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An integrated approach for predicting the fate of reintroduced populations

A thesis presented
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Abstract

I provide a comprehensive account of the fate of a reintroduced population of North Island robins (*Petroica longipes*) at Tawharanui Regional Park, a predator-free peninsular site in the Auckland Region. All factors affecting the success of reintroductions do so through survival, reproduction, or dispersal. I use an integrated Bayesian approach to assess the impact these factors have on population persistence. I estimated population growth by combining vital rates (survival and reproduction) using 9 years of post-release monitoring data. There was no change to estimates when informative priors that accounted for site-to-site variation were included. I determined that despite low recruitment, the population will persist under current circumstances. I then focused on what was causing low recruitment by distinguishing juvenile survival from permanent natal dispersal. Habitat fragmentation prevented juvenile dispersal out of the park, and juvenile survival was low with most mortality occurring within four months of fledging. It is low juvenile survival that is causing low recruitment, indicating the habitat quality is marginal. Despite this, current habitat quality and connectivity is sufficient to maintain a population, but there may be implications for management if connectivity is increased in the future. Finally, I assessed whether it would be sensible to harvest this population as their location makes them a convenient source for future reintroductions. I projected population dynamics 10 years into the future and examined the implications of a one-off harvest on population persistence. Whilst there was negligible chance that the population would go extinct, a harvest at any level reduced the number of females in the population throughout the 10 years, with larger harvests causing a greater reduction. My results can be used within a decision analysis framework to facilitate the decision of whether Tawharanui would be a suitable source population for future reintroductions.

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Chapter 1

General Introduction

New Zealand Conservation

New Zealand’s long geographic isolation from other land masses has enabled the development of unique biota, and resulted in one of the highest levels of endemism in the world (Gibbs, 2006). Geographical isolation acted as a barrier to plant and animal colonisation, enabling biota to live in the absence of mammalian predators (Gibbs, 2006). This led to the loss of anti-mammalian predation responses in endemic birds, and the development of several unique traits, including gigantism and flightlessness (Holdaway, 1989; Maloney & McLean, 1995). It is widely acknowledged that these unique traits make island birds highly vulnerable to introduced predators (Vitousek et al., 1997; Mack et al., 2000). As a result, the pre-human New Zealand avifauna was much more diverse and abundant than what exists today (Holdaway, 1989).

Human colonisation changed New Zealand’s biota dramatically. Since human arrival approximately 800-1000 years ago (Wilmshurst & Higham, 2004), a large number of species have gone extinct and many that remain are threatened with extinction (Holdaway, 1989, 1999). These losses have been largely attributable to habitat loss and fragmentation, as well as the ongoing impacts of exotic mammalian predators (Saunders & Norton, 2001). The first mammalian predators were the kiore, or Polynesian rat (*Rattus exulans*), and the kuri (*Canis familiaris*), or Polynesian dog which were introduced at the time of Polynesian arrival. Subsequent European colonization in the late 18th Century brought many additional mammalian predators, including the ship rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*), feral cat (*Felis catus)* and mustelids (*Mustela spp.*) (Holdaway, 1989). Rats and mustelids are widely recognized as the primary factor responsible for the historic and current declines of New Zealand fauna (Holdaway, 1989; Clout, 2001; Innes et al., 2010). Since human arrival, almost a third of bird species (41% of those being endemic) in New Zealand have gone extinct (Innes et al., 2010).

Human arrival has also caused significant loss of forest habitat. Historically New Zealand consisted of large tracts of continuous forest below the alpine zone (Ewers et al., 2006). Polynesian and European colonisation caused the destruction of nearly three quarters of indigenous forest cover, and the remainder is heavily fragmented (Ewers et al., 2006). The role of habitat fragmentation in species decline is well recognised (Saunders et al., 1991; Vitousek et al., 1997). This is especially relevant in New Zealand, as the fauna consists of a large number of animals that are found predominantly in continuous forest throughout their life cycle (Innes & Hay, 1991) and many are unwilling to cross large gaps of open pasture (Richard & Armstrong, 2010). In many regions, habitat loss and fragmentation has caused the local or regional extirpation of endemic fauna (Innes et al., 2010). These losses have evoked efforts to reverse defaunation through the intentional movement of animals into restored habitat.

Reintroduction Biology in New Zealand

Reintroduction biology is a relatively new field of research that is designed to improve conservation translocations. Conservation translocations are the intentional movement of organisms from one place to another, where conservation of the target species is the primary objective (Hodder & Bullock, 1997; Seddon et al., 2012; Armstrong et al., 2015). Conservation translocations include reintroductions, the re-establishment of a species to part of its historic range from which it has been extirpated, and are designed to conserve species and fulfil restoration objectives (IUCN, 1987; Seddon et al., 2007; Armstrong et al., 2015). Reintroductions to predator-free or predator-controlled areas are the main type of conservation translocation focused on in New Zealand, as they often provide a means to restore locally extinct populations (Sarrazin, 2007).

Conservation translocations have a much longer history than reintroduction biology. Early attempts to translocate New Zealand birds date back as far as 1863 (Miskelly & Powlesland, 2013), with the first recognised conservation translocations occurring from 1895 to 1907 (Armstrong et al., 2015). They started to become a major conservation strategy in New Zealand during the 1960s, leading to an almost exponential increase in the number of translocations, both in New Zealand and worldwide (Seddon et al., 2012). There are now > 1100 documented conservation translocations of New Zealand fauna, and most these have involved birds (Sherley et al., 2010; Miskelly & Powlesland, 2013; Armstrong et al., 2015). Conservation translocations have become a well-established conservation tool and are used to improve our understanding of reintroductions at various levels (Seddon et al., 2007; Armstrong & Seddon, 2008).

Historically reintroduction success rates have been low. Poor planning and little to no monitoring of early reintroductions meant that the causes of failure remained unknown (Seddon et al., 2007). This prompted the formation of the IUCN reintroduction specialist group (RSG) in 1988 to provide guidance for reintroduction programmes (IUCN, 1987; IUCN, 2013). The RSG emphasized that for projects to be feasible, they needed to be well planned and their results monitored. This caused a substantial increase in post-release monitoring, facilitating a shift in the literature from predominately descriptive accounts of reintroductions to the use of more powerful methodologies such as quantitative modelling (Armstrong et al., 2015). Accurate modelling requires a reasonable understanding of the mechanisms regulating population growth. Models that estimate vital rates (survival and reproduction) and predict population growth are used to guide a range of decisions to reduce the risk of reintroduction failure (Seddon et al., 2007; Converse et al. 2013). If density dependent processes are regulating a population, it may be able to be sustainably harvested. Populations that can be harvested with minimal cost in terms of viability, may be considered as potential source populations for future reintroductions.

New Zealand has become a world leader in reintroduction biology. Species recovery and restoration initially focused on offshore islands where predators could be eradicated. This proved to be highly successful in many recovery attempts of threatened species (Armstong & McLean, 1995; Towns et al., 1997). Despite these successes, it became clear that it would not be possible to sustain New Zealand’s indigenous biodiversity on offshore islands alone (Saunders & Norton, 2001). Therefore, the more ambitious challenge of restoration projects on the New Zealand mainland (North and South Islands) were attempted. Predator control programmes have now been implemented in many mainland reserves, which (depending on the level of control and susceptibility of the species) has created opportunities to reintroduce locally extirpated species (Saunders & Norton, 2001). In recent years there has been an increase in the number of fenced ‘mainland island’ sanctuaries established where predators have been eradicated (Innes et al., 2012). However, there are numerous factors that make reintroductions to mainland islands more challenging and they have had lower success than island reintroductions.

One of the challenges facing reintroduction of birds to mainland sites is the increased capacity for dispersal out of managed mainland areas into unsuitable surrounding landscape. The open water that surrounds ‘true’ islands acts not only as a barrier for invasive predators, but also as a barrier that prevents reintroduced birds from leaving. Mainland reintroductions can fail in the short term due to immediate dispersal of individuals post-release, and in the long term due to continued dispersal away from the reintroduction site (Richardson et al., 2015). Most attempts to deal with dispersal of reintroduced populations, have focused on initial post-release dispersal without fully acknowledging the effects of ongoing dispersal (Richardson et al., 2015). Natal dispersal of juveniles can compromise the persistence of populations when the dispersal rate is high in relation to the recruitment rate (Andrews, 2007). Dispersal and mortality can have similar costs because individuals that disperse will not contribute demographically or genetically to the population (Le Gouar et al., 2012). This emphasises that the mechanisms regulating reintroduced populations over both the short and long-term need to be understood. Focused monitoring increases our understanding of these mechanisms, enabling managers to adopt appropriate strategies to maximise reintroduction success.

One decision that managers or scientists need to make is how long to continue a study before they can be confident that the reintroduction has been successful and that the population will persist (Armstrong & Ewen, 2013). There is a bias in the literature toward short-term studies, partly due to the low success rates of early reintroductions and partly due to constraints caused by funding or duration of postgraduate degrees (Armstrong & Ewen, 2013). Cost-efficient decision making is an essential component of any reintroduction, yet many mainland reintroductions have relied on intuitive decisions and carried out a ‘release and see’ approach (Parlato & Armstrong, 2012). Long term monitoring of mainland reintroductions could enable a greater understanding of the complex interactions of various factors (e.g. natal dispersal, invasive species management) that apply to mainland sites. This knowledge can aid the overall goal of the establishment self-sustaining populations on the mainland.

Study species – North Island Robin

Most mainland reintroductions have been of the North Island (NI) robin (*Petroica longipes*), or toutouwai, a small (26-32g) insectivorous forest passerine (Higgins & Peter, 2002). The NI robin is a separate species to the South Island robin (*P. australis*) which is also found on Stewart Island. This divergence was first based on morphological characteristics that include differing plumage pattern and body size (Holdaway et al., 2001), and later reinforced by mitochondrial DNA sequencing research (Miller & Lambert, 2006).

Our knowledge on robins comes almost exclusively from populations in managed protected areas. Prior to European colonisation, NI robins were widely distributed throughout the North Island as well as neighbouring offshore islands (Higgins & Peter, 2002; Heather et al., 2005). Their natural range has now been restricted to a few remnant forest fragments and exotic plantations in the central North Island, and populations on Little Barrier and Kapiti Islands (Heather et al., 2005; Higgins & Peter, 2002). Habitat loss and predation drove this range restriction. Other than small populations derived from mainland reintroductions (Wenderholm Regional Park in 1999, Hunua Ranges in 2001, Waitakere Ranges; in 2005, Tawharanui Regional Park in 2007, and most recently Shakespear Regional Park in 2016), NI robins are still absent from many mainland forest areas in the Auckland region (Lovegrove, 2007).

The breeding season for NI robins spans from September to February (Armstrong et al., 2000; Powlesland et al., 2000). Adults are sedentary, typically monogamous and occupy permanent territories (Higgins & Peter, 2002). Females lay up to three clutches, each containing two to three eggs (Armstrong et al., 2000; Powlesland et al., 2000). Fledglings are fed for four to seven weeks and stay in the natal territory for up to ten weeks (Armstrong et al., 2000). Juveniles usually undergo an initial dispersal phase before establishing a permanent territory. Both juveniles and females are light grey in colour, and males display delayed plumage maturation where their plumage darkens over time (Armstrong et al., 2000; Higgins & Peter, 2002). Juveniles become sexually mature by the start of the following breeding season and reproductive success of first year birds is similar to older birds (Dimond & Armstrong, 2007).

Robins are one of the most commonly reintroduced species in New Zealand (Miskelly & Powlesland, 2013). They are easy to work with (i.e. capture and monitor) as they are highly inquisitive, responsive to playback and can be easily trained to come to mealworms (*Tenebrio molitor*). Unlike other New Zealand native bird species (e.g. saddlebacks. *Philesturnus* spp.), they can co-exist with introduced predators that are maintained at low levels. Furthermore, many populations have been monitored post-release and data on demographic rates collected using consistent methodology (Parlato & Armstrong, 2012; Miskelly & Powlesland, 2013). These factors make them a good species for reintroduction to a restored site. Often the reintroduction of species with a higher threat status will only be considered after the successful establishment of robins. Several species were reintroduced to Tawharanui Regional Park after the successful establishment of NI robins.

Study Population

Tawharanui Regional Park is a 550-ha mainland sanctuary approximately 80 km north of Auckland, New Zealand (Figure 1.1). It is located on the Tokatu peninsula and owned by the Auckland Council. Tawharanui was run as a coastal farm park until the mid-1990s when the council began exploring the concept of developing Tawharanui as a ‘mainland island’.

One hundred and seventy hectares (ha) of the total area is comprised of pasture and is still farmed with sheep and cattle. Remaining forested areas are in several discrete fragments and have been fenced off. The main forested areas are comprised of kanuka (*Kunzea ericoides*) scrub/forest, manuka (*Leptospermum scoparium*) scrub and pohutukawa-puriri-broadleaf forest (*Metrosideros excelsa* and *Vitex lucens*) (Singers et al., 2015). There are also small fragments of kauri-podocarp-broadleaf (*Agathis australis* and *Podocarpus*) forest as well as wetland, woodland, exotic grassland, and sand dune areas. The community group Tawharanui Open Sanctuary Society Incorporated (TOSSI) was formed in 2002 and Tawharanui is now operated by the Auckland Council in partnership with TOSSI. In 2006 Tawharanui was officially opened as New Zealand’s first Open Sanctuary that integrates conservation, recreation and farming operations (Murdoch, 2008).

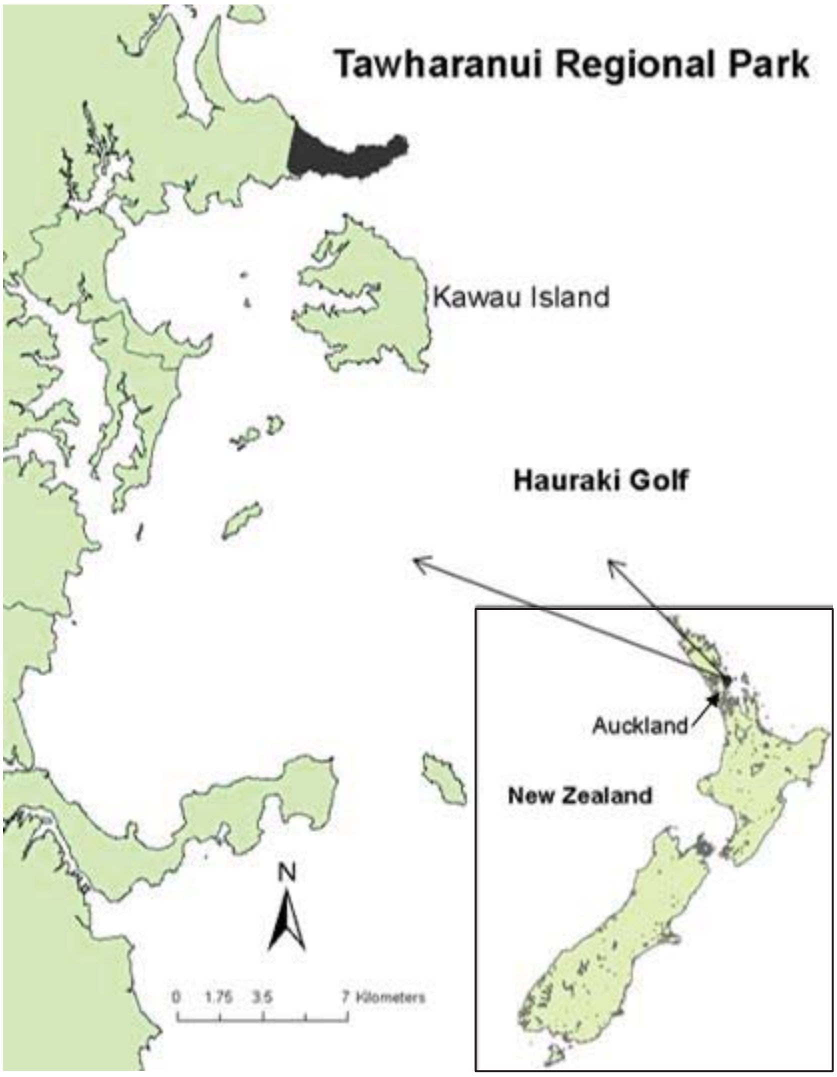

Figure 1.1. Location of Tawharanui Regional Park on the east coast, north of Auckland City.

In 2004 a 2.7 km coast-to-coast predator exclusion fence was installed isolating 550 ha of the peninsula from introduced mammals (Maitland, 2011). Extensive mammal control followed including an aerial poison drop of brodifacoum. All mammal species except mice (*Mus musculus*) and rabbits (*Oryctolagus cuniculus*) were eradicated. Potential incursion pathways include the coastal ends of the fence and as stowaways in visitor vehicles. A number of species including rats, cats (*Felis catus*) and stoats (*Mustela erminea*) periodically re-enter the park but they are usually detected and targeted for prompt removal (Maitland, 2011). There has only been one occasion in 2008 when an *in-situ* breeding population of the ship rat (*Rattus rattus*) was recorded. Conservation outcomes are generally achieved despite these incursions and the sanctuary generally remains free of mammalian predators.

Since the establishment of the predator fence, many native flora and fauna species have recovered and several others have been reintroduced. Productivity of existing native lizard and bird species increased, and bellbirds (*Anthornis melanura*) *s*elf-introduced themselves from Hutaratu (Little Barrier Island) in 2005. Seven native bird species were reintroduced from 2006 to 2014. North Island robins were the second species reintroduced to Tawharanui. The other reintroduced species are: The North Island brown kiwi (*Apteryx mantelli*) in 2006 and 2007, whitehead (*Mohoua albicilla*) in 2007, pateke (*Anas chlorotis*) in 2008 and 2010, kakariki (*Cyanoramphus novaezelandiae*) in 2009 and 2010, and North Island saddleback (*Philesturnus rufusater*) in 2012 and most recently 10 takahe (*Porphyrio hochstetteri*) in 2014.

Twenty-One North Island robins were reintroduced to Tawharanui Open Sanctuary from Tiritiri Matangi in March 2007. There was a sex bias in this initial translocation as it comprised 15 males and 6 females. Consequently, four additional females were captured on private land near Puhoi later in 2007 and translocated to Tawharanui to increase the number of females in the founding population. There was no mortality before release during any of the translocations to Tawharanui. The Puhoi birds were a satellite population, derived from the 21 robins reintroduced to Wenderholm Regional Park in 1999, which also originated from Tiritiri Matangi (Dimond & Armstrong, 2007).

Demographic data have been collected on the Tawharanui robin population since its release. Despite low post-release dispersal and high annual productivity, recruitment has remained low. The main hypothesis for this low recruitment has been that juvenile robins are dispersing out of the park into the surrounding unprotected habitat. However, in contrast to observations at Wenderholm Regional Park where many birds dispersed (Andrews, 2007), very few robins have been located outside of Tawharanui.

Aim and Thesis outline

This thesis is centred around three chapters which are presented as individual research papers to facilitate future publication in scientific journals. Due to this structure, some repetition between chapters is inevitable. However, it is minimised where possible.

In Chapter 2, I estimate survival and fecundity and combine these models to estimate λ (finite rate of increase) with nine years of post-release monitoring data, to predict the fate of the population under current circumstances. I then manipulate the amount of data available and add informative priors to assess the effect of using informative priors and determine how many years of data are required to be confident of population persistence.

In Chapter 3, I examine the survival and movement patterns of juvenile NI robins from fledging to recruitment. My aim was to determine whether low recruitment into this population is caused by high mortality and/or dispersal out of the park. I also investigate whether habitat fragmentation is preventing dispersal from Tawharanui or affecting movement within it.

In Chapter 4, I investigate whether it is sensible to harvest the Tawharanui NI robin population. I expand the population model from Chapter 2 to project population dynamics 10 years into the future, and examine the implications of a one-off harvest on population persistence. My aim was to help facilitate the decision of whether Tawharanui is a suitable source population for potential future reintroductions in the region.

Chapter 5 is a summary of the main findings of the previous three chapters, followed by the contributions this study has made to the field of reintroduction biology, and suggestions for future research.

Chapter 2

Predicting the persistence of reintroduced populations

Photo Credit: Jonas Kotlarz

Abstract

Monitoring is an essential component of any reintroduction programme, but can be costly. One way to potentially reduce monitoring cost is to model population dynamics within a Bayesian framework that incorporates prior information on expected survival and reproduction rates. I used this approach to predict the fate of a reintroduced population of North Island robins (*Petroica longipes*) at Tawharanui Regional Park, a predator-free peninsular site in the Auckland Region. I combined survival and fecundity models to estimate λ (the finite rate of increase) using 9 years of post-release monitoring data, and assessed how precision improved as years of data were added. I then evaluated the usefulness of informative priors, which I obtained by analysing data from 9 other reintroductions while accounting for random site-to-site variation. I found an ambiguous effect of density on fecundity, so estimated λ under models with and without density dependence. Under either model, with all 9 years of data the 95% credible interval for λ was > 1, demonstrating that this population has a high probability of persistence. However, 7 years of data were required before λ and its associated uncertainty were > 1, and this requirement was not reduced when informative priors were used. Informative priors enabled λ to be predicted when no Tawharanui data were available. However, the informative priors had low precision due to the large amount of random variation between reintroduction sites. This meant their effect was negligible once any Tawharanui data were available.

Introduction

Species reintroduction is a costly exercise that has historically had a low rate of success (Griffith et al., 1989; Fischer & Lindenmayer, 2000; Griffiths & Pavajeau, 2008). It is well recognised that reintroductions have previously suffered from insufficient monitoring and that failure to learn from monitoring may have contributed to the poor success rate (Lyles & May, 1987; Griffith et al., 1989; IUCN, 2013). Increased monitoring has improved the ongoing management of reintroduced populations and helped to guide strategies for future reintroductions (Seddon et al., 2007). It has also facilitated the development of quantitative models to make predictions about population dynamics, which can be used to guide a range of decisions.

The reintroduction literature largely consists of descriptive accounts of reintroductions (Seddon et al., 2007), but there has been an increasing use of predictive modelling to reduce the risk of reintroduction failure (Converse & Armstrong, 2016). Models for reintroduced populations can be used to make predictions for new sites before reintroduction, and are also useful for predicting population persistence under current conditions to assess whether future management is likely to be required. A population model is a type of predictive model that uses demographic data to provide estimates of population growth rates, abundance, short-term establishment, and long-term population persistence. Regardless of the strategy used to establish a population, the reintroduction will ultimately be unsuccessful if the population is unable to persist (Armstrong & Seddon, 2008). Estimates of positive population growth are a key component in ensuring continued persistence. The quality and quantity of data limit the precision of these estimates. Therefore, accounting for uncertainty in estimates and decision making is an essential component of quantitative modelling (Beissinger & Westphal, 1998).

Advances in computational statistics have enabled the development of complex models, which are typically needed for ecological inference and prediction (Clark, 2005). The recent advent of Bayesian hierarchical modelling has gained widespread acceptance among scientists due to the potential to accommodate high dimensional problems without the need for explicit integration (King et al., 2009; Link & Barker, 2009). Hierarchical models allow a much more flexible approach to modelling the status of reintroductions. They recognise uncertainty by allowing random site-to-site variation to be accounted for (Parlato & Armstrong, 2012), whilst also having the capability to evaluate complex variation from small data sets (Clark & Gelfand, 2006). This is especially relevant when modelling demographic data from species reintroductions as they often involve small data sets, especially in the initial years following reintroduction.

The basic concept behind Bayesian inference is that prior knowledge and new data can be combined using a model to produce posterior knowledge (McCarthy, 2007). A data-derived informative prior is where data from past studies are incorporated into a model. Although most ecologists are motivated by the relevant outcomes of previous studies, many only incorporate this information implicitly in their sampling designs or discussions of their results (McCarthy & Masters, 2005). In a similar manner, the incorporation of prior knowledge in analyses is not yet common practice in reintroduction biology. A major advantage of using informative priors is that they can be highly cost-effective because they may reduce the amount of data needed before useful predictions can be made (McCarthy & Masters, 2005; Gedir et al., 2013). This is particularly applicable to reintroduced populations as it can enable useful predictions to be made sooner than what would otherwise be possible, freeing up resources that can be allocated to other management areas.

Cost-efficient decision making is an essential component of any reintroduction. To date, decisions about reintroductions have been largely intuitive (Converse et al., 2013). One decision that managers or scientists need to make is how long to continue monitoring before they can be confident that a population will persist (Armstrong & Ewen, 2013). Projecting the trajectory or fate of a population is famously ‘data hungry’ (Possingham et al., 1993). It is impossible to construct demographic models before a reintroduction takes place unless prior information is used, and models constructed with minimal data soon after release may also be relatively worthless (South et al., 2000; Parlato & Armstrong, 2012). Long-term monitoring has the advantage of enabling continuous improvement of the understanding of dynamics of populations. It also allows models to include data-based estimates of factors that influence the population in the long term, including density-dependent regulation and environmental stochascity (Armstrong & Ewen, 2013). However, long-term monitoring diverts resources (Likens, 1983; Taylor, 1989), and prior information may increase cost-efficiency by enabling management decisions to be reached with less data.

Chapter Aim

I used Bayesian inference to model the dynamics of a reintroduced population of North Island robins (*Petroica longipes*), while incorporating prior information. The North Island robin is one of the most commonly reintroduced species in New Zealand (http://rsgoceania.squarespace.com/nz/), and most populations are monitored post-release as they are easy to monitor. North Island robins present an ideal scenario for modelling the usefulness of prior information as multiple reintroductions have taken place, their biology and threats are well understood, and demographic data were collected using consistent methodology. I incorporated prior distributions for survival and reproduction parameters, from a model created by Armstrong and Parlato (2012) that combined multiple reintroduction sites to create parameter estimates that accounted for site-to-site variation.

My aim was to predict the fate of the population under current circumstances and determine how many years of data were required to be confident of population persistence. I estimated vital rates (survival and reproduction) and combined these to determine lambda (λ) 'the finite rate of increase' with all nine years' post-release monitoring data. I then manipulated the amount of data available and added informative priors. Finally, I compared the precision of these estimates to assess the effect of using informative priors, and discussed how my results can benefit management over the long-term.

Methods

Species and Study Area

The North Island (NI) robin is a small (26-32g) forest passerine endemic to New Zealand (Higgins & Peter, 2002). NI robins can live in both native and exotic forest and are mainly insectivorous, feeding on small invertebrates on the forest floor and amongst bark on tree trunks (Higgins & Peter, 2002; Heather et al., 2005). At the time of European settlement, they were widespread throughout the North Island and nearby offshore islands. Habitat clearance and introduction of mammalian predators caused their steady decline and they are now patchily distributed on the mainland. Adult robins are territorial. They rarely leave a territory after establishment and both sexes will actively defend their territory against conspecific intruders. They are easy to detect and monitor due to their inquisitive nature, and this has made them the subject of many reintroduction projects (Miskelly & Powlesland, 2013).

NI robins are socially monogamous and their breeding season typically spans from September to February. Females can lay up to three clutches per season and after hatching fledglings can stay in their natal territory for up to 10 weeks (Armstrong et al., 2000). Juveniles undergo an initial dispersal phase shortly after fledgling and many disperse before establishing a territory. Juveniles become sexually mature by the start of the following breeding season. Provided they survive the first winter, the survival and reproductive success of first year birds has been found to be similar to that of older birds (Armstrong & Ewen, 2002; Dimond & Armstrong, 2007).

The study area is Tawharanui Regional Park, a 550-ha peninsula site approximately 80 km north of Auckland New Zealand. The park operates as an open sanctuary that integrates recreation, conservation, and farming. One hundred and seventy hectares of the total area is pasture and is farmed with sheep and cattle. Forested areas have been fenced off and are in several discrete fragments. Auckland Council operates the park in partnership with the Tawharanui Open Sanctuary Society (TOSSI). Intensive predator control, combined with the installation of an open ended 27 km predator exclusion fence in 2004, has caused the eradication of all mammal species except mice (*Mus musculus*), and there is ongoing monitoring for incursions (Maitland, 2011). Species eradicated include the ship rat (*Rattus rattus*), house cat (*Felis catus*), stoat (*Mustela erminea*) and brush-tailed possum (*Trichosurus vulpecula*). In March 2007, 21 North Island robins were translocated from Tiritiri Matangi to Tawharanui. A male sex bias in this initial translocation led to two supplementary translocations in July and August 2007, when four additional females were captured on private land near Puhoi and translocated to Tawharanui.

Data Collection

Annual surveys were performed from 2007 to 2016 to generate data on survival of colour-banded individuals. These were performed by Tim Lovegrove and other Auckland council staff during September at the start of each breeding season. Fecundity data were obtained through weekly checks of known robin pairs. These checks consisted of recording the breeding status (non-breeding, number of eggs, chicks, fledglings) of each nest, generating data on the number of young fledged over the season by each pair.

Pairs were usually located by walking through the territory, but lure tapes were occasionally used when pairs were not easily found. Nests were located by feeding mealworms (*Tenebrio molitor*) to the birds. During incubation, the male would call the female off the nest, or if the chicks had hatched, either parent would take mealworms to the nest. Nestlings were typically banded 9-12 days after hatching (Parker et al., 2016), resulting in 660 chicks being banded on the nest between 2007 and 2016. There were only a few instances (4), where young birds were caught using a claptrap or hand net and banded as fledglings. It was not possible to colour-band all chicks every year as some nests were inaccessible and the occasional nest was missed during monitoring. However, the number of unbanded birds has remained relatively low, and most (> 95%) of the population has always been banded.

Due to the number of pairs increasing (9 in 2007 to 37 in 2016), the nests could not all be monitored through to fledging. To keep maintained consistency between years, chicks were considered to have fledged if they survived to banding age. The number considered fledged was therefore slightly higher than the number recorded as leaving the nest, but data from the 2015-2016 breeding season suggests that the proportion of monitored chicks that died between banding and fledging was quite small (< 1%; Chapter 3).

Modelling

OpenBUGS (version 3.2.3) was used to model the data. OpenBUGS is an open-source version of the WinBUGS software package (Spiegelhalter et al., 2007). It uses Markov Chain Monte Carlo (MCMC) techniques to fit Bayesian hierarchical models, which allow the incorporation of multiple random effects. It also facilitated integrated population modelling (Schaub & Abadi, 2011), whereby fecundity and survival data were modelled simultaneously to generate population projections that fully account for parameter uncertainty and covariance. Models were run for up to 50,000 iterations with an initial burn in of 5,000 samples after checking convergence by examining the chains and autocorrelation plots.

Generation of Informative Priors

I generated informative priors using Parlato and Armstrong’s (2012) model, which integrated demographic data from 10 reintroduction sites to predict what would happen at a proposed reintroduction site. I adapted this model by removing the two years of Tawharanui data that had been included, and used the model to generate prior distributions for four parameters: 1) mean fecundity (number of fledglings per female), 2) random effect of individual female on fecundity, 3) probability of an adult surviving one year, and 4) the probability of a juvenile surviving from fledgling to adulthood (Table 2.1). The priors for the survival parameters are specific to peninsular sites, as Parlato and Armstrong (2012) found apparent survival of juveniles to be lower on peninsular than non-peninsular sites, and the significance of this effect was retained when the Tawharanui data were removed. They hypothesised that apparent juvenile survival was lower at peninsular sites because juveniles dispersed along forest edges into unprotected habitat outside the site.

Table 2.1. Informative and uninformative prior distributions for key parameters in the population model for North Island robins reintroduced to Tawharanui. The informative priors are based on data for 9 robin reintroductions other sites. The normal distributions (*N*) show means and standard deviations, and the uniform distribution (*U*) shows the range.

Parameter	Informative	Uninformative
a.f	*N*(1.27, 0.38)	*N*(0, 10)
sd.fem.f	*N*(0.23, 0.09)	*U*(0, 1)
a.phi	*N*(-1.76, 0.60)	*N*(0, 10)
b.age.phi	*N*(3.05, 0.95)	*N*(0, 10)

*a.f, intercept term for log of mean fecundity (number of fledglings per female); sd.fem.f, standard deviation for random effect of individual female on log fecundity; a.phi, intercept term for logit of probability of a juvenile surviving from fledgling to adulthood and staying at Tawharanui; b.age.phi, difference between logit annual adult female survival and logit juvenile survival.

Modelling Tawharanui Data

I initially modelled the Tawharanui data using uninformative priors (Spiegelhalter et al., 2007), and started by examining the effects of all variables I believed may affect survival or fecundity. Uninformative priors were taken to be normally distributed for main parameters (regression coefficients) and uniformly distributed for hyper-parameters (standard deviation of random effects). I then reduced the model by removing fixed effects if their 95% credible intervals included zero, and removing random effects if the lower portions of their posterior distributions were concentrated near zero (Kéry & Schaub, 2012).

Fecundity was modelled with a log link function and Poisson error distribution. The full fecundity model included a fixed effect of density and two random effects, one for the individual female and the other for year. Some females occurred over multiple years causing pseudo-replication in the data. Including the random female effect allowed variation among individual females and ensured that the results were robust to this pseudo-replication. Age was not considered as previous studies suggest that age of female robins does not affect their fecundity (Dimond & Armstrong, 2007).

Survival was modelled using a state-space formulation of the Cormack-Jolly-Seber (CJS) model. This is where the probability of a bird being seen is dependent on both its survival and re-sighting probabilities (Kéry & Schaub, 2012; McCarthy et al., 2012). Both survival and re-sighting were modelled with logit link functions and Bernoulli error distributions (Schofield et al., 2009). Survival surveys were conducted annually at the start of each breeding season, and the difference in the time interval between the translocation and first annual survival survey (6 months) was corrected for. The full survival model included fixed effects of age (adult vs juvenile), sex (adults only), and translocation (first 6 months' vs later adult survival) as well as a fixed effect for density on juvenile survival. An effect of banding age was also included to correct for the higher survival probability expected in the four juveniles banded as fledglings, compared to those banded in the nest. Random annual variation on juvenile survival was included to allow for changes in survival over time due to weather and other factors.

Annual abundance was also estimated as this enabled me to observe how population size had changed over time, and model density dependence in survival and fecundity. There were two components to estimating yearly abundance: estimating the number of banded birds alive at each survival survey based on the CJS model, and estimating the number of unbanded birds present. I assumed that detection probability was equal for banded and unbanded birds. I obtained separate estimates for males and females and then combined these to estimate the total.

Estimating Population Growth

The reduced model was used to derive the finite rate of increase, which is given by:

$$\lambda = s_a + \frac{1}{2} s_j f,$$

where s_a is annual adult survival probability, f is the mean number of fledglings per female per year and s_j is the apparent juvenile survival probability (probability of both surviving from fledging until adulthood and staying at Tawharanui). I generated λ with both informative priors and uninformative priors (Tables 2.1, 2.3). For both approaches I added the Tawharanui data one year at a time to assess how the precision of the λ estimate and usefulness of the priors changed with the amount of data available.

Results

Abundance

The Tawharanui population has increased over time from 22 birds in 2007 to about 80 birds in 2016 (Figure 2.1). There was a slow increase from 2007 to 2011 followed by a more rapid increase after the 2011 breeding season, and the population size has remained relatively constant from 2014 to 2016.

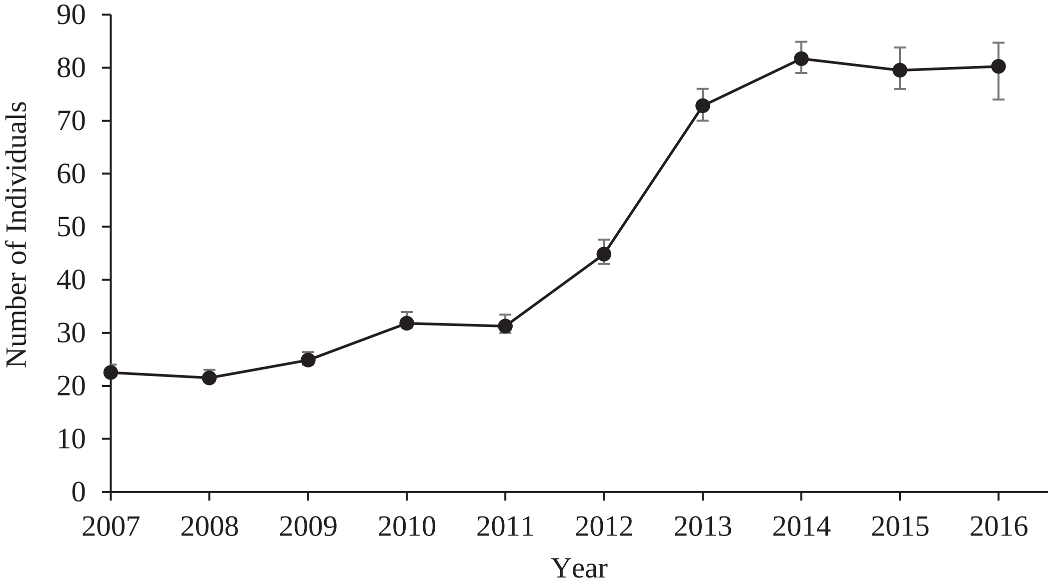

Figure 2.1. Growth of the North Island robin population reintroduced to Tawharanui. Points show estimated numbers at the start of each breeding season, with 95% credible intervals.

Fecundity

There was a trend for fecundity to decrease as population size increased, but this effect was ambiguous (Table 2.2, Figure 2.2). Thus, there were two fecundity models with similar support: a 'constant' model and a 'density' model. Under the constant model, an average female was estimated to have 3.8 fledglings, whereas under the density model this was expected to decline from 4.8 to 3.3 fledglings as the population grew from 0 to 80. While there was random variation in fecundity among individual females, there was no evidence of random variation among years (Table 2.2).

The precision of fecundity estimates depended on both the model and amount of data available (Figure 2.3). The 'constant' model was supported for the first 7 years, as it took

8 years before the posterior distribution for the density effect to be narrow enough that it no longer included 0. The ambiguity of the density effect for the final two years, means both models will provide reasonable estimates for 8 or 9 years of data (Figure 2.3).

Table 2.2. Means and credible limits (CL) for parameters in the full model and reduced models of fecundity and survival of North Island robins at Tawharanui Regional Park. These estimates are based on all 9 years of data with uninformative priors.

Parameter [a]	**Full Model**			**Reduced Model** [b]		
	mean	**2.5% CL**	**97.5% CL**	**mean**	**2.5% CL**	**97.5% CL**
a.f	1.52	1.24	1.78	1.52	1.30	1.72
b.d.f	-0.48	-1.04	0.09	-0.48	-0.86	-0.08
sd.fem.f	0.21	0.09	0.33	0.21	0.06	0.34
sd.yr.fem.	0.10	0.00	0.30			
a.phi	-1.05	-1.98	-0.01	-1.44	-1.95	-0.93
b.age.phi	2.12	0.09	4.63	2.70	2.16	3.26
b.bfl	2.65	0.53	5.22	1.82	0.37	2.87
b.d.juvphi	-0.83	-2.62	0.95			
b.sex.adphi	-0.29	-5.59	2.98			
b.trans	2.70	-1.01	14.11			
sd.yr.adphi	0.25	0.01	0.84			
sd.yr.juvphi	0.58	0.17	1.23	0.66	0.30	1.30
a.p	2.29	1.73	3.04	2.22	1.86	2.64
sd.yr.p	0.49	0.03	1.69			

[a] a.f, intercept term for log of mean fecundity (number of fledglings per female); b.d.f, effect of density (birds/ha) on log fecundity; sd.fem.f, standard deviation for random effect of individual female on log fecundity; sd.yr.fem, standard deviation for the random effect of year on log fecundity; a.phi, intercept term for logit of probability of a juvenile surviving from fledgling to adulthood and staying at Tawharanui; b.age.phi, difference between logit annual adult female survival and logit juvenile survival; b.bfl, effect of being banded as a fledging on logit juvenile survival; b.d.juvphi, effect of density on logit juvenile survival;

b.sex.phi, difference between males and females in logit adult survival; b.trans; difference between logit survival probability in the first 6 months after translocation versus later; sd.yr.adphi, standard deviation for random annual variation in logit juvenile survival; sd.yr.juvphi, standard deviation for random annual variation in logit adult survival; a.p, intercept for logit of re-sighting probability; sd.t.p standard deviation for random annual variation on logit re-sighting probability.

[b] Fixed effects removed if 95% credible intervals included zero, random effects removed if 95% credible intervals centred near 0.

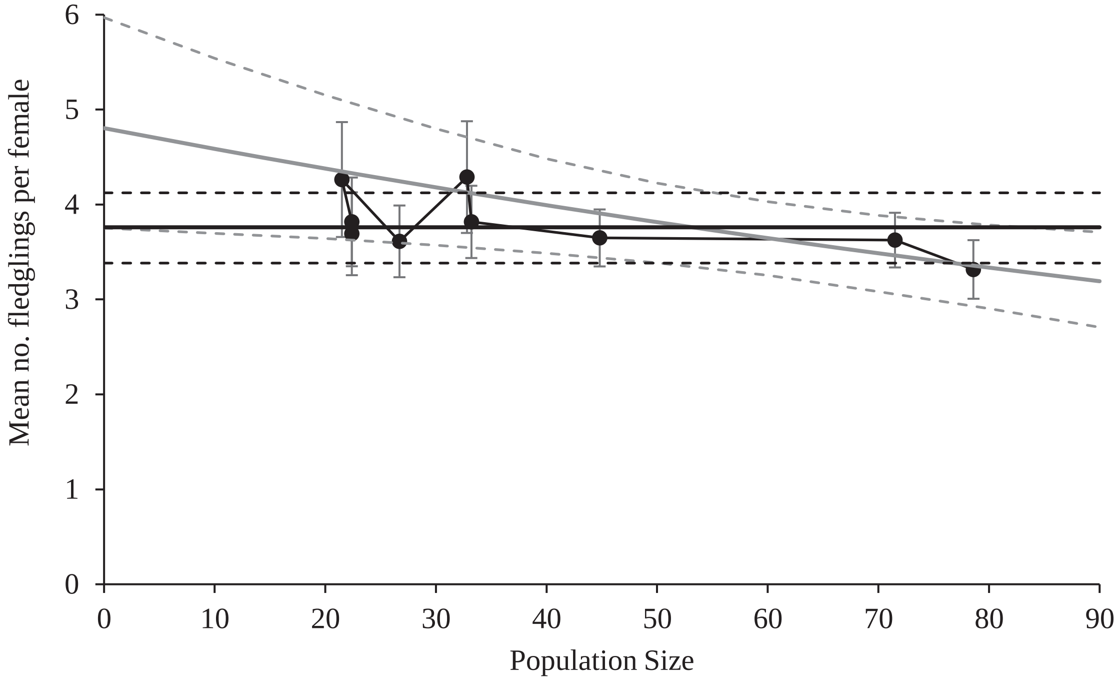

Figure 2.2. Changes in mean fecundity (fledglings per female) of North Island robins at Tawharanui Regional Park in relation to breeding population size. Dots show annual estimates with 95% credible intervals. The grey curve shows the estimated relationship between fecundity and density, whereas the black line shows the estimated fecundity if density dependence is excluded from the model. Dotted lines show 95% credible intervals. Both models had uninformative priors for all parameters.

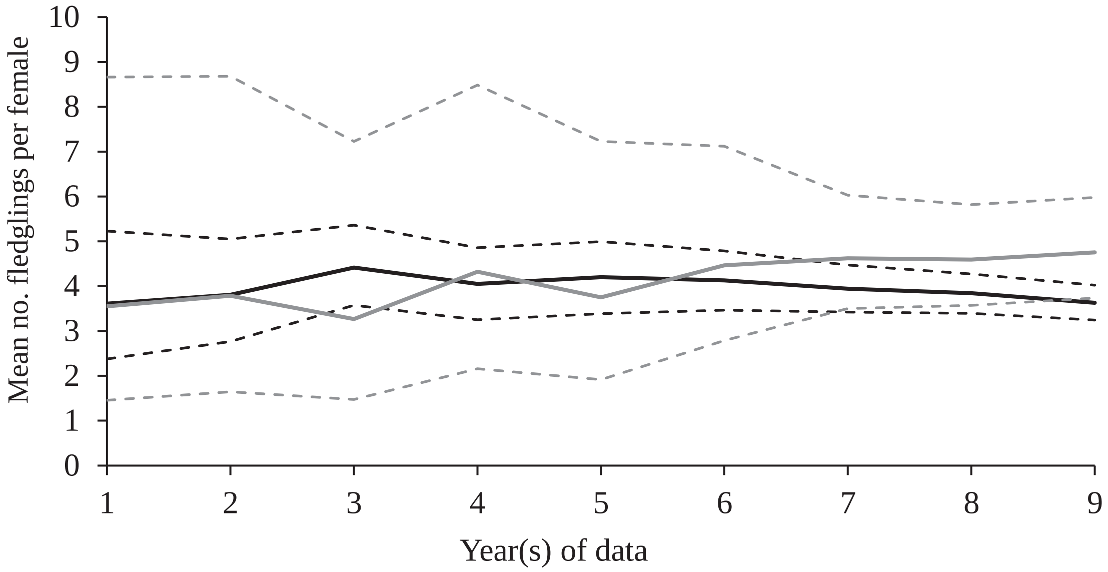

Figure 2.3. Changes in the estimated mean number of fledglings per female for North Island robins at Tawharanui Regional Park, as a function of the number of years of monitoring data available. Black lines show estimates of the intercept based on a constant model, and grey lines show estimates of the intercept based on the density-dependent model. Dotted lines show 95% credible intervals. All models had uninformative priors for all parameters.

Survival

Adult survival was relatively constant (ca. 0.78) over time (Figure 2.4, Table 2.2), so we removed the random time effect on adult survival from the model. The fixed sex and translocation effects were also removed as there was no evidence for a difference in survival between males and females, or between survival over the first 6 months and later adult survival (Table 2.2). Juvenile survival was considerably lower than adult survival and varied from 0.14 to 0.38 among years (Figure 2.4). There was no evidence that density dependence caused this variation, as the 95% credible interval for the density effect of juvenile survival was centred near 0 (Table 2.2), and there was no decrease in juvenile survival over time (Figure 2.4). The probability of re-sighting a bird at each survey was 0.90, and this was constrained to be constant over time as the 95% confidence interval for the random year effect was centred near 0 (Table 2.2).

The precision of adult survival estimates increased as more data became available (Figure 2.5). For juvenile survival, random annual variation became apparent after 5 years of data were available (posterior distribution no longer concentrated near zero), so the model selected changes at this stage, increasing the accuracy of the estimates but reducing precision (Figure 2.5).

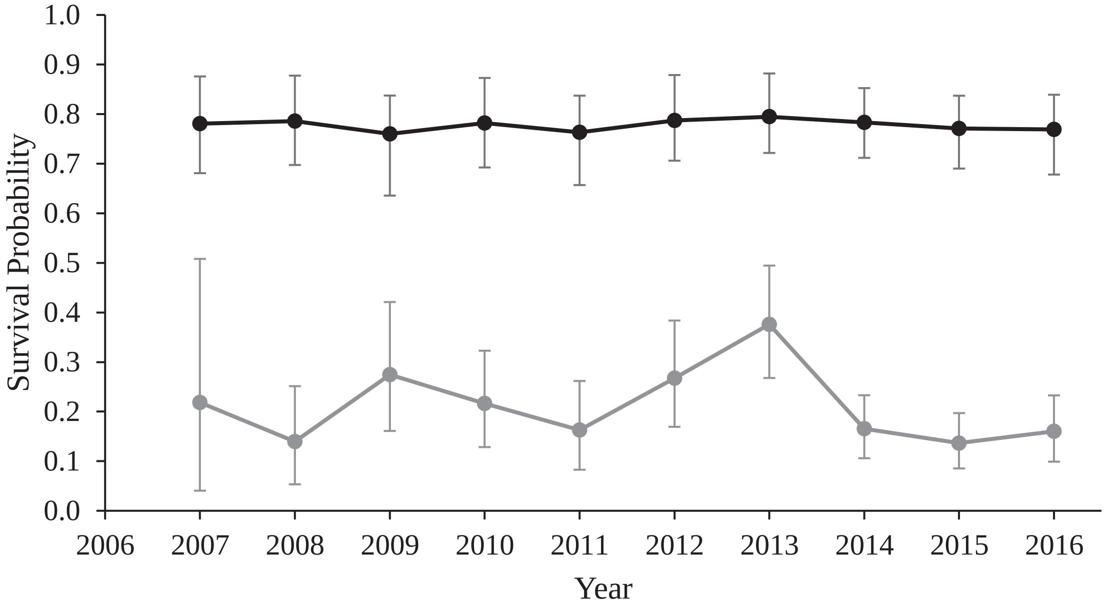

Figure 2.4. Estimated annual survival of adult (black) and juvenile (grey) North Island robins at Tawharanui under a model with random year effects, with uninformative priors used for all parameters. Error bars showing 95% credible intervals.

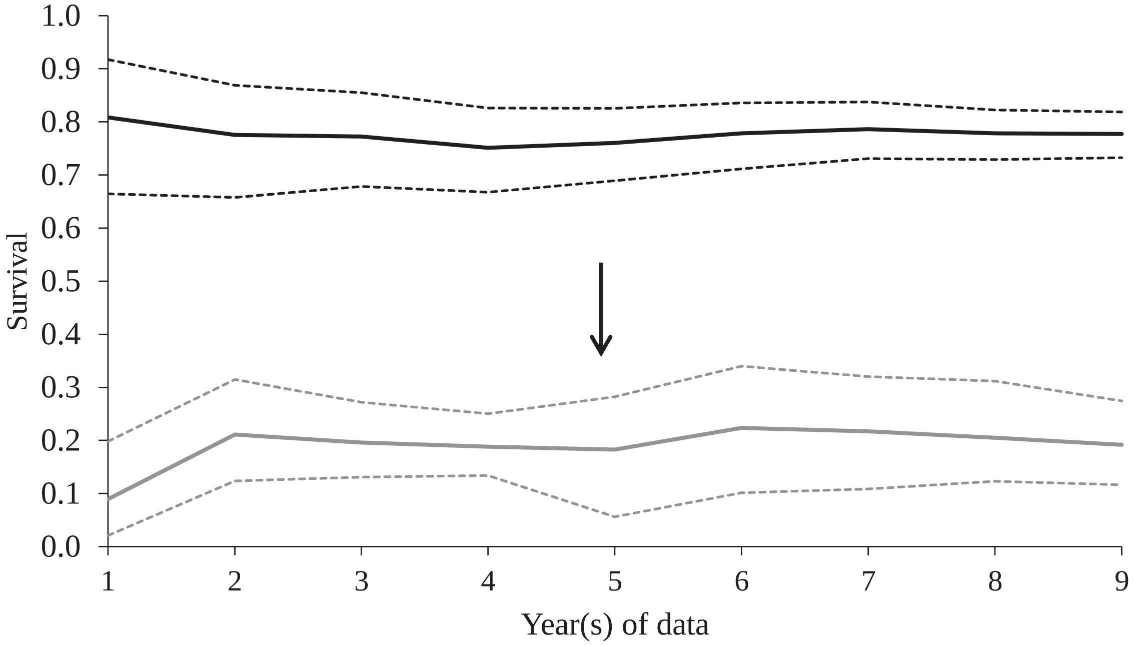

Figure 2.5. Changes in the estimated survival probabilities of adult (black) and juvenile (grey) North Island robins as a function of the number of years of monitoring data available.

Solid lines show estimates and dotted lines show 95% credible intervals. All variables in the reduced model fitted to all 9 years of data are included, except for the random year effect on juvenile survival which was added when 5 years of data were available (black arrow). Uninformative priors were used for all parameters.

Population Growth

Because it was unclear which was the best fecundity model, λ was estimated using models with and without the density effect on fecundity included. After 9 years of monitoring, the model with no density dependence gave a λ estimate of 1.13, with a lower 95% credible interval near 1 (Table 2.3). The model including density dependence gave a slightly higher λ estimate of 1.23 at zero density, but the lower credible limit was also near 1 due to the greater standard deviation under this model.

Table 2.3. Finite rate of increase (λ) and carrying capacity (K) estimates for the North Island robin population at Tawharanui Regional Park. The first row gives estimates based only on prior data from 9 other reintroduction sites. All other rows show estimates after 9 years of monitoring the Tawharanui population, with and without the ambiguous density effect on fecundity. K was only estimated when the density effect (DD) was included. Separate estimates are shown for when informative (I) and uninformative (U) priors were used. λ decreases with population growth under the density dependent model, and the values shown are for 0 density.

				λ			**K**	
Tawharanui data	**Prior**	**DD**	**mean**	**2.5% CL**	**97.5% CL**	**mean**	**2.5% CL**	**97.5% CL**
No	I	N/A	1.08	0.76	1.66	N/A	N/A	N/A
Yes	U	No	1.13	0.99	1.30	N/A	N/A	N/A
Yes	U	Yes	1.23	1.03	1.48	192	27	516
Yes	I	No	1.11	0.99	1.25	N/A	N/A	N/A
Yes	I	Yes	1.20	1.02	1.40	260	21	546

The mean λ was above 1 but its 95% credible interval was not always above 1 for all years of data availability (Figure 2.6). The lower credible limit for λ was below 1 until 3 years of data became available. It then fluctuated and remained around 1 for 7 years of data onwards (Figure 2.6). The apparent reduction in precision after 5 years is due to the addition of the random year effect to juvenile survival.

Informative priors enabled λ to be predicted when no Tawharanui data were available. Overall, informative priors produced lower upper credible limits and slightly higher lower credible limits. They also increased precision by giving narrower credible intervals, when the random year effect on juvenile survival was added to the model at 5 years (Figure 2.6).

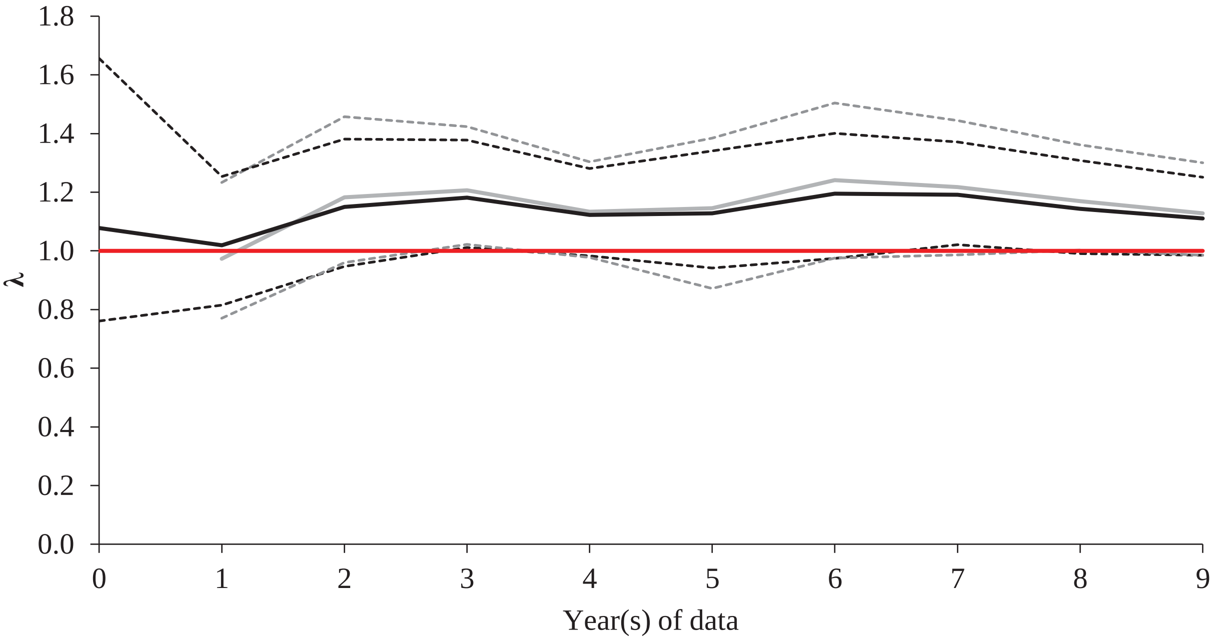

Figure 2.6. Changes in the estimated finite rate of increase (λ) of the reintroduced North Island robin population at Tawharanui Regional Park as a function of the number of years monitoring data available. Black lines show estimates (solid lines) and 95% credible intervals (dotted lines) using informative priors, whereas grey lines show estimates and 95% credible intervals using uninformative priors. The red line shows a λ value of 1, meaning the population is expected to persist. Both models shown here exclude density-dependence in fecundity.

Discussion

Models for reintroduced populations are useful for predicting population persistence under current conditions, to assess whether future management is likely to required. I combined survival and fecundity models for a reintroduced NI robin population, and estimated λ the 'finite rate of increase' within an integrated Bayesian framework. I found an ambiguous density effect on fecundity so estimated λ under models with and without density dependence. Under either model, with all 9 years of data the 95% credible interval for λ was >1, demonstrating that this population has a high probability of persistence under current circumstances. Both informative and uninformative priors gave reasonable parameter estimates after 1 year of data, and the number of years monitoring required was not reduced when informative priors were used.

Population models that include estimates of vital rates are useful, as inferences based on population trends alone can be misleading (Armstrong & Reynolds, 2012). The reintroduced NI robin population at Tawharanui increased in size from 2011-2013, followed by the population remaining at approximately 80 for the next three years. This can potentially create the impression that the population has reached carrying capacity. However, this is misleading as carrying capacity would be much larger under the minor (but ambiguous) density dependence in fecundity (Table 2.3), and there was no evidence of a density effect on juvenile survival. The trend in abundance can be explained by random annual variation in apparent juvenile survival. This random variation was attributed to chance environmental fluctuations.

Inbreeding depression can potentially cause changes in vital rates over time, and therefore affect the viability of small reintroduced populations. It is defined as the loss of fitness due to mating of close relatives, and is usually only expected to affect population persistence over long time frames as it has a gradual effect (Frankham et al., 2002). Inbreeding was demonstrated to reduce juvenile survival, but have no detectable effect on fecundity in a study of a reintroduced robin population conducted over a similar timeframe (Jamieson et al., 2007). However, effects on population dynamics were expected to be negligible for time frames < about 100 years (Jamieson, 2011). My focus was on estimating whether λ > 1 in the immediate future, as otherwise the population will not persist long enough for any genetic consequences to impact population growth.

My model enables prediction of the medium-term fate of this reintroduced population under current environmental and management circumstances. I emphasize that the incorporation of uncertainty around estimates is vital. Inclusion of parameter uncertainty may show that there is considerable risk that a reintroduced population will decline, even though λ is estimated to be > 1 (Armstrong et al., 2006). The lower credible limit of the λ distribution needs to be > 1 for conclusions about success to be robust to estimation error. This risk is illustrated in this case study. Although λ for the prior model (which does not contain any Tawharanui data) was above one (λ=1.08), its lower credible interval was well below one (λ LCL=0.76), meaning there was great uncertainty about whether the reintroduction would be successful. When the Tawharanui data were added, manipulation of the amount of data available showed that the credible limits for λ only reached 1 after 7 years of data. Environmental stochasticity affects these data requirements, as it will always take several years before a random year effect can be estimated. Here I found that random annual variation in juvenile survival could not be estimated and accounted for, until five years of data were available. This means that our initial survival estimates with fewer years of data could have been biased as they failed to consider annual variation.

The analysis was conducted in a Bayesian framework where prior information and the site-specific data both influence the results. Data from 9 other reintroduced populations were used to generate informative priors for the parameters. Informative priors enabled λ to be predicted when no Tawharanui data were available. Unsurprisingly, this model had the largest amount of variation surrounding its estimate of λ. The results showed that it took only 1 year of post-release data for estimates to become considerably more precise. This applied for models with both informative and uninformative priors. The period over which monitoring is required will depend on how close λ (and its associated uncertainty) is to 1, the amount of data collected each year, and the level of annual variation. The precision of the prior information depends on the variation among reintroduction sites, which in turn is affected by the number of sites and the amount of data available at each site.

The priors' ability to bias results is reduced when variation among sites is accounted for. Otherwise priors have the potential to cause bias in parameter estimates, especially for small data sets, and need to be interpreted carefully to ensure that the priors are not in conflict with the data (Gedir et al., 2013). In a similar manner, priors based on expert opinion can be used to improve the precision of model predictions from small data sets

(Martin et al., 2005). This is where a large portion of controversy surrounding Bayesian inference stems from, as the validity of this improvement is affected by how well the subjectivity of expert opinion is accounted for (Spiegelhalter et al., 2000; Pan & Yontay, 2016). As my priors were 'data-derived' using independent data from other sites, I avoided the issues of lack of independence and subjectivity.

It is important that models are run with both informative and uninformative priors and the entire suite of plausible models used to draw inferences (Gedir et al., 2013). Informative priors are currently not commonly used in Bayesian models for reintroductions (Canessa et al., 2016). This may be because insufficient data are available or the data not being in a format that can be easily analysed. It has been only recently that data from multiple reintroduction events became readily available (Parlato & Armstrong, 2012). In our case study, both informative and uninformative priors generated reasonable parameter estimates after one year of post-release data. The similarity of the results supports the reliability of estimates generated with uninformative priors, whilst demonstrating that informative priors also provide a logical basis in model predictions.

Monitoring generates vital information that can be used to evaluate the specific project outcomes, whilst informing the wider discipline of reintroduction biology (Nichols & Williams, 2006; Ewen, 2012; Goldsmith, 2012). Ideally reintroduction programmes require long-term monitoring, so focused monitoring that is linked to decision making is necessary to refine and adjust management strategies (Canessa et al., 2016). I used an initial demographic model with only data from other sites, and updated this model as post-release monitoring data for Tawharanui became available. This approach can be widely applied to other reintroduced populations, as it promotes the improvement of knowledge over time, which enables management strategies to be adjusted accordingly.

Chapter 3

Distinguishing juvenile survival from natal dispersal in a reintroduced population with low recruitment

Photo Credit: Jonas Kotlarz

Abstract

Detailed data on survival rates from fledgling to recruitment are rare in the literature. Most survival studies focus on ‘apparent juvenile survival’ which does not distinguish between permanent dispersal and true mortality. I estimated juvenile survival for a reintroduced North Island (NI) robin (*Petroica longipes*) population with low recruitment. I modelled different types of juvenile survival data (re-sighting, radio-telemetry, recruitment) within an integrated framework to determine the life-stages between fledging and adulthood where high mortality was occurring, and to distinguish mortality from dispersal. I determined that low juvenile survival is causing low recruitment. Overall there was a 16% chance a juvenile would survive to adulthood, and most mortality occurred within 6 weeks of fledging. Only 50% of juveniles survived to independence (ca. 4 weeks), and < 25% of juveniles survived to the end of the radio-tracking period (14 weeks), after which juvenile survival matched adult survival. Low juvenile survival indicates that habitat quality is marginal. Juveniles moved between closely connected habitat fragments, but low lying vegetation < 3 m and large pasture gaps > 110 m prevented them from dispersing from the park. Despite low juvenile survival, current habitat quality and connectivity is sufficient to maintain a population. I improved information on juvenile dispersal and survival rates from fledgling to recruitment, both areas where there is limited knowledge. I have demonstrated the clear advantages of distinguishing natal dispersal from juvenile mortality, both in terms of the ongoing and future management of reintroduced populations.

Introduction

In recent years, the focus of species reintroduction in New Zealand has shifted from predator-free offshore islands to areas on the mainland (i.e. 'Mainland Islands'), where predators have been either eradicated or reduced to very low densities. Numerous factors make reintroductions to mainland areas more challenging (e.g. habitat size and connectivity), and thus they have had lower success than island reintroductions. For a reintroduced population to be self-sustaining, population additions (births and immigration) must exceed losses (death or emigration) over the time-period of interest (Converse & Armstrong, 2016). Juvenile survival and dispersal are both critical factors that can influence reintroduction success. Mainland reintroductions regularly display low recruitment where too few juveniles remain within protected areas to replace adult losses (Lovegrove et al., 2002; Kemp et al., 2015).

Survival estimates are essential for estimating population persistence. Previous research has predominantly focused on apparent juvenile survival, which is the probability of a juvenile remaining within a defined area, and surviving to the next breeding season (Gardali et al., 2003; Schaub et al., 2012). Apparent survival does not distinguish between whether juvenile mortality is occurring during early life-stages (e.g. nestling, fledging), or whether juveniles are dispersing out of managed areas. This is an area where there is a considerable knowledge gap. The life-history stages where mortality and/or dispersal is limiting population growth, need to be evaluated in the context of the entire life cycle. Estimates at each life-stage from fledging to adulthood can distinguish dispersal from mortality. However, it is difficult to estimate survival over life-stages that involve dispersal as dispersal data are both costly and difficult to obtain.

Radio-telemetry can greatly improve data quality by distinguishing dispersal from mortality (Armstrong & Ewen, 2013). It enables the fate of individuals (and hence the reasons behind low recruitment) to be known. It also gives precise information about the timing of dispersal and can help to reveal information about which individuals survive and which die. This can lead to greater understanding of causes of death as bodies can be recovered for necropsy. However, even with radio telemetry, these inferences are not always clear with small animals. This is due to the short battery life and limited detection range of small transmitters. Telemetry can also be labour intensive and costly; therefore, small sample sizes generally limit studies. Nevertheless, the transmitters' ability to distinguish survival from mortality makes them highly useful for filling significant knowledge gaps.

Dispersal can compromise success in the short-term but also be critical to the long-term sustainability of reintroduced populations. Mainland reintroductions can fail due to post-release dispersal and ongoing dispersal away from the reintroduction site (Richardson et al., 2015). To date, most research has focused on reducing or mitigating post-release dispersal, without fully acknowledging the impacts of ongoing natal dispersal (Richardson et al., 2015). Natal dispersal patterns exhibit different traits to post-release dispersal as translocated individuals often exhibit a stress response (Adams et al., 2013), which causes different dispersal tendencies to those under normal conditions. Dispersal has similar costs to mortality as individuals that disperse and settle away from the release area will not contribute demographically or genetically to the population, increasing the risk of reintroduction failure (Le Gouar et al., 2012). Over the long-term this can cause genetic consequences such as reduced genetic variation.

Management of dispersal requires the consideration of all factors that contribute to the persistence of a species after reintroduction (Armstrong & Ewen, 2013; Richardson et al., 2015). In predator-free areas, habitat quantity, quality and connectivity are the most common factors implicated in the failure of reintroductions (Richardson et al., 2015). Reintroductions can fail when managed sites are small with a high level of connectivity to nearby unmanaged forest (Richardson et al., 2015). Poor habitat quality and high landscape connectivity have been key factors associated with low individual establishment probability and poor long-term persistence. Restoration of habitat, for example through predator control, may be futile when the habitat is highly connected. Unsurprisingly, the reintroduction of species with medium to high dispersal propensity to highly connected sites have shown a high risk of failure. It is essential that habitat quality, quantity, and connectivity be considered in combination with species dispersal propensity to optimise reintroduction success.

Understanding the dispersal behaviour of species in fragmented landscapes is fundamental to ensure their persistence (Wiens, 2001; Lens et al., 2002). The spatial arrangement and vegetation composition of habitat fragments can affect the movements of individuals. Species gap crossing abilities can affect their distribution in fragmented landscapes (Richard & Armstrong, 2010). Forest-dependent species are seldom adapted for movement in open areas, and wide gaps between habitat fragments can inhibit their movements (Lees & Peres, 2009; Robertson & Radford, 2009). The level of recommended habitat connectivity for species persistence in fragmented landscapes, can be determined by combining landscape structure with individual dispersal pathways.

Chapter Aim

This chapter examines the survival and movement patterns of juvenile North Island robins (*Petroica longipes*) at Tawharanui Regional Park. My main aim was to determine whether low recruitment into this population (Chapter 2) is caused by high mortality and/or dispersal out of the park. Over the 2015-16 breeding season re-sighting data were collected from fledging to independence and radio-telemetry data were collected during independence. Recruitment data (i.e. number of juveniles surviving to 2016-17 breeding season) were collected in a single survey in September 2016. I combine these data and model weekly and cumulative juvenile survival over life-stages (newly fledged, older fledgling, newly independent, older independent and post-radio tracking) from fledging to adulthood.

I then determine the predicted accessibility of different vegetation areas at Tawharanui, by extrapolating Richard and Armstrong's (2010) result that gaps in forest cover >110 m limit the movement of NI robins. I use the radio-telemetry data to calculate individual dispersal pathways and combine each pathway with the predicted accessibility of different vegetation areas to determine whether habitat fragmentation is affecting movement within, or preventing dispersal from Tawharanui.

Methods

Species and Study Area

The North Island (NI) robin is a small (26-32g) forest passerine endemic to New Zealand (Higgins & Peter, 2002). Their diet is mainly composed of invertebrates found on the forest floor and amongst bark on tree trunks (Higgins & Peter, 2002; Heather et al., 2005). NI robins are territorial and have particularly high detectability due to their inquisitiveness and strong response to territory lure calls. They are socially and genetically monogamous and nesting typically occurs from September to February. Females produce two to three young per brood and can have up to three broods per season. The incubation period is approximately two to three weeks (ca.17 d), and chicks fledge (i.e. leave the nest) within 3 weeks (ca. 19-21d) of hatching. Adults will feed juveniles for a minimum of four weeks after fledging, during this time juveniles remain within their parent's territory and no dispersal occurs (Armstrong et al., 2000). Juveniles then undergo an initial dispersal phase and many disperse before establishing a territory.

NI robins have declined in range since human colonisation. They originally occurred throughout forested areas in the North Island but have been extirpated from > 90% of their original range due to forest clearance and predation by introduced mammals (e.g. ship rats *Rattus rattus*). Although they are not classified as threatened, many local restoration programmes are attempting to recover populations through translocation and predator management (Parlato, 2014). They are often one of the first species reintroduced to a new site as they are easy to detect and monitor and are more robust to predation than other more highly endangered endemic species (e.g. NI saddlebacks *Philesturnus rufusater*).

The study was conducted at Tawharanui Regional Park, a 550-ha peninsula site approximately 80 km north of Auckland, New Zealand. The park operates as an open sanctuary that integrates recreation, conservation, and farming. One hundred and seventy ha of the total area of the park is pasture, and forested areas exist in several discrete fragments. The main forest fragments that provide habitat for robins are all similar in species composition and consist of kanuka scrub/forest, manuka scrub and pohutukawa-puriri-broadleaf forest (Singers et al., 2015). Auckland Council operates Tawharanui in partnership with the Tawharanui Open Sanctuary Society (TOSSI). Intensive predator control, combined with the installation of an open ended 27 km predator exclusion fence in 2004, has caused the eradication of all mammal species except mice (*Mus musculus*), and there is ongoing monitoring for incursions (Maitland, 2011). In 2007 21 North Island robins were reintroduced to the largest fragment (Ecology Bush) and have since spread to two other main fragments (Possum Gully and Takatu Bush) (Figure 3.1).

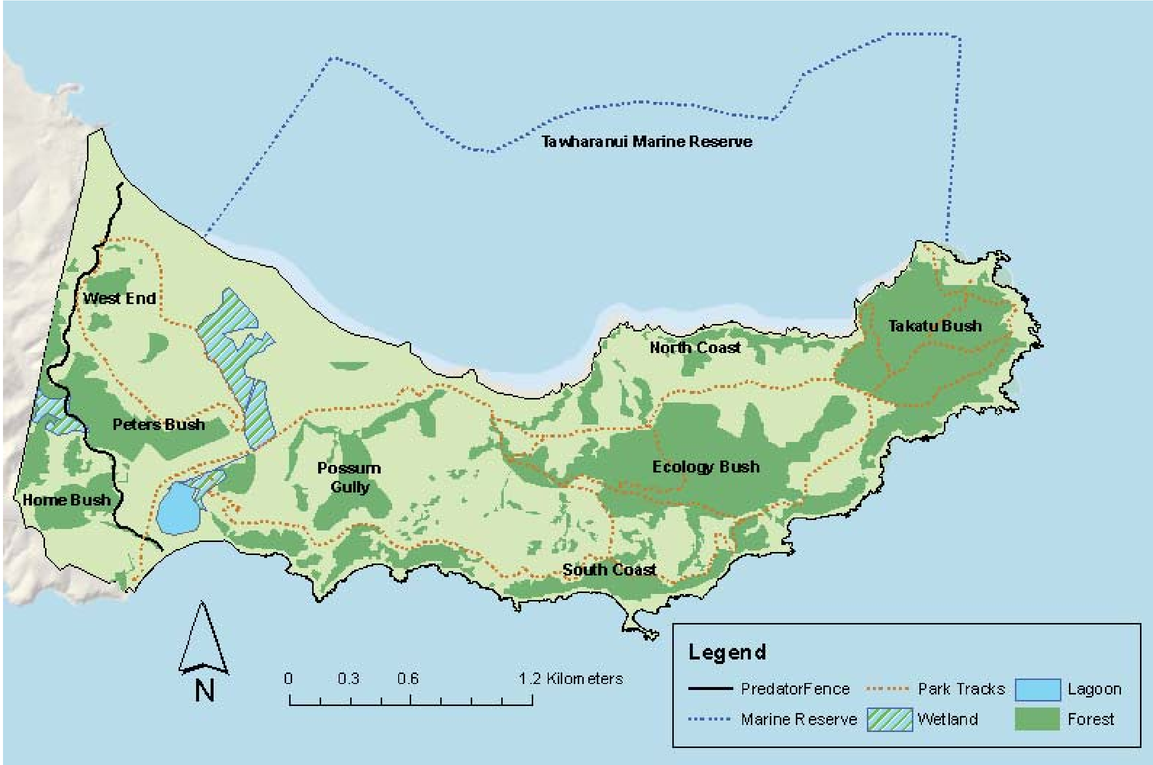
Tawharanui Marine Reserve
West End
Peters Bush
Home Bush
Possum Gully
North Coast
Takatu Bush
Ecology Bush
South Coast
N
0
0.3
0.6
1.2 Kilometers
Legend
PredatorFence
Park Tracks
Lagoon
Marine Reserve
Wetland
Forest

Figure 3.1. Map of Tawharanui Regional Park showing the main boundaries, natural features, and tracks. North Island robins are present in Possum Gully, Ecology Bush, and Takatu Bush, and absent from the North and South Coast fragments, Home Bush, Peter's Bush, and West End Bush.

Data collection

Post-fledging data for dependent juveniles and radio telemetry data for independent juveniles were collected between September 2015 and March 2016. Juveniles were banded on the nest 9-12 days after hatching. I typically checked nests at least once before the chicks fledged, and then visited territories approximately once a week during the initial four weeks after the chicks fledged. NI robins can be trained to take meal worms (*Tenebrio molitor*). After the young left the nest, I determined whether adults were feeding fledglings, by giving them meal worms and recording the band combinations of the fledglings fed. If the adults showed no signs of feeding fledglings, suggesting the fledglings had died, I still visited on at least two further occasions so that I could estimate the probability of failing to detect live chicks.

Radio transmitters (Holohil BD-2, 1.05g) were attached to a sample of 20 juveniles > 4 weeks after fledging to obtain data on their subsequent survival and movements. The sample size is reflective of the number of available transmitters and number of juveniles able to be monitored adequately by one person. At least one juvenile from each of the three forest patches with robin territories was radio tagged, enabling me to record movements within and between habitat fragments in the park.

Juveniles were captured using a hand net or Potter trap after training them to come to the ground to feed on meal worms, and the transmitters were attached using a Rappole harness around the legs (Rappole & Tipton, 1991) (Figure 3.2). Juveniles were then tracked every one to three days using a TR4 receiver (Telenics, Arizona, USA) and a handheld Yagi antenna (Sirtrack electronics, Havelock North, New Zealand), until they died or the transmitter fell off or its battery ran out (approximately 42 days). On each occasion, I sighted the bird to confirm whether it was alive and recorded its coordinates using a GPS (Global positioning system). Juveniles were typically caught four to six weeks after fledging whilst in their natal territory. However, to extend the age range where juveniles were tracked, transmitters were also attached to three older juveniles (8 to 9 weeks after fledging) encountered outside the natal territory, and a second transmitter was attached to two juveniles after the battery ran out. Where possible, the spent transmitters were removed after monitoring. The sex of radio-tagged birds was determined from DNA extracted from feathers (Norris-Caneda & Elliott, 1998).

Juvenile survival data covering the end of the radio-tracking period to adulthood were collected in a single survival survey in September 2016. Any pair changes to established territories were recorded, and other suitable habitat areas within the park searched. The 2015-16 juveniles could be distinguished from previous years' juveniles as all chicks receive a unique colour band combination. The number of juveniles from the 2015-16 breeding season observed in the September 2016 survey enabled recruitment to be estimated.

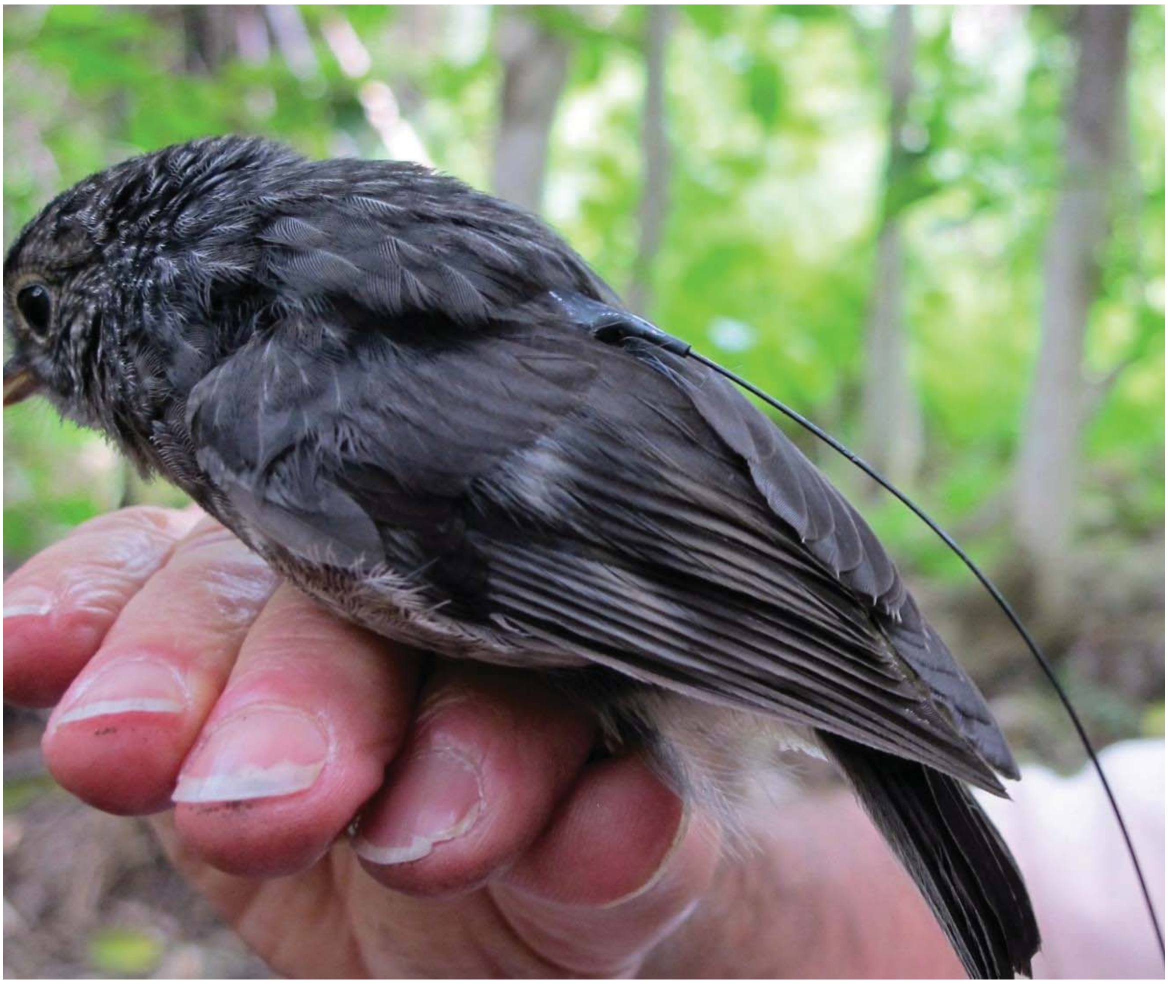

Figure 3.2. Juvenile North Island robin with radio transmitter attached using a Rappole harness.

Juvenile Survival Modelling

I created a model that estimated weekly survival probabilities for each of five stages: "newly fledged" (0-2 weeks after fledging), "older fledgling" (2-4 weeks after fledging), "newly independent" (4-6 weeks after fledgling), "older independent" (6-14 weeks after fledging) and "post-radio tracking" (> 14 weeks after fledging). Mortality was able be distinguished from dispersal over the first four stages as juveniles do not disperse within four weeks of fledging, and radio tracking occurred over weeks 4 to 14. Mortality could not be distinguished from dispersal during the final "post-radio tracking" stage. I also included an early/late effect in the model (acting in parallel to the stage effects), as previous years' data showed chicks born later in the breeding season were less likely to recruit. Juveniles were divided into those that fledged "early" (before 1 December) and "late" (after 1 December).

I used the Bayesian updating software OpenBUGS (version 3.2.3) to model the data as it allows simultaneous modelling of post-fledgling, radio-telemetry, and recruitment data within an integrated framework by combining a state-space formulation of the Cormack-Jolly-Seber (CJS) model and "known fate" model. I modelled survival probabilities with logit link functions and Bernoulli error distributions (Schofield et al., 2009). Uninformative priors that were normally distributed were used for survival parameters. The model was run for up to 50,000 iterations with an initial burn in of 10,000 samples after checking convergence by examining the chains.

A state-space formulation of the Cormack-Jolly-Seber (CJS) was used to model post-fledgling and recruitment data. The CJS model assumes the probability of a bird being seen is dependent on both its survival and re-sighting probabilities (McCarthy, 2007; Kéry & Schaub, 2012). An uninformative prior was used to model detection probability for post-fledgling data. The post-fledgling data were used to model survival from fledgling to independence, covering the "newly fledged" and "older fledgling" stages. For logistic reasons, post-fledgling monitoring checks were not synchronised among territories or conducted at even intervals, causing "ragged data". Our modelling approach allowed for this by generating a separate encounter history for each bird. The recruitment data were obtained in a single survey. These data were used to model survival from the end of the radio-tracking period to adulthood, covering the "post-radio tracking" stage. An informative prior (0.898 ± 0.019) was used for detection probability of recruited birds as it was known from previous annual survival surveys (Chapter 2).

Radio-tracked juveniles were modelled throughout the initial 10 weeks of independence (4 to 14 weeks after fledgling) as "known fate" data. The fate of each radio-tagged juvenile was known at each check because they were sighted and their fate (dead or alive) confirmed. This means that detection probability was 1 over the "newly independent" and "older independent" stages. The data for radio-tagged juveniles were also "ragged", as there were a few occasions when they could not be checked on the same day.

Juvenile Dispersal

Spatial analysis of dispersal data was conducted in ArcMap 10.2 (ESRI, Redlands, California, USA). A map was created that predicted the accessibility of different vegetation areas within Tawharanui for dispersing juvenile robins. This map was based on extrapolation of Richard and Armstrong's (2010) result that gaps in forest cover > 110 m limit NI robin movements. A 55 m buffer was applied around all areas of forest (defined as woody vegetation > 3 m high), and areas outside this buffer were predicted to be un-crossable. Dispersal maps, which show the actual movements of radio-tracked juveniles during their dispersal stage, were generated to test whether these movements were consistent with the predicted accessibility. These maps were created by plotting the GPS coordinates for all radio-tracked juveniles onto aerial photographs and connecting the main steps to determine dispersal pathways for all juveniles that were tracked until 'dispersal', i.e. until they moved > 100 m.

Results

Juvenile Survival

Over the 2015-16 breeding season 109 juveniles were banded. Fifteen of these were re-sighted as recruits during the September survival survey. With detection accounted for, the probability of a juvenile surviving and remaining at Tawharanui from banding to recruitment was 0.160 with a standard error of 0.037. Separation of juveniles into those that fledged 'early' and 'late' showed a higher survival for 'early' juveniles (Table 3.1, Figure 3.3). The probability of an 'early' juvenile recruiting was 0.221 ± 0.058 and a 'late' juvenile recruiting was 0.105 ± 0.044.

Juvenile survival on the nest after banding was high (0.972 ± 0.043). Survival then declined immediately after fledging, and during the initial weeks of independence. Independence occurred between 4 and 6 weeks after fledging. The earliest a juvenile reached independence was 28 days post-fledging and the latest was 41 days post-fledging. Approximately half (0.544 ± 0.069) of the 'early' juveniles survived from banding to the minimum (4-week post-fledging) time-period for independence, and survival of 'late' juveniles was even lower at 0.378 ± 0.073 (Figure 3.3). Most of this mortality occurred during the 'newly fledged' stage, i.e. within 2 weeks after fledgling. These survival estimates account for detection probability for checks during the post-fledging period. This probability was estimated to be 0.739 ± 0.035.

Table 3.1. Weekly survival probabilities with associated standard errors and lower and upper 95% credible limits (LCL, UCL), for juvenile North Island robins from fledging (ca. 21 days after hatching) to recruitment at Tawharanui Regional Park. Separate estimates are shown for juveniles that fledged 'early' (before 1 December 2015) and juveniles that fledged 'late' (after 1 December 2015).

		Early				Late			
Stage	**Wks after fledging**	**Mean**	**Sd**	**LCL**	**UCL**	**Mean**	**Sd**	**LCL**	**UCL**
Newly fledged	0-2	0.757	0.047	0.667	0.850	0.642	0.061	0.527	0.763
Older fledgling	2-4	0.983	0.032	0.884	1.000	0.972	0.049	0.824	1.000
Newly independent	4-6	0.769	0.074	0.607	0.903	0.660	0.096	0.465	0.840
Older independent	6-14	0.964	0.023	0.913	0.998	0.939	0.039	0.852	0.995
Post radio-tracking	> 14	0.996	0.005	0.982	1.000	0.993	0.010	0.966	1.000

Less than 25% of the juveniles that fledged survived to the later stages of independence. The probability of a juvenile surviving from fledging to the end of the radio-tracking period was 0.245 ± 0.070 for an 'early' juvenile and 0.125 ± 0.049 for a 'late' juvenile. During independence, most mortality occurred during the 'newly independent' stage (4 to 6 weeks after fledging) (Table 3.1). Apparent juvenile survival was close to 100% after the end of the radio-tracking period (14 weeks after fledging) to recruitment (Figure 3.1). This meant that there was no confounding dispersal effect on juvenile survival, as almost no disappearances occurred during the "post-radio tracking" stage when mortality could not be distinguished from dispersal.

Juvenile Dispersal

The accessibility map predicted that juveniles would be able to disperse between habitat fragments within the park, but not able leave it, due to a dispersal barrier on the western side of the park (Figure 3.4). The dispersal pathways of the radio-tracked juveniles supported this prediction as none of the 20 juveniles radio-tagged over the 2015-16 breeding season left the park (Figures 3.5, 3.6). Ten of these radio-tagged juveniles were female, 7 were male and sex could not be determined for the remaining 3 due to insufficient

DNA on the feathers collected. Dispersal pathways were calculated for the 14 juveniles that moved > 100 m, and these include three birds that dropped their transmitters.

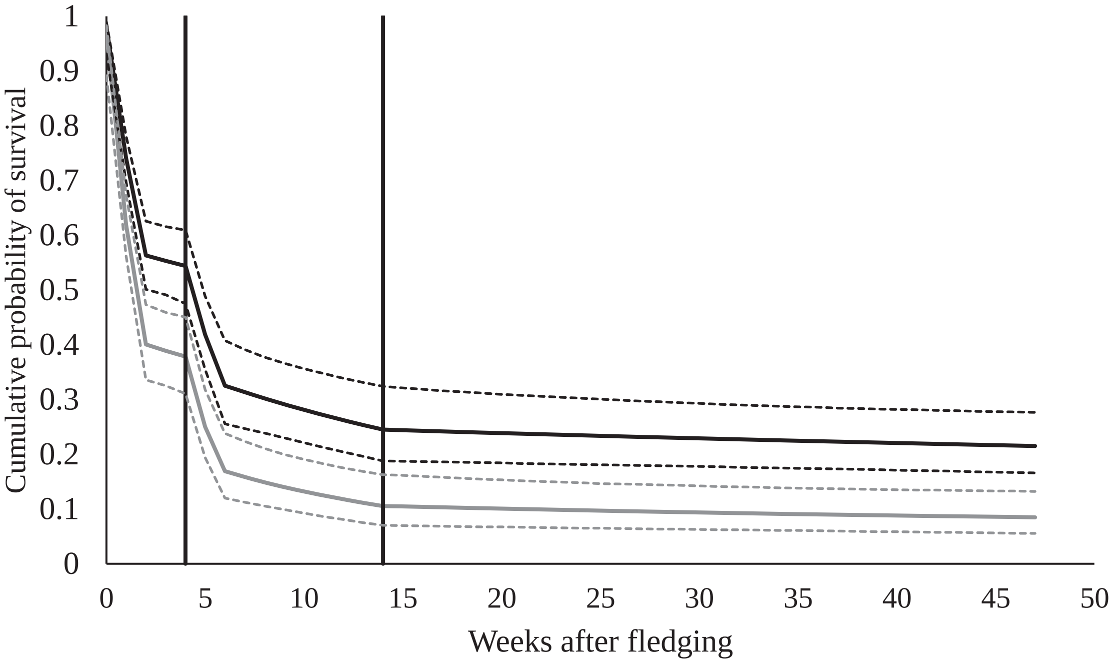

Figure 3.3. Estimated cumulative survival probability of juvenile North Island robins at Tawharanui Regional Park as a function of weeks after fledging. Black lines show estimates and standard errors for juveniles that fledged early (before 1 December) and grey lines show estimates and standard errors for juveniles that fledged after 1 December. The region between the vertical lines is the time-period (weeks 4 to 14) during which independent juveniles were radio-tracked.

Dispersal pathways show that juveniles can travel between the three main areas of forest and to closely connected patches of regenerating forest that were not suitable for establishment of a permanent robin territory due to the absence of an understory and leaf litter layer (Figure 3.5, 3.6). The pathways also show that they travelled to the South Coast, an area within the park where no robins had been previously sighted and there are no known adult territories.

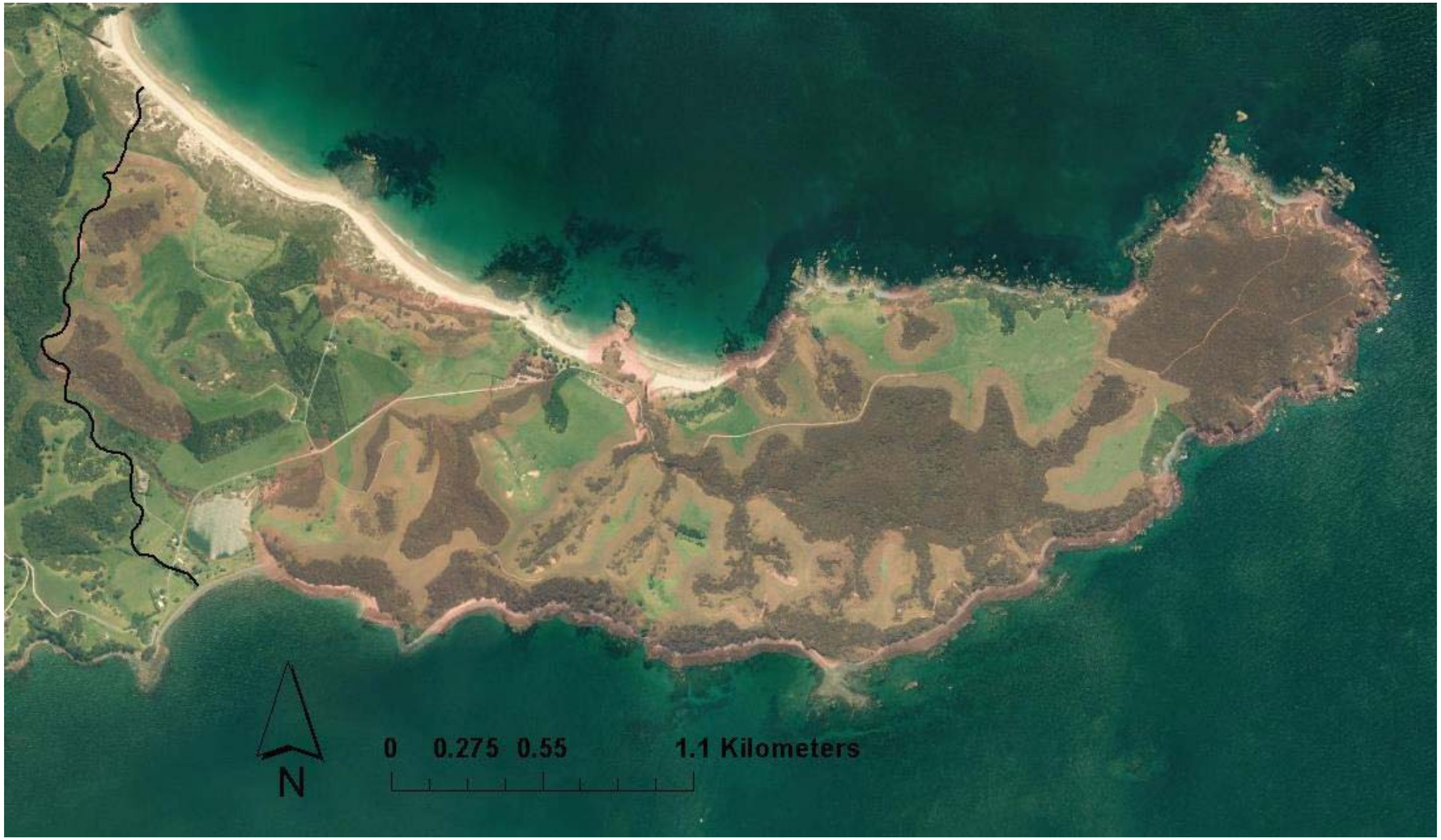

Figure 3.4. Predicted accessibility of different vegetation areas at Tawharanui based on Richard and Armstrong's (2010) estimate that gaps in forest cover > 110 m limit North Island robin movements. The black line shows the predator exclusion fence. The pink shading shows a 55 m buffer to all areas of vegetation > 3 m within Tawharanui, and areas outside of this buffer were predicted to be un-crossable.

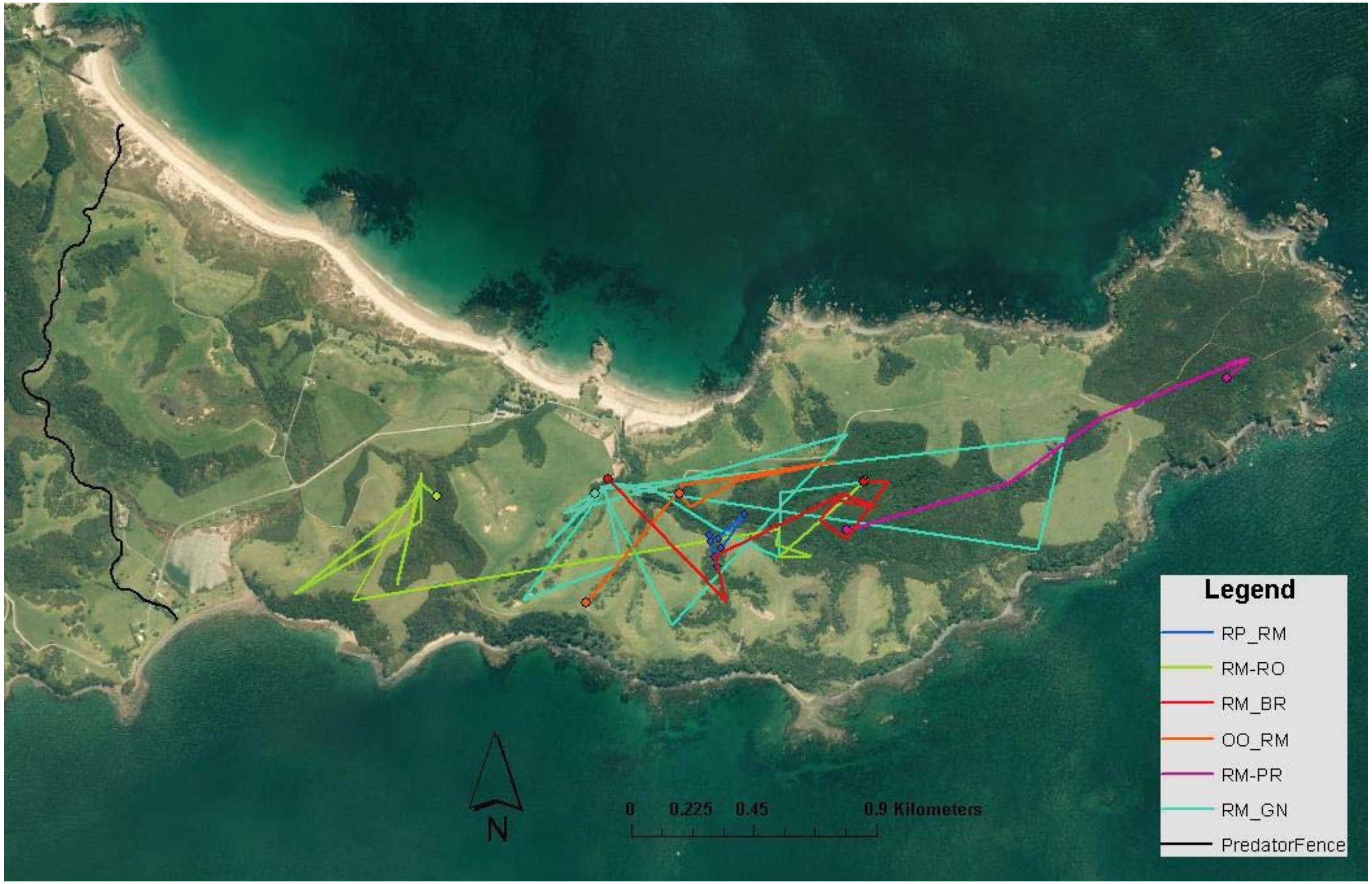
Legend
RP_RM
RM-RO
RM_BR
OO_RM
RM-PR
RM_GN
PredatorFence
N
0
0.225
0.45
0.9 Kilometers

Figure 3.5. Dispersal pathways of radio-tagged female juvenile North Island robins that travelled > 100 m at Tawharanui Regional Park from November 2015 to February 2016.

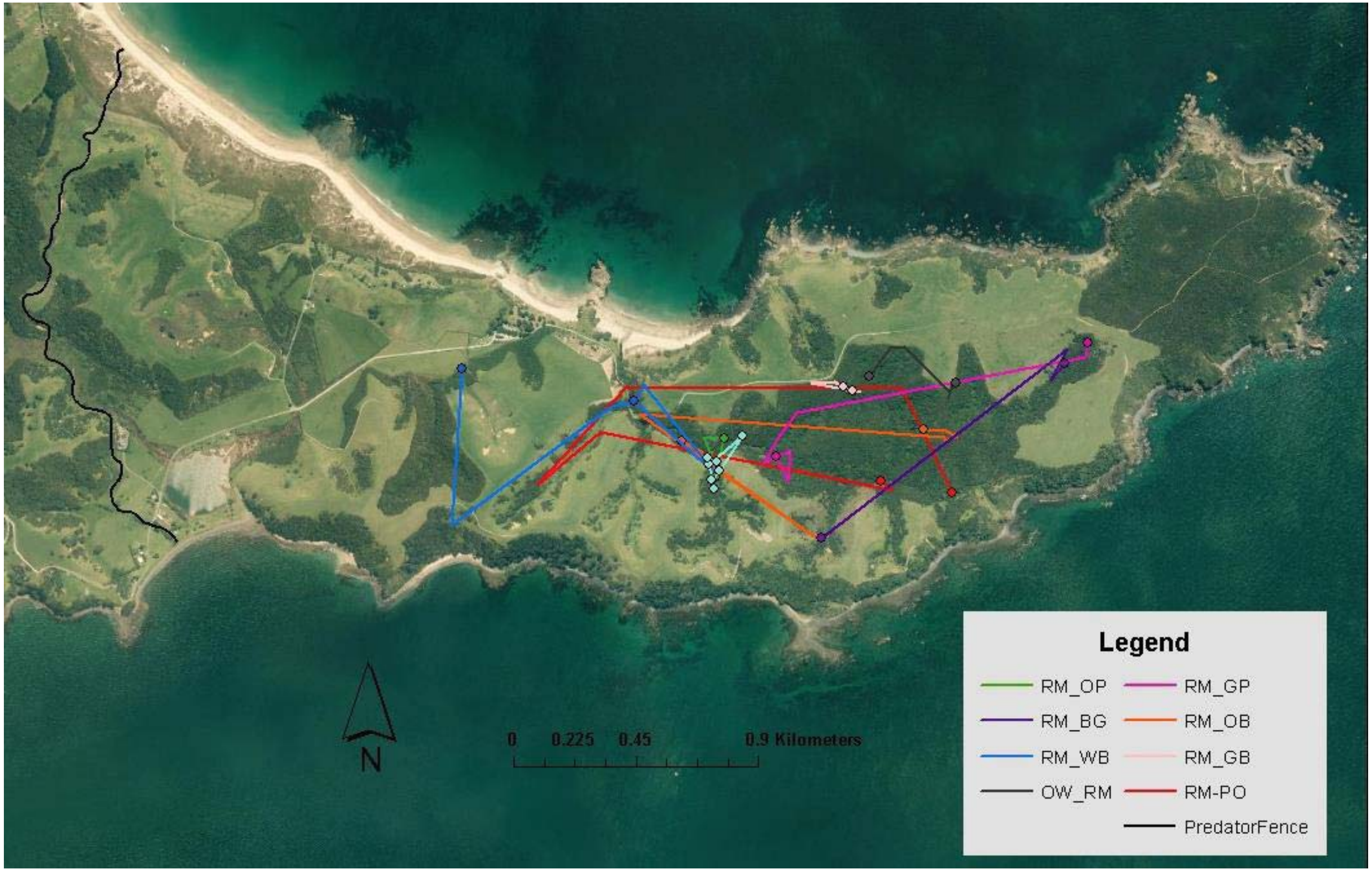
Legend
RM_OP
RM_GP
RM_BG
RM_OB
RM_WB
RM_GB
OW_RM
RM-PO
PredatorFence
N
0
0.225
0.45
0.9 Kilometers

Figure 3.6. Straight-line dispersal pathways of radio-tagged juvenile North Island robins that travelled > 100 m at Tawharanui Regional Park from November 2015 to February 2016. All birds displayed are male, except RM_GB and RM_PO whose sexes were unknown.

Discussion

Low juvenile survival is causing the low recruitment of the reintroduced NI robin population at Tawharanui (Chapter 2). I modelled different types of juvenile survival data (post-fledgling, radio-telemetry, recruitment) within an integrated framework to determine the stages between fledging and adulthood where high mortality was occurring, and to distinguish mortality from dispersal. Overall, there was only a 16% chance that a juvenile from the 2015-16 breeding season would survive to adulthood, and most mortality occurred within 6 weeks of fledgling. Juveniles that fledged after 1 December had considerably lower survival than those that fledged earlier in the breeding season, a similar result to what was found at Tiritiri Matangi (Dimond & Armstrong, 2007). Dispersal did not confound juvenile survival estimates as almost no juveniles disappeared after radio-tracking, which was the only time period between fledging and recruitment where mortality could not be distinguished from dispersal.

Weekly survival was lowest in the initial two weeks after fledging. Only about half the chicks banded survived to four weeks after fledging, to the minimum age of independence. High mortality immediately after fledging is well documented (Anders et al., 1997; Rush & Stutchbury, 2008; Low & Pärt, 2009), and likely causes are predation and starvation. Shortage of food at high densities is likely to limit robin populations (Dimond & Armstrong, 2007). However, there is no indication that juvenile survival at Tawharanui is being limited by density (Chapter 2). High mortality is likely to be due to avian predation and food shortage due to poor habitat quality. Predation by owls (Morepork *Ninox novaeseelandiae*) has been observed for both young naive fledglings and adult robins (Dimond & Armstrong, 2007), although the numbers lost to this predation remain largely unknown. Fledglings also have high nutritional requirements and are completely dependent on their parents for food. This can be a very laborious task for adults as they feed 2-3 fledglings each brood. It is unclear why most juveniles die as fledglings after leaving the nest, and not before. Nevertheless, it is reasonable to expect some juveniles will be lost to starvation.

Survival was also low four to six weeks after fledging during the 'early independence' stage. Less than 25% of juveniles were estimated to survive to 14 weeks after fledging, their subsequent weekly survival (0.996) was consistent with the 79% annual survival estimated for adults (Chapter 2). Early independence is normally associated with low survival, as dispersing juveniles are inexperienced, have low social skill and poor locomotory skills (Marchetti & Price, 1989; Salinas-Melgoza & Renton, 2007). The survival of newly-independent animals will be particulary low in habitat where food availability is limited. It is well recognised that non-favourable conditions limit food availablity, reducing habitat quality (White, 2008). Tawharanui has a large amount of dry and exposed coastal vegetation along the edges of the peninsula, which are poor quality habitat for NI robins.

Landscape connectivity affects habitat quality by influencing dispersal movements. Functional landscape connectivity is the degree to which species movement is facilitated or impeded between different elements of a landscape (Taylor et al., 1993). All models of landscape connectivity need to be corroborated with actual dispersal data (Richard & Armstrong, 2010). My juvenile dispersal pathways supported the accessibility map predictions in showing that habitat fragmentation was affecting dispersal at Tawharanui. Many adult territories at Tawharanui are aggregated within a fragmented habitat matrix. Newly independent juveniles would often sit on the edge of their natal territories, with further exploration appearing to be difficult due to the aggression of neighbouring pairs, or prohibited by large gaps of pasture. I found juveniles could disperse through closely connected patchy habitat where there were no established robin territories, but they did not cross pasture gaps over 110 m or travel through vegetation < 3 m in hight. They dispersed between habitat fragments within the park but appeared to be unable to leave due to a dispersal barrier on the western side caused by extensive pasture and other low vegetation.

Low recruitment for NI robin populations has also been found at three other peninsula sites: Wenderholm Regional Park, Glenfern and Cape Kidnappers (Parlato & Armstrong, 2012). Wenderholm is a peninsular site where a reintroduced robin population bred successfully for nearly 10 years before it died out. There was very high dispersal from Wenderholm and too few young birds stayed within the park to replace adult losses (Andrews, 2007). Tawharanui has different dispersal patterns as it is a larger reserve with more discrete forest patches and lower connectivity. My results show factors causing low recruitment differ between peninsular sites and they do not support the hypothesis that peninsulas facilitate juvenile dispersal along forest edges inland (Parlato & Armstrong, 2012).

Detailed data on survival rates from fledgling to recruitment are rare in the literature. Most studies of annual survival suffer from the inability to distinguish between permanent dispersal and true mortality (Gardali et al., 2003). This is mainly due to the difficulty and cost of obtaining data after independence. Radio-tracking juveniles during their dispersal phase allowed me to bridge a knowledge gap as it enabled mortality to be distinguished from dispersal. It is unlikely that the mortality observed was related to their transmitters as most juveniles survived at least a week after transmitter attachment. Most small bird species are unable to survive more than a day or two without food (Newton, 1998). Except for two juveniles, all mortalities occurred within three days of when their parents stopped feeding them. This supports my earlier conclusion that some inexperienced juveniles are unable to forage properly and most probably starve. The usual limitations associated with transmitters (short battery life, limited detection range) were reduced for my study, as most mortality occurred before the end of the radio-tracking period.

Despite low juvenile survival, the robin population at Tawharanui is expected to persist under current circumstances (Chapter 2). However, regeneration on the western side will increase the risk of dispersal out of the park, which could have both positive and negative implications. Whilst it is important to acknowledge that some level of immigration and emigration together will be required in the long-term for genetic viability, emigration is likely to result in mortality for individuals that disperse into unmanaged areas outside the park. If dispersal exceeds recruitment (as per Wenderholm) the population may die out.

My study provides information that can be useful for predicting the fates of other reintroductions in mainland landscapes. I improved information on juvenile dispersal and survival rates from fledging to recruitment, both areas where there is limited knowledge. It is low juvenile survival that is causing low recruitment, indicating the habitat quality is marginal. Although habitat fragmentation highly influenced dispersal pathways, current habitat quality and connectivity is sufficient to maintain a population. Revegetation needs to be considered carefully as increased connectivity will have implications for future management of the park. My results demonstrate the clear advantages of distinguishing natal dispersal from juvenile mortality, both in terms of the ongoing and future management of reintroduced populations, and for predicting the suitability of sites for future reintroductions

Chapter 4

Assessing the potential to harvest a reintroduced population for further translocations

Abstract

Reintroductions require source animals which must be harvested from existing populations. Harvesting of a source population needs to be sustainable. I was asked to assess whether it would be sensible to harvest the North Island (NI) robin (*Petroica longipes*) population at Tawharanui Regional Park, as their location makes them a convenient source for future reintroductions. I predicted the impact of a one-off harvest on the persistence of the Tawharanui population. I projected population dynamics 10 years into the future and used a female-only stochastic model to compare the population's response when 5, 10, 15 or 20 females were harvested. Population dynamics were projected with and without density dependence, as there was an ambiguous density effect on fecundity. With no harvest, the median number of females increased from 33 to 68 over 10 years for the model with density dependence in fecundity, and to 124 for the model without density dependence. The lower prediction limits for the number of females were 23-25 for both models. While the probability of extinction within 10 years was < 0.01 for all scenarios, a one off-harvest at any level was predicted to reduce the population in 10 years. The lower prediction limits were ≤ 15 females for the higher harvest levels. In the event of a proposed NI robin reintroduction, my predictions can be used within a decision analysis framework to facilitate the decision of whether Tawharanui is a suitable source population.

Introduction

Sustainable harvesting is harvesting that allows population numbers to be maintained or increased over time (López-Hoffman et al., 2006). Harvesting strategies can be addressed through population modelling (Pöysä, 2004). Accurate modelling requires reasonable understanding of the mechanisms regulating populations (Armstrong & Reynolds, 2012). Rapid population growth after establishment can cause density dependence, potentially providing an opportunity for sustainable harvesting. As density increases, food and space availability decreases, in turn decreasing survival and/or fecundity. Harvesting is direct manipulation of density, so density dependence may enable populations to be harvested with minimal cost in terms of viability (Caughley & Sinclair, 1994; Armstrong & Ewen, 2002; Pöysä, 2004). Sustainable harvesting can be applied to any situation where organisms are removed from populations. One of these situations is translocation of threatened species for reintroduction.

Species reintroductions require source populations. Animals for translocation must be harvested from an existing population, whether it be a remnant population, reintroduced population, or captive population. Remnant populations of endangered species are likely to have higher genetic diversity but be living in sub-optimal habitat at lower densities, due to extensive habitat clearance and/or impacts of introduced species. Reintroduced populations are generally released into habitat that has been restored, for example through predator control. Improved habitat quality can cause rapid population growth and density dependence. Therefore, reintroduced populations may be the best candidates for harvesting for future translocations (Armstrong & Ewen, 2002). In any case, for harvesting to be sensible the impacts to the source population need to be outweighed by the benefits of the reintroduction (Seddon et al., 2007; Armstrong & Reynolds, 2012).

Decision analysis provides a framework for optimal choices about the numerous components of reintroductions. It can be used to facilitate the decision about whether a source population is the optimal choice for future reintroductions. Decision analysis breaks complex problems into smaller steps and focuses on objectives, while making decisions to overcome common human errors in judgement. This involves articulating a key question, defining objectives, identifying a set of alternative management actions, and then weighing up the costs and benefits of these actions (Converse & Armstrong, 2016). Demographic models link objectives with alternative actions by providing predictions of system responses to each of the management actions (Armstrong & Reynolds, 2012). Population predictions are essential for determining the impact of harvesting, and can be used to assess whether harvesting is sustainable in the context of the dynamics of the source population.

Chapter Aim

This chapter examines the implications of a one-off harvest on the persistence of a reintroduced population of North Island (NI) robins (*Petroica longipes*) at Tawharanui Regional Park. My aim was to help facilitate the decision of whether Tawharanui is a suitable source population for potential future reintroductions in the region. I expanded the population model created for this reintroduced population (Chapter 2) to project population dynamics 10 years into the future, and simulated a one-off harvest in March 2017. I used a female-only stochastic harvest model and compared the population's predicted response to different numbers harvested. I modelled four different scenarios: harvest of five females, harvest of 10 females, harvest of 15 females, harvest of 20 females.

Methods

Species

North Island (NI) robins are small (26-32g) forest passerines endemic to New Zealand (Higgins & Peter, 2002). Forest clearance and predation by introduction mammals has caused them to become extirpated from > 90% their original range. They are territorial, insectivorous birds that typically form monogamous life-bonds. Their breeding season spans from September to February, during which they produce up to three clutches, each containing one to three eggs. Many local restoration programmes are attempting to recover NI robin populations through translocation and predator management (Parlato, 2014). They are often one of the first species reintroduced to a new site as they are easy to detect and monitor, and are more robust to predation than other more highly endangered endemic species. Consequently, there are frequent requests to harvest some existing populations for reintroductions.

Study Site and Population

Tawharanui is a 500 ha mainland peninsula site, approximately 80 km north of Auckland New Zealand. Auckland Council owns Tawharanui Regional Park. In 2004 a coast-to-coast predator exclusion fence was installed. Ongoing extensive predator control has eradicated all mammalian pest species except mice (*Mus musculus*) and rabbits (*Oryctolagus* *cuniculus*). In 2006, Tawharanui was opened as New Zealand’s first open sanctuary that combines recreation, conservation, and farming (Murdoch, 2008). NI robins were the second avian species translocated, and since their reintroduction a further five species including takahae (*Porphyrio hochstetteri*), whitehead (*Mohoua albicilla*) and NI saddleback (*Philesturnus rufusater*) have been translocated to Tawharanui.

Twenty-one NI robins were translocated to Tawharanui from Tiritiri Matangi in March 2007. There was a sex bias in this initial translocation as it comprised 15 males and 6 females. Consequently, four additional females were captured on private land near Puhoi later in 2007 and translocated to Tawharanui to increase the number of females in the founding population. There was no mortality before release during any of the translocations to Tawharanui. The Puhoi birds were a satellite population derived from the population reintroduced to Wenderholm Regional Park in 1999, which also originated from Tiritiri Matangi (Dimond & Armstrong, 2007). The Tiritiri Matangi population is a reintroduced population itself. Fifty-eight robins were released on Tiritiri Matangi in 1992 and 1993, and 36 of these founders (22 male, 14 female) survived to the 1994-1995 breeding season.

Demographic data have been collected on the Tawharanui NI robin population since its release. Annual survival surveys were performed from 2007 to 2016 by Auckland Council staff during September at the start of each breeding season. Data on fecundity (number of fledglings per female) were obtained through weekly checks of known robin pairs. The population has increased over time from 22 birds in September 2007 to approximately 80 birds in September 2016 (Chapter 2). Because Tawharanui would be the most convenient source population for further robin reintroductions in the Auckland Region, I was asked to assess whether it would be sensible to harvest this population.

Modelling

Modelling was conducted in OpenBUGs in an integrated framework where the population model (Chapter 2) was expanded to include a harvesting component. The population model included demographic stochasticity in all vital rates and environmental stochasticity in apparent juvenile survival. Expansion of that model enabled uncertainty in parameter estimation to be propagated into population projections. My initial model (Chapter 2) combined survival and reproduction data from nine years of monitoring (2007 to 2016). Modelling of these vital rate data indicated that fecundity and adult survival were relatively constant between years, whereas apparent juvenile survival (probability of a fledgling surviving to the next breeding season and remaining at Tawharanui) varied between years. However, this variation in juvenile survival was unrelated to population density. In contrast, there was tentative evidence that fecundity declined slightly as density increased. Consequently, when predicting effects of harvesting I used two alternative population models, one with and one without the density effect on fecundity included.

I used a female-only population model to generate projections 10 years into the future with no harvest and for each of the four harvesting scenarios (Figure 4.1). The model accounts for detection probability (Chapter 2) when estimating the initial number of females in September 2016, when 30 females were found in the survey. The total number of female fledglings each year was estimated by sampling from a Poisson distribution based on the expected number of fledglings. This expected number was obtained by multiplying the number of females in September by the expected number of fledglings per female estimated in the model, and multiplying by 0.5 to get the number of female fledglings. All harvesting scenarios specify a one-off harvest during the first year of projections in March 2017. I modelled adult and juvenile survival to March 2017, then removed the number harvested and modelled survival for a further 6 months to September 2017 (Figure 4.1). Adult survival probability was calculated annually and the 6 month difference in time interval corrected for, to get the probability of surviving until March 2017. Juvenile survival probability is calculated over 6 months and is assumed to be equal to adult survival after the harvest, as after four months juvenile survival is consistent with adult survival (Chapter 3). For the following 9 years, I modelled adult and juvenile survival to September (Figure 4.1).

I also included a population ceiling to avoid unrealistic growth. Robin density has been estimated as high as 5 birds/ha (Dimond & Armstrong, 2007). Based on the areas of forest that contain established territories, I calculated that Tawharanui currently has 110 ha of robin habitat. This gives a maximum of 550 robins, which I divided by half (assuming a 1:1 sex ratio) to get an approximate population limit of 275 females. The model truncated the number of females at the start of each breeding season so it would not exceed 275.

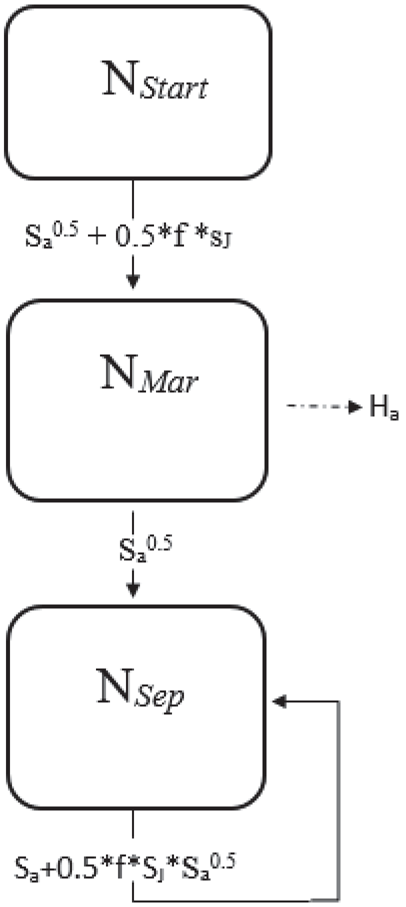

Figure 4.1. Flow of female-only stochastic model used to project population dynamics 10 years into the future, with a one-off harvest in March 2017. N_{Start} is the number of females in September 2016, N_{Mar} is the number of females in March 2017, N_{Sep} is the number of females in September for the remaining 9 years projected. H_a is the number harvested. The solid arrows represent the expected proportional increases or decreases based on the vital rates (S_J, juvenile survival to March, after which juveniles are considered adults; S_a annual adult survival; f, mean female fecundity which was estimated with and without density dependence.

Results

Population Projections without Harvesting

With no harvest, population dynamics projected 10 years into the future indicated that the population would continue to persist with negligible chance of extinction, although the prediction intervals around population size are quite large (Figure 4.2). With detection accounted for, the median number of females was 33±2 in September 2016. This increased to 68±39 over 10 years for the model with density dependence in fecundity, and to 124±84 for the model without density dependence (Figure 4.2, Table 4.1). The inclusion of density dependence reduced uncertainty in the upper prediction limits, but the lower prediction limit was between 23 and 25 females for all years, irrespective of whether density dependence was included (Figure 4.2, Table 4.1).

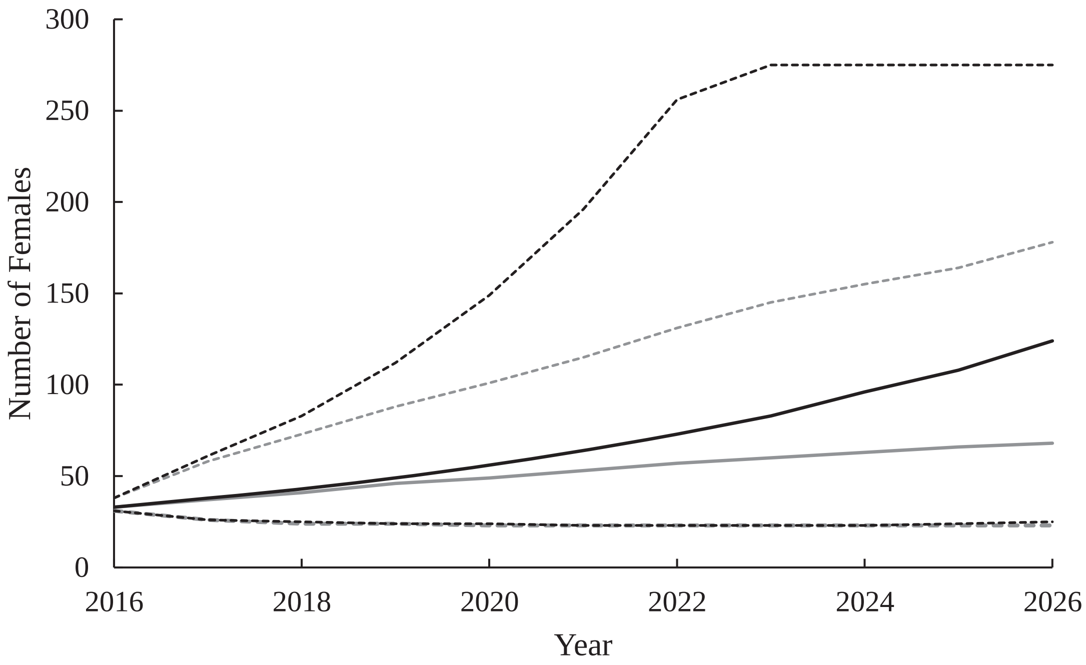

Figure 4.2. Projected dynamics of the Tawharanui robin population over the next 10 years if no harvest is conducted. Grey lines show projections based on a model with density dependence in fecundity, and black lines show projections from a model with no density dependence. Solid lines show medians and dotted lines show 95% prediction intervals.

Population Projections with Harvesting

Harvesting at any level reduced the number of females in the population throughout the 10 years, with larger harvests causing a greater reduction (Figure 4.3, Table 4.1). When density dependence was excluded a higher number of females were predicted under all harvest levels, but the prediction intervals were very wide (Table 4.1). The lower prediction limits for the numbers of females were similar for models with and without density dependence. The probability of extinction was low (< 0.01) under all harvesting scenarios, but the lower prediction limits were ≤ 15 for the higher harvest levels (Table 4.1).

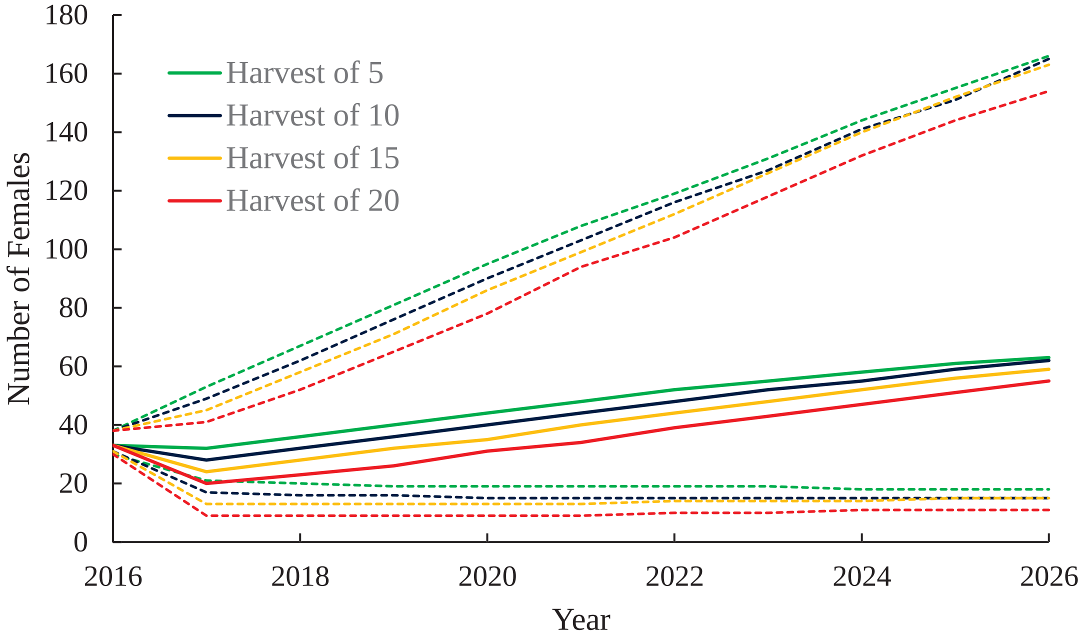

Figure 4.3. Projected dynamics of the Tawharanui robin population over 10 years under four possible harvests in March 2017: harvest of 5 females, harvest of 10 females, harvest of 15 females, harvest of 20 females. Solid lines show median numbers of females and dotted lines show 95% prediction intervals. These projections are based on the model with density dependence in fecundity. Projections for the model with no density dependence are similar but have higher upper prediction limits (Table 4.1).

Table 4.1. Comparison of medians and 95% prediction limits (LPL, UPL) for the number of females in the Tawharanui robin population in 2026 under four different levels of harvest, with and without density dependence in fecundity.

No. females harvested	**No Density dependence**			**Density dependence**		
	Median	**LPL**	**UPL**	**Median**	**LPL**	**UPL**
0	124	25	275	68	23	178
5	101	18	275	63	18	166
10	96	15	275	62	15	165
15	79	12	275	59	15	163
20	65	8	275	55	11	154

Discussion

Simulation of different harvest levels enabled me to make predictions that can be used to assess whether it is sensible to harvest the Tawharanui NI robin population. A one-off harvest at any level was predicted to cause a reduction in population over the next 10 years, with larger harvests causing a greater reduction. While the probability of extinction within 10 years was close to 0 for all harvest levels, the lower prediction limits for the number of females in the population were also very low for the higher harvest levels.

An integrated framework was used in the modelling, enabling uncertainty in estimates to be fully accounted for (Schaub & Abadi, 2011). Inclusion of parameter uncertainty is important for population projections as it will increase the further estimates are projected into the future. It may also show that there is considerable risk that the population will decline. Population projections at Tawharanui showed that in the absence of a harvest the median number of females was predicted to double in size over the next 10 years. However, the lower prediction limits were between 23 and 26 females for all projected years, which is lower than the current number of females in the population. While there appears to be no risk of extinction in the next 10 years, there is risk of the population declining, meaning that it may go extinct over a longer time frame.

Genetic variation in reintroduced populations can be important over long time frames. My population model does not incorporate genetic effects into its estimates, as any such effects would likely to be negligible in the time frame considered (Jamieson, 2011). However, an understanding of the population’s genetic history is essential when considering the potential long-term effects of harvesting. Using a reintroduced population as a source has the potential to cause future genetic issues. The Tawharanui NI robin population has undergone a “double-bottleneck” as it is derived from the Tiritiri Matangi population that also had a small number of founders. Populations that remain small are especially vulnerable to inbreeding depression. Inbreeding depression is expected to have minimal effect on populations that expand relatively quickly after establishment (Allendorf & Luikart, 2009), but the population growth at Tawharanui is gradual so this is an area where there is scope for more exploration and research.

The benefits of reintroduction will probably only outweigh the impacts to the source population if density dependence is regulating the source population. Density dependence is notoriously difficult to estimate (Newton, 1998; Knape & de Valpine, 2012; Lebreton &

Gimenez, 2013). This was demonstrated for the NI robin population on Tiritiri Matangi Island. Although density dependence was regulating the population via low juvenile survival 6 years after reintroduction, this effect was ambiguous with random variation in juvenile survival (Armstrong & Ewen, 2002). A harvest was conducted and the model refined and adapted using post-harvest data, giving stronger evidence of density-dependent regulation (Dimond & Armstrong, 2007). At Tawharanui there is no indication that juvenile survival regulates the population, but there is tentative evidence for weak density-dependence in fecundity. Consequently, population dynamics at Tawharanui were projected under two models, due to an ambiguous density-dependence effect on fecundity (Chapter 2). Although the model with no density dependence predicted a much higher median number of females after 10 years, both models displayed similar lower prediction limits. After a one-off harvest at any level, the population did not increase to the size estimated without a harvest, reflecting the weak or absent density dependence in the models.

A decision analysis framework can be used for choosing optimal management actions for reintroduction projects (Converse & Armstrong, 2016). Such a framework is particularly important for controversial decisions, such as the removal of animals from a population that is not being regulated by density dependence. I predicted outcomes with respect to one likely objective in such a decision, namely the persistence of the Tawharanui population. There is scope for considering this issue further within a decision analysis framework. This would involve defining objectives (e.g. persistence of the new reintroduced population, save money), and alternative management actions (e.g. no reintroduction, reintroduction using Tawharanui as the source, reintroduction using alternative source), and then weighing the competing objectives. I was asked to assess whether a harvest of the Tawharanui NI robin population would be sensible. My results can be used to facilitate the decision of whether Tawharanui would be a suitable source population for future reintroductions. This versatile approach can be adapted to inform any decision about the harvesting of a well-studied source population

Chapter 5

General Discussion

Reintroduction is increasingly being used for species recovery and restoration (Seddon et al., 2014). It is widely recognized that the factors influencing reintroduction outcomes need to be understood and analysed to improve the success of existing and future reintroductions (Sarrazin & Barbault, 1996; Ewen & Armstrong, 2007; Sutherland et al., 2010). All factors affecting the success of reintroductions do so through survival, reproduction, or dispersal. Quantitative models are useful for helping to better understand these factors, and the impact they have on population persistence. Modelling generates vital information that can be used to evaluate species-specific project outcomes, whilst informing the wider discipline of reintroduction biology. For my study, all modelling was conducted in an integrated Bayesian framework. I provide a comprehensive account of the fate of a reintroduced NI robin population under current circumstances.

The conditions at the reintroduction site need to be sufficient to allow growth and long-term persistence. In Chapter 2 I estimated λ by combining survival and fecundity (fledglings per female) models using 9 years of post-release monitoring data. I also assessed how precision improved as years of data were added, and evaluated the usefulness of prior information by incorporating informative priors that accounted for random site-to-site variation. My model determined that despite low apparent juvenile survival, the population would persist under current circumstances. It took 7 years of data before λ and its associated uncertainty were > 1, and this requirement was not reduced when informative priors were used. The informative priors were data-derived, meaning they avoided many of the controversies surrounding the use of prior information for Bayesian Inference. However, they had to account for a large amount of unexplained variation between reintroduction sites, and this reduced the precision of their predictions. Thus, informative priors enabled λ to be estimated when no Tawharanui data were available, but had negligible effect once any Tawharanui data were available. My approach promotes the improvement of knowledge over time, by showing how the integration and manipulation of the amount of data, can provide useful guidance for managers. An obvious application of this approach, is to use the prior model to predict parameters for a proposed reintroduction, and then update these parameters as site-specific post-release monitoring data become available. Alternatively, it can also be applied to other populations where there are already monitoring data available. In either case, this approach provides predictions of the fate of the population, which enables management strategies to be refined and adjusted accordingly.

Focused monitoring that is linked to decision making is necessary to refine and adjust management strategies (Canessa et al., 2016). The Tawharanui NI robin population has low recruitment, and this caused its persistence to initially appear uncertain. Therefore, in Chapter 3 I focused on distinguishing juvenile survival from permanent natal dispersal. I combined different types of juvenile survival data (re-sighting, radio-telemetry, recruitment), and modelled juvenile survival at each life-stage from fledging to recruitment. I determined that it is low juvenile survival that is causing the low recruitment of the population. Low recruitment is characteristic of peninsular sites (Parlato & Armstrong, 2012), and I found that the factors driving low recruitment differ between peninsula sites. At Tawharanui, low juvenile survival was attributed to limited food and non-favourable environmental (weather) conditions, whereas at Wenderholm (another peninsular site) low juvenile survival was caused by dispersal out of the reintroduction site (Andrews, 2007). Identification of reintroduction sites where the surrounding landscape is more likely to inhibit dispersal out of the managed area is essential to avoid dispersal-related reintroduction failure (Le Gouar et al., 2012). Tawharanui fits this criterion, as habitat fragmentation prevented juvenile dispersal out of the park. Whilst current habitat quality and connectivity is sufficient to maintain a population at Tawharanui, if connectivity is increased in the future, there will be implications for the management of the park.

The frequency of reintroductions in New Zealand has increased in recent years, creating an increase in demand for animals for reintroduction (Saunders & Norton, 2001). In Chapter 4, I assessed whether it would be sensible to harvest the NI robin population at Tawharanui, as their location makes them a convenient source for future reintroductions. I projected population dynamics 10 years into the future and examined the implications of a one-off harvest on population persistence. Whilst there was negligible chance that the population would go extinct, a one-off harvest at any level reduced the number of females in the population throughout the 10 years, with larger harvests causing a greater reduction. Even under the smallest harvest level, the population did not increase to the size estimated if no harvest is performed. My results reflect the weak or absent density dependence in the population, as it is less likely that harvesting will be sustainable if density dependence is not regulating the source population. My results can be used within a decision analysis framework to facilitate the decision of whether Tawharanui would be a suitable source population for future reintroductions. The modelling approach used throughout each of my chapters can be easily replicated or adapted to inform a wide range of decisions about reintroduced populations.

My study has made the following contributions to the field of reintroduction biology:

- **Modelling within an integrated Bayesian framework enabled me to fully account for uncertainty in estimates.**
  This approach allows simultaneous modelling of diverse sources of data, and fully accounts for uncertainty, whilst enabling predictions to be more reflective of the information available. In Chapter 2, I integrated demographic data (survival and fecundity) into a single model with random effects, and uncertainty in estimates was propagated into population projection projections in Chapter 4. In Chapter 3, I integrated different types of survival data (re-sighting, radio-telemetry, recruitment), and could account for the differences in detection and monitoring intensity between these data. The integrated approach allows greater flexibility in the monitoring and data requirements for population inference.
- **Prior information that incorporated site-to-site variation was incorporated into the population model.**
  To my knowledge, this is the first time that informative priors that account for site-to-site variation have been used in Bayesian models for reintroductions. There was a high level of variation in population growth rates among the sites that were combined to generate the informative priors. Therefore, although informative priors did not reduce uncertainty in estimates for my study, they will continue to provide a logical basis in model predictions, as our knowledge of the factors affecting the fate of reintroductions continues to improve.
- **Improved information on juvenile survival and natal dispersal**
  Focused monitoring provides insight into where important uncertainties lie, and therefore guides where greater certainty can lead to better management. In Chapter 3 I focused my monitoring efforts on juvenile survival and natal dispersal. In doing so, I contributed to an area where a significant knowledge gap exists, both in terms of NI robin management at Tawharanui and the wider discipline of reintroduction biology. Distinguishing between natal dispersal and juvenile survival enabled me to evaluate their respective influences on predicting reintroduction outcomes. I improved juvenile survival estimates by estimating survival at each life-stage from

fledging to recruitment, and contributed to knowledge of how habitat quality and connectivity affect both juvenile survival and dispersal.

Finally, I would like to point out some issues that were raised and lead to recommendations for further research.

- Landscape connectivity is a useful predictor of survival and dispersal. Currently, only a combination of both the landscape structure and species-specific movement behaviour will yield a meaningful value of connectivity (Kindlmann & Burel, 2008). Such connectivity indices have been developed for NI robins (Richard & Armstrong, 2010; Parlato & Armstrong, 2012), but are not applicable to peninsulas. This means that my informative priors for survival parameters in Chapter 2 are specific to peninsula sites. General relationships between landscape connectivity and landscape structure are lacking (Kindlmann & Burel, 2008), and this is an area where further research and development could prove highly beneficial for the management of reintroduced populations.

- Parlato and Armstrong (2012) suggested that natal dispersal inland via vegetation along coastal boundaries, is what causes low juvenile survival of NI robins at peninsular reintroduction sites. I propose an alternative hypothesis, where the large amount of dry and exposed areas of coastal vegetation along peninsula edges are poor quality habitat for NI robins and contribute to low juvenile survival. This is an issue that should be considered when predicting the suitability of sites for future reintroductions. There is scope for future work that considers the differences in habitat quality between coastal/peninsula areas and areas inland. This can be expanded further to the more general issue of the need to identify and accurately model the key habitat factors affecting site suitability (Osborne & Seddon, 2012).

- My models do not incorporate any genetic effects into estimates. Genetic variation in reintroduced populations can be important over long time frames. Research is needed to predict how the genetic make-up of reintroduced populations affects their growth and persistence over the longer term. Such predictions would require estimating the effects of genetic diversity on survival and reproduction and then projecting the impacts using population modelling (Armstrong & Seddon, 2008).

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