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Predicting reintroduction outcomes using data from multiple populations

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Abstract

Predicting reintroduction outcomes before populations are released is inherently challenging. Reintroductions typically involve small data sets from specific locations, making it difficult to know whether results from individual case studies are more widely applicable. However, a number of species have now been reintroduced to multiple sites, providing an opportunity to move beyond the inferences possible from single-site studies. I present a novel approach where data from multiple reintroduced populations are modelled simultaneously, allowing *a priori* predictions that account for random variation among sites to be made before new reintroductions are attempted. I construct models using data from multiple reintroductions of the North Island robin (*Petroica longipes*) to identify important factors influencing population establishment, vital rates and growth across existing reintroduction sites, and use the best supported models to make predictions for a candidate reintroduction site under alternative management scenarios. My results indicate that rat tracking rate (an index of rat density) and the surrounding landscape at reintroduction sites are important for both establishment and growth of reintroduced robin populations, and that sourcing founders from habitat similar to that at the reintroduction site (forest type and predators present) is also important for post-release establishment. I then extend the multi-population approach to integrate data from multiple species, and use the resulting model to predict growth of a reintroduced population at a range of predator densities when the candidate species for reintroduction (the North Island saddleback, *Philesturnus rufusater*) has never been observed in the presence of those predators. I predict saddleback population growth at different rat tracking rates using the relationship modelled for North Island robins, with the strength of the relationship adjusted to account for the greater vulnerability of saddlebacks to predation. The relative vulnerability to predation of saddlebacks (and 24 other New Zealand forest bird species) is estimated by measuring range contraction following the arrival of introduced mammalian predators on New Zealand's mainland. My results suggest that saddlebacks could be successfully reintroduced to sites with very low rat densities. This study illustrates how an integrated approach to modelling reintroductions improves the information available to managers, providing guidance about site suitability and appropriate management measures. For species reintroduced to multiple sites, integrated models provide an ideal opportunity to develop understanding over time of the key drivers of reintroduction success.

I dedicate this thesis to

my Mum, who never ceases to inspire

and

my Dad, whose love and support know no limits

Preface

I have had a love of nature for as long as I can remember. I think, perhaps, it stemmed from the time I spent as a child on our family's beautiful bush-clad property on Great Barrier Island. To this day, I am filled with a sense of peace and awe whenever I am in native forest, along with a deep knowledge that this is my happy place. It was this love of the natural world that led me to do a Bachelor of Science majoring in Zoology. I still remember the day I was sitting in a lecture, listening to someone called Doug Armstrong talk about something called "reintroduction". That hour changed my life. I knew instantly that I wanted to be involved with reintroductions – they fulfilled all of my idealistic dreams of conserving native species and helping to redress the effects of humans on the world. I was sold. And so I embarked on a Masters project to study one of the first North Island robin reintroductions to a New Zealand mainland site. After completion of my Masters, I worked in conservation jobs in New Zealand and overseas; but always dreamt of doing a reintroduction-related PhD. Dream became reality when I was awarded a Doctoral scholarship from Massey University, meaning I was lucky enough to have the autonomy to develop my own research topic. I knew I wanted to contribute towards increasing reintroduction success, so I set out to develop an approach that could help us learn from past reintroductions to improve the outcomes of those carried out in the future. This was a somewhat ambitious undertaking, as I had little quantitative modelling experience; but I figured PhDs are all about learning, and modelling was the means to the end I was after. I have since come to greatly enjoy the challenge of writing code although, I must confess, not quite as much as I enjoy the challenge of finding a well hidden nest.

So here it is, after all these years, my attempt at contributing to the field of reintroduction biology. I hope that in some way, the work in this thesis will benefit reintroduced individuals and populations, and will make the hard decisions faced by the dedicated people who manage them a bit easier.

Table of Contents

Abstract i

Preface v

Acknowledgements ix

Co-authors xi

Chapter 1 1

Research aim – a multi-population approach 4

New Zealand context 5

North Island robins – a model species 7

A multi-species approach 7

Summary 9

Chapter 2 11

Abstract 12

Introduction 12

Methods 15

Results 20

Discussion 25

Chapter 3 29

Abstract 30

Introduction 30

Methods 32

Results 38

Discussion 43

Chapter 4 47

Abstract 48

Introduction 48

Methods 50

Results 55

Discussion 58

Chapter 5 63
Abstract 64
Introduction 64
Methods 66
Results 73
Discussion 77
Chapter 6 83
Next steps 92
References 96
Appendix 112

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I am very grateful to the team at Landcare Research who gave me access to a workstation for my GIS work. Mapping every piece of woody vegetation (including individual trees) within 2 kilometres of reintroduction site boundaries took a decidedly long time (months and months…), and their friendliness and banter helped keep me sane. I am especially grateful to Peter Newsome who taught me the art of landcover mapping and who has shown me nothing but kindness. I would also like to thank Mike Tuohy for helping me start in the world of ArcGIS, as well as the organisations that gave me access to aerial imagery: Landcare Research, Terralink International Limited, Department of Conservation, Auckland Regional Council and Hawkes Bay Regional Council; and the Ornithological Society of New Zealand for providing distributional data.

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And my parents. I owe so much to my Mum, who encouraged me to pursue my dreams. Her love and belief in me has helped get me through. She, who was unable to see me get to this point, but who knew I could do it. I love you forever Mum. This is for you. Huge thanks to my Dad, who has given me sage advice throughout my PhD and has dedicated so much time to helping me finish this thesis – he has enriched my children’s life with the time he’s given them. For that I am eternally grateful.

And finally, to my husband Craig, whose support has been unwavering throughout. Every day I appreciate his kindness, generosity, insightfulness, and integrity, and I feel so fortunate to have him as my partner in life. His love enabled me to make this journey. Since the start of this PhD we have been joined by Cohen and Grayson, our two beautiful children, who are the light and joy of my life. They make me soar.

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Co-authors

While this thesis is my own original work, all four research chapters include input from one or both of my supervisors that warrants co-authorship.

Doug Armstrong (Ecology Group, Massey University)

As my primary supervisor, Doug has worked extensively with me to develop my research ideas and provide guidance on data analysis and interpretation. He reviewed all chapters (including manuscripts for publication), and has collaborated with me on every part of this research. He is consequently co-author on Chapters 2-5.

John Innes (Landcare Research)

As my secondary supervisor, John provided advice on my research concepts and his suggestions for Chapter 4, in particular, were invaluable. John reviewed Chapters 1, 4 and 6, and is a co-author on Chapter 4.

Chapter 1

General Introduction

In the face of the current biodiversity crisis (Blaustein and Kiesecker 2002, Turner et al. 2007) there has been a growing global awareness of the need to conserve threatened species (Butchart et al. 2004) and restore damaged ecosystems (Aronson and van Andel 2006). Reintroductions of species into habitat from which they were extirpated are increasingly being used for species recovery and to fulfil biodiversity or restoration objectives (Sarrazin and Barbault 1996, Seddon et al. 2007). Reintroduction has become a popular and widely applied conservation tool (Armstrong and Seddon 2008, Seddon et al. 2012), often providing the last chance to restore locally extinct populations within management timeframes (Sarrazin 2007).

Awareness of reintroduction as an effective conservation option grew as a result of some high profile reintroduction successes in the 1970s and 1980s (Seddon et al. 2007). However, reintroduction success has historically been poor (e.g. Griffith et al. 1989, Wolf et al. 1996) and this situation was exacerbated by the fact that there was little or no monitoring of early reintroductions so the causes of failure remained unknown (Seddon et al. 2007). These issues led to numerous calls in the literature for greater monitoring of reintroductions (Kleiman 1989, Armstrong and McLean 1995, Sarrazin and Barbault 1996, Hein 1997) and prompted formation of the World Conservation Union (IUCN) Reintroduction Specialist Group (RSG) in 1988 to provide guidance for reintroduction programmes and improve success rates (IUCN 1987, IUCN/SSC 1998, 2013). Since this time there has been a substantial increase in monitoring and in the number of peer-reviewed publications in the reintroduction literature, and there is now a recognised field of reintroduction biology (Seddon et al. 2007). This growing body of knowledge has allowed progressively more challenging reintroductions to be attempted (e.g. Armstrong and Davidson 2006); but despite how far reintroductions and their underlying science have come in the last 30 years (Moehrenschlager et al. 2013), failures remain common and probably less than half of reintroduction programmes can be considered successful (Sarrazin 2007).

Given the limited success of reintroductions, analysis of factors influencing reintroduction outcomes is crucial to improve the success of future programmes (Ewen and Armstrong 2007, Sutherland et al. 2010, Le Gouar et al. 2012, IUCN/SSC 2013). Although there has been a huge increase in both the number of reintroductions and their related publications, reintroduction research so far has largely been retrospective evaluations of techniques or specific parameters that are easily measured, rather than focusing on factors that may be more important to the successful establishment and long-term persistence of a reintroduced population (Seddon et al. 2007). This has limited our ability to learn from past mistakes and gain reliable knowledge to improve reintroduction success (Seddon et al. 2007). It is increasingly recognised that research and monitoring should focus on acquiring a better understanding of the habitat conditions

needed for populations to grow (Armstrong and Seddon 2008) and how management can improve the likelihood of reintroduction success throughout the phases of the reintroduction process (McCarthy et al. 2012, Converse et al. 2013).

The key phases affecting the dynamics of reintroduced populations are release, growth and regulation (Sarrazin 2007) or, more generally, establishment and persistence (Armstrong and Seddon 2008), and it is important to distinguish factors that might influence each of these phases (Armstrong and Seddon 2008). While the ultimate goal of any reintroduction is population persistence (Seddon 1999), this is only achievable if the population survives the establishment phase. There is often elevated mortality and dispersal immediately after release, meaning that populations can fail to establish even if conditions at the new site would enable persistence once established (Armstrong and Seddon 2008). Nevertheless, establishment of reintroduced individuals can be facilitated at various levels; for example, in the choice of which individuals to release (e.g. Masuda and Jamieson 2012), the release techniques used (e.g. Devineau et al. 2011) or through habitat management in the reintroduction area (e.g. Moorhouse et al. 2009). However, if habitat at the release site is unsuitable for population persistence, then efforts to maximise establishment success will be misplaced and will waste the lives of reintroduced individuals as well as precious conservation resources (Armstrong and Wittmer 2011). Understanding the conditions necessary to enable persistence at the new site is therefore fundamental to any responsible reintroduction attempt.

Population persistence requires positive growth after release, and this should be the main target for reintroduction programmes (Armstrong and Seddon 2008). Habitat quality (including food supply, predators, competitors and parasites) is the primary determinant of long-term persistence of populations, so the effectiveness of reintroduction programmes will depend on how well we understand the ecological requirements of species (Hirzel et al. 2004). The importance of habitat quality for reintroduction success has been highlighted throughout the literature (e.g. Macdonald et al. 2000, Armstrong and Seddon 2008, Osborne and Seddon 2012, IUCN/SSC 2013), and reintroduction failures are commonly attributed to insufficient knowledge of species' habitat requirements (Cook et al. 2010). Gaining a better understanding of what constitutes suitable habitat for a species is therefore essential for improving reintroduction success. Vital rates (survival and reproduction) are the only direct measure of habitat quality (Armstrong 2005) so assessments of habitat quality should be explicitly linked to demography for the species in question (Hall et al. 1997). In fact, all biological factors (whether genetic, environmental or behavioural in origin) affect population viability by acting on survival and reproductive rates so a good knowledge of a species' demography is essential for evaluating their potential effects on reintroduction success (Sarrazin and Barbault 1996). Demographic

analyses can therefore make a valuable contribution to effective management of reintroduction efforts (Converse et al. 2013).

Although decisions about reintroductions have remained largely intuitive to date, there has been increasing use of population modelling to analyse demographic data collected after reintroductions (Armstrong and Reynolds 2012, Converse et al. 2013). Population models can be used to predict population growth rates, project future trends, estimate probabilities of establishment or persistence, and provide a quantitative basis for comparing alternative management strategies (Beissinger and Westphal 1998, Armstrong and Reynolds 2012). Importantly, modelled relationships can then be used to make predictions before new reintroductions take place, providing guidance to managers about site suitability and appropriate measures to improve reintroduction success. The challenge is that reintroductions, by their very nature, often involve small data sets from distinct locations, so data from individual reintroduction attempts may be inadequate for thorough evaluation of factors affecting reintroduction success across a species' range (Jachowski et al. 2011). Analyses of data from single sites are also limited to factors that can be manipulated within that site (for example, release techniques). Potentially more important factors, such as habitat quality or connectivity, only vary among sites so analysing data from multiple sites is necessary to evaluate their influence on reintroduction outcomes.

Research aim – a multi-population approach

Using data from multiple sites provides more certainty that identified relationships are general (Johnson 2002) and therefore applicable to other sites, and also makes it possible to use small data sets that would otherwise have little predictive power. There are now numerous examples where single species have been released into multiple sites for conservation purposes (e.g. Le Gouar et al. 2008, Linklater et al. 2011) and these multiple releases provide a valuable opportunity to move beyond the inferences that can be derived from single-site studies. However, a framework for integrating demographic data from multiple reintroduced populations has been lacking from the reintroduction literature.

The aim of this thesis is to develop an integrated approach for multi-population inference that builds on results from other reintroduction programmes to better understand the key influences on reintroduction outcomes across sites, thereby improving predictions and enabling effective management to improve reintroduction success. Integrating data from multiple reintroductions allows more precise predictions to be made, especially for populations for which data are sparse,

and allows projections that account for random site-to-site variation to be made before new reintroductions are attempted. The importance of random variation (e.g. unexplained variation among sites, females or years) is being increasingly recognised by ecologists, and its estimation enables results to be extrapolated to populations beyond the study sample (Bolker et al. 2009). Recent advances in population modelling through the use of Bayesian hierarchical models (King et al. 2010) have made it possible to integrate data from multiple reintroduced populations into a single model with random effects, allowing random case-by-case variation to be accounted for. Bayesian methods therefore provide an ideal framework for developing my multi-population approach, and I have used Bayesian modelling throughout this thesis to analyse data on New Zealand bird populations. Moreover, Bayesian inference is ideal for modelling reintroductions because data from existing reintroduced populations can be used to make predictions for proposed reintroductions, and these prior distributions can then be updated when post-release monitoring data become available (McCarthy et al. 2012).

New Zealand context

New Zealand has a long history of reintroductions (Craig et al. 2000), and these have played a crucial role in the recovery of threatened bird species and the restoration of damaged ecosystems (Miskelly and Powlesland 2013). Since 1895, there have been over 1100 translocations (mostly reintroductions) of 55 different species, with at least 148 releases since 2000 alone (Miskelly and Powlesland 2013). Reintroductions have formed an integral part of New Zealand conservation because, for many species, the cause(s) of original extirpation are now generally well understood, resulting in extensive efforts to address those factors in order to reverse declines of extant populations and allow re-establishment of locally extinct species.

Like many oceanic islands, New Zealand's lengthy geographic isolation has resulted in a unique biota that evolved in the absence of mammalian predators. Since human arrival approximately 1000 years ago (Wilmshurst and Higham 2004), there have been numerous declines and extinctions of native species (Holdaway 1989, 1999). These losses have been largely attributable to habitat loss and impacts of introduced pests (Saunders and Norton 2001), with predation by introduced mammals such as rats (*Rattus* spp.) and mustelids (*Mustela* spp.) widely recognised as the primary factor responsible for historic and current declines of New Zealand fauna (King 1984, Holdaway 1989, Clout 2001, Innes et al. 2010). Consequently, effective ecological restoration in New Zealand is not possible without control or eradication of introduced mammals (Atkinson 2001).

Until the late 1900s, most species recovery and restoration programmes were focused on offshore islands where mammalian predators could be eradicated (Towns et al. 1997), and reintroductions to these locations were notable for their high rates of success (Armstrong and McLean 1995). Inspired in part by the success of these offshore island initiatives, substantial conservation resources are now being channelled into restoration projects on New Zealand's mainland (North and South Islands). The greater accessibility of mainland sites, combined with a strong public conservation ethic (Smuts-Kennedy and Parker 2013), has simultaneously brought about a shift from primarily government-led projects to community-based conservation groups increasingly playing a key role in restoring mainland ecosystems (Parker 2013). Predator control programmes have now been implemented in many mainland reserves, and this in turn has created opportunities to reintroduce locally extirpated species (Saunders and Norton 2001). However, in contrast to the high success rates of island reintroductions, reintroductions to mainland sites have had lower success. Reintroducing species to mainland sites presents a new set of challenges to those faced on offshore islands. For example, there may be increased capacity for dispersal out of managed mainland areas into unsuitable surrounding habitat. The problem of ongoing dispersal out of target areas is becoming increasingly recognised as an important consideration for reintroduction programmes (e.g. Tweed et al. 2003, Stamps and Swaisgood 2007, Le Gouar et al. 2012). Dispersal and mortality can have similar costs because individuals who disperse and settle away from the reintroduction area will not contribute demographically or genetically to the population (Le Gouar et al. 2012). Probably the major challenge, however, is that mainland reserves are subject to ongoing mammalian repopulation, either by reinvasion (unless predator-proof fences are erected and even these remain subject to incursions) or by *in situ* breeding. Nevertheless, intensive predator control can reduce predators to low levels (Saunders and Norton 2001) and many studies have shown the effectiveness of control programmes for improving survival and reproduction of native bird species in mainland reserves (e.g. Powlesland et al. 1999, Moorhouse et al. 2003, Innes et al. 2004, Armstrong et al. 2006a, Armstrong et al. 2006b). Therefore, the important question facing managers is not whether predator control is an appropriate strategy, but what level of control is necessary for reintroduced populations to grow (Armstrong et al. 2006a).

Although ongoing control programmes can potentially reduce introduced predators to levels where many native species can be successfully re-established (Sinclair et al. 1998), it is often unclear *a priori* what those levels will be and whether habitat has been adequately restored for the species to survive (Ewen and Armstrong 2007). As such, many of the mainland reintroductions to date have relied on intuitive decisions and have been carried out with a "release and see" approach, which stems from the limited information available to guide decisions about release site suitability. Nevertheless, data collected from these past

reintroductions provides a valuable opportunity to develop population models to identify the key factors influencing establishment and persistence at mainland sites, and predict how reintroduced populations will respond to alternative management regimes (Armstrong and Reynolds 2012, Converse et al. 2013).

North Island robins – a model species

In this thesis I use data from multiple reintroductions of North Island robins (*Petroica longipes*) to develop an integrated modelling approach that allows the general drivers of population establishment and growth to be identified, and allows *a priori* predictions that account for random variation among sites to be made before reintroductions are attempted. North Island robins are a small insectivorous forest-dwelling passerine endemic to New Zealand, and are usually the first species reintroduced into unfenced mainland areas with predator control (Ewen and Armstrong 2007). The species was historically found over the entire North Island, but is now restricted to the central North Island and some offshore islands (Higgins and Peter 2002). Robins are susceptible to predation, primarily by exotic ship rats (*Rattus rattus*) (Brown 1997, Powlesland et al. 1999), but also other exotic mammals such as stoats (*Mustela erminea*) and native avian predators such as morepork owls (*Ninox novaeseelandiae*). Robins are often the initial species selected for reintroduction, mainly because they are easy to work with (i.e. capture and monitor) and because they are less threatened than other species (Armstrong 2000). Consequently, robins are one of the most commonly reintroduced species in New Zealand (Miskelly and Powlesland 2013, http://rsg-oceania.squarespace.com/nz/) and most populations have been monitored post-release. North Island robin reintroductions therefore present an ideal scenario for developing an integrated modelling approach because multiple reintroductions of one species have taken place, the biology of the species and its threats are well understood, and data on demographic rates have been collected using consistent methodology.

A multi-species approach

The successful establishment of reintroduced species signifies clear progress towards ecosystem restoration, and can lead to consideration of reintroductions of more threatened species. This has been seen in New Zealand where reintroductions of endangered species have been attempted following the establishment of North Island robins (e.g. Sullivan 2006). Although robins have been identified as a useful species for assessing habitat suitability (including risk from introduced predators) before reintroductions of more threatened species are contemplated (Armstrong 2000), species clearly differ in their vulnerability to predation and this needs to be taken into account when evaluating site suitability. Some species (e.g. hihi, *Notiomystis cincta*) rapidly disappeared from the mainland following the arrival of mammalian predators and only

avoided extinction by surviving on offshore island refuges free of mammalian predators, whereas other species (e.g. grey warbler, *Gerygone igata*) have remained relatively widespread and common on the mainland to the present day. Understanding how vulnerable endemic taxa are to predation is clearly important for conservation management, and is becoming increasingly pertinent with species previously extinct on the mainland now being considered for reintroduction to mainland sites with mammalian predators present at a range of densities (e.g. Armstrong and Davidson 2006, Richardson 2009).

Reintroductions of extirpated species back to unfenced areas on New Zealand's mainland are an exciting prospect for New Zealand conservation, but are inherently risky given ongoing reinvasion by predators (Armstrong and Davidson 2006) and the lack of available information about the amount of predation by exotic mammals that mainland populations can withstand. There have been two reintroductions of mainland extirpated species to unfenced sites on New Zealand's mainland to date, with North Island saddlebacks (*Philesturnus rufusater*) reintroduced to Boundary Stream Mainland Island in 2004 and hihi reintroduced to Ark in the Park in 2007. Both of these reintroduced populations are now extinct, indicating a need for reliable models to evaluate the level of management required for populations to grow in the presence of predators (Armstrong and Davidson 2006). However, predicting reintroduction outcomes is particularly difficult when the species being considered for reintroduction no longer co-exists with the identified threats in any location.

Making inferences about species when data are lacking is a well-recognised challenge in conservation biology, and has led to the development of surrogate-species concepts such as indicator species (Morrison 1986) where data from other species are used to make inferences about a species (or group of species) of interest. However, these approaches are limited by their assumption that the surrogate species will be a reliable indicator of population response in the target species, which may not be valid given that species often respond differently to threatening processes (Verner 1984, Landres et al. 1988, Lindenmayer et al. 2002). The relationship between species and their indicators is likely to depend on the extent to which shared ecological drivers impact on populations (Hoare et al. 2013) so extrapolating from one species to another is difficult unless the relative response of populations can be estimated. As part of my research, I have attempted to build on the idea of using data from other species to estimate population parameters for a species of interest (Landres et al. 1988) by developing a more sensitive framework that accounts for differential species responses to key ecological drivers when modelling population growth. I use this framework to predict population growth of a mainland-extirpated species reintroduced to a mainland site with mammalian predators present.

Summary

Given the limited success of many reintroduction attempts, it is crucial that reliable models are developed; both to understand important factors affecting reintroduction outcomes, and enable credible *a priori* predictions for new populations in new situations. However, assessing the conditions needed for population establishment and persistence at a new site before release is often challenging, particularly given there are usually no data available for the species at the site (Armstrong and Seddon 2008). With reintroductions of single species into multiple sites increasingly being undertaken, valuable opportunities to build on results from past programmes are arising. However, a framework for integrating demographic data from multiple populations has been lacking to date. Integrating data among multiple populations provides more certainty that identified relationships are general, enables consideration of factors that vary among sites, and allows predictions to be made for existing or proposed reintroductions when data are lacking. Importantly, this approach also enables unexplained site-to-site variation to be accounted for when evaluating what is required for a reintroduced population to establish and persist at a new site. An even greater challenge is presented, however, when the species being considered for reintroduction no longer coexists with the identified threats in any location, making it impossible to use data from other sites. Data from other species can potentially be used to make inferences about the species of interest, but it is then necessary to account for differential effects of key threats on each species' demographic rates. The goal of this thesis is to develop a modelling framework that allows integration of data from multiple populations and, ultimately, multiple species to enhance the predictive capability of models used to evaluate site suitability and enable targeted management to improve reintroduction success.

This thesis is centred around four research chapters, each written as stand-alone papers. While this format leads to some inevitable repetition, I have tried to minimise this where possible and have used a standardised format throughout to make the thesis more cohesive in its entirety.

In Chapter 2, I show how Bayesian modelling can be used to identify general drivers of establishment and to account for random site-to-site variation when making predictions for new sites. I model establishment data for North Island robins reintroduced to 14 sites where introduced mammals are controlled, and use the resulting model to predict individual establishment probability at a candidate reintroduction site under alternative management scenarios.

Chapter 3 describes how models were constructed using vital rate data available from robin populations reintroduced to 10 sites, and identifies important influences on survival and

fecundity (fledglings per female) across sites. Given the importance of population growth for persistence of reintroduced populations, I show how the resulting models can be used to project population growth at these sites and a proposed reintroduction site under different levels of predator control, while accounting for random variation in demographic rates among sites.

Understanding differential species responses to key ecological drivers is important for effective management of reintroductions, particularly if successful attempts lead to consideration of reintroductions of more threatened species. Because introduced mammalian predators are the main cause of New Zealand bird declines, in Chapter 4 I evaluate the vulnerability of New Zealand's surviving endemic forest bird species to impacts of introduced mammalian predators, and identify key life history attributes underlying this vulnerability.

Chapter 5 presents a modelling approach that integrates data from multiple species and sites to predict growth of a reintroduced population at a range of predator densities when the candidate species for reintroduction (the North Island saddleback in this case) has never been observed in the presence of those predators. I initially use demographic data from saddleback populations reintroduced to three predator-free sites to estimate growth at a new site in the absence of mammalian predators. Population growth at different predator densities is then predicted using a relationship modelled for reintroduced North Island robins (Chapter 3), with the strength of the relationship adjusted to account for the greater vulnerability of saddlebacks to predation (Chapter 4). The model is then extended to incorporate site-specific random effects on demographic rates, and the resulting model is used to predict growth of a saddleback population reintroduced to a mainland site with predator control where robins have previously been released.

In aggregate, this work will increase the number of successful reintroductions and the chances that reintroduced animals – many of which are threatened species – survive release and subsequently breed. Besides the intrinsic value and ethical rights of these individuals, it is expensive to catch animals for translocation and to maintain source populations that are healthy enough to sustain harvest. In New Zealand, most founders are sourced from offshore islands, many of which were made pest-free by eradication, or from mainland sanctuaries where pests are targeted by trapping and poisoning. Both are expensive, and using modelling to improve the effectiveness of releases will minimise the loss of intrinsically, financially and genetically valuable individuals in future reintroductions.

Chapter 2

Predicting post-release establishment using data from multiple reintroductions

Parlato, E. H. and D. P. Armstrong. 2013.

Biological Conservation 160:97-104.



Release of North Island robins (*Petroica longipes*) into Little Windy Hill Reserve. Photo: Graham Parker

Abstract

For any reintroduction it is important to maximise the probability of released individuals establishing in the target area (settling and surviving to breed). Factors influencing establishment have typically been studied at single sites, making it impossible to assess factors that vary at the site level (e.g. connectivity) or quantify unpredictable variation among sites. Using data from 14 reintroductions of the North Island robin (*Petroica longipes*) to native forest reserves, we show how Bayesian modelling can be used to identify general drivers of establishment and to account for site-to-site variation when making predictions for new sites. High landscape connectivity and high rat tracking rates (a density index) at reintroduction sites were key factors associated with lower individual establishment probabilities. Habitat similarity between source and release sites was also important, as robins sourced from native forest had higher establishment than those from exotic pine forest. Previous predator experience appeared to affect establishment in sites with mammalian predators, as founders sourced from sites with these predators had higher establishment than those from other sites. Our approach can be applied to a wide range of species that are being reintroduced to multiple sites, providing guidance on source and release site selection, efficacy of management interventions, and the numbers of individuals to release to achieve desired initial population sizes. The results are not only applicable to these particular species, but can be used to predict site suitability for reintroductions of species with similar dispersal behaviour or other ecological characteristics.

Introduction

Reintroduction is increasingly used to re-establish populations of threatened species within their historical ranges (Sarrazin and Barbault 1996, Seddon et al. 2007). However, many reintroduction attempts are unsuccessful (Griffith et al. 1989, Wolf et al. 1996, Sarrazin 2007) and the underlying causes of failure are rarely well understood (Fischer and Lindenmayer 2000, Letty et al. 2007, Dickens et al. 2010). Analysis of factors influencing reintroduction outcomes is therefore important to improve the success of future reintroduction programmes (Sarrazin and Barbault 1996, Ewen and Armstrong 2007, Sutherland et al. 2010, Le Gouar et al. 2012).

The two key phases affecting the dynamics of reintroduced populations are establishment and persistence (Armstrong and Seddon 2008). While the ultimate goal of any reintroduction is population persistence (Seddon 1999), this is only achievable if the population survives the establishment phase. There is often elevated mortality (e.g. Calenge et al. 2005, Kreger et al. 2006) and dispersal (e.g. Moehrenschlager and Macdonald 2003, Tweed et al. 2003) immediately after release, meaning that reintroductions can fail during the establishment phase

even if conditions at the new site would enable persistence once established (Armstrong and Seddon 2008). Dispersal and mortality can have similar costs because individuals who disperse and settle away from the reintroduction area will not contribute demographically or genetically to the population (Le Gouar et al. 2012).

Because individuals are lost soon after release, the effective initial population size, commonly defined as the number of individuals that survive to the breeding season, is often much lower than the number of individuals released (Armstrong and Seddon 2008, Armstrong and Wittmer 2011). This in turn can exacerbate problems faced by small populations, including demographic stochasticity, environmental stochasticity, Allee effects and loss of heterozygosity. Maximising initial population size is therefore an important consideration for any reintroduction.

The most obvious approach to increase the initial population size is to release more individuals. The benefit of larger release groups is widely cited in the literature (e.g. Griffith et al. 1989, Wolf et al. 1998, Deredec and Courchamp 2007). However, releasing more individuals has a trade-off with impact on the source population (Armstrong and Wittmer 2011) and can also have financial and logistical repercussions. There may also be a trade-off at an individual and ethical level, as larger founder groups can result in more individuals being lost due to post-release dispersal or mortality.

An alternative to releasing more individuals is taking measures to reduce post-release mortality or dispersal, thereby increasing the probability of founders settling in the reintroduction area. Population establishment is dependent on the probability of reintroduced individuals establishing at the new site, so understanding the key determinants of individual establishment is important for reintroduction success. Post-release survival and dispersal can be affected by various aspects of a reintroduction; including the translocation process (e.g. release strategy, Devineau et al. 2011), characteristics of the individuals involved (e.g. age or sex, Moehrenschlager and Macdonald 2003, Masuda and Jamieson 2012), conditions at the reintroduction site (e.g. predator levels, Moorhouse et al. 2009), similarity between release and source sites (Stamps and Swaisgood 2007, Roe et al. 2010, Lawrence and Kaye 2011), and the habitat matrix surrounding the reintroduction site (La Morgia et al. 2011). Establishment of reintroduced individuals can therefore be facilitated at various levels; although the most appropriate and effective measures will depend on the species in question. For example, riparian brush rabbits (*Sylvilagus bachmani riparius*) held longer in enclosures before release had higher post-release survival (Hamilton et al. 2010), whereas delayed release of stitchbirds (*Notiomystis cincta*) lowered survival compared to birds released immediately (Castro et al. 1995).

Analysis of data collected after reintroduction can provide crucial information about factors affecting establishment of individuals post-release. Importantly, modelled relationships can then

be used to make predictions before new reintroductions take place, providing guidance to managers about site suitability and appropriate measures to improve reintroduction success. However, identification of factors influencing post-release establishment is often based on data from single sites (e.g. Tweed et al. 2003, Jõgar and Moora 2008, Roe et al. 2010, Bernardo et al. 2011). While these studies can provide valuable insights for the site in question, factors influencing success throughout a species' range may not be apparent in results from a single site (Jachowski et al. 2011). Using data from reintroduction attempts at multiple sites provides more certainty that identified relationships are general (Johnson 2002) and therefore applicable to other sites. Analyses of data from single sites are also limited to factors that can be manipulated within that site (for example, release techniques or supplementary feeding). Potentially more important factors, such as habitat quality or connectivity, only vary among sites so analysing data from multiple sites is necessary to evaluate their influence on reintroduction outcomes.

There are numerous examples where single species have been released into multiple sites for conservation purposes. In New Zealand and Australia, more than 40 vertebrate species have each been translocated to at least 5 different sites (e.g. http://rsg-oceania.squarespace.com/nz/ , Short 2009). In southern Africa, most large herbivores (e.g. Van Houtan et al. 2009, Linklater et al. 2011) and carnivores (e.g. Hayward et al. 2007) have been reintroduced to multiple sites. There are also examples from other parts of the world, including Griffon vultures (*Gyps fulvus*) in France (Le Gouar et al. 2008) and black-footed ferrets (*Mustela nigripes*) in North America (Jachowski et al. 2011). These multiple releases create a unique opportunity to integrate data among sites to identify the key influences on reintroduction outcomes, while also accounting for any unexplained site-to-site variation in population parameters. The results obtained would not only be applicable to the species that have already been reintroduced to multiple sites, but could be used to predict site suitability for reintroductions of species with similar dispersal behaviour or other ecological characteristics.

We present an approach whereby data from multiple reintroduced populations are integrated into a Bayesian hierarchical model to identify important factors influencing post-release establishment. We model establishment data for North Island robins (*Petroica longipes*) reintroduced to 14 sites, and show how the resulting model can be used to make predictions for a candidate reintroduction site under alternative management scenarios. The strength of our approach is the ability to model the general influences on establishment while accounting for site-to-site variation, thereby enhancing predictive capability and enabling targeted management to improve reintroduction success.

Methods

Species and reintroductions

The North Island robin is a small (26-32 g) insectivorous forest passerine endemic to New Zealand. The species was historically found over the entire North Island, but is now restricted to native forest remnants and exotic plantations in the central North Island, as well as some offshore islands (Higgins and Peter 2002). Robins are susceptible to predation, primarily by exotic ship rats (*Rattus rattus*) (Brown 1997, Powlesland et al. 1999), but also other exotic mammals such as stoats (*Mustela erminea*) and native avian predators such as morepork owls (*Ninox novaeseelandiae*). Their breeding season is generally from early September to February, and juveniles become sexually mature by the start of the breeding season after that in which they fledge.

North Island robins were reintroduced to 15 different sites (31 ha - 1100 ha forested area) between 1997 and 2007 and analysable data were available for 14 of these (Table 2.1). Thirteen of the sites were on the North Island and two (Glenfern, Windy Hill) were on Great Barrier Island, a ca. 28,500 ha island off the north-east of the North Island. Reintroductions always occurred between March and August. Pre-release monitoring was conducted at all sites prior to reintroduction and no robins were found. Birds were caught from the wild and were released immediately on arrival at the release site. Robins typically undergo a period of dispersal post-release, and become sedentary once pairs and territories are established in the breeding season. All sites, including the proposed site, were managed to control introduced mammalian predators. At the time of reintroduction, two sites were fenced to exclude mammalian predators, which were eradicated after fencing, hence those species were expected to be absent. Another site was fenced but had openings for vehicle access, so mammalian predators remained present. All reintroductions were to areas of native forest, and birds could potentially disperse into unmanaged forest in the surrounding landscape. One site also had an exotic pine forest plantation within its boundary.

Data collection

We compiled data to assess the probability of released individuals establishing at each reintroduction site, where "establishment" is defined as surviving and remaining at the site until the start of the breeding season (late August). We specifically modelled return rates, which are the proportions of released individuals that remain at the site and are detected (Martin et al. 1995, Cam et al. 2005), as it was impossible to separately estimate establishment and detection probabilities from the data available for some sites. We included data on return rates from initial reintroduction attempts only, so any supplementary translocations in subsequent years were

Table 2.1 Characteristics of 14 North Island robin reintroduction sites and one proposed reintroduction site.

Site	Month and year reintroduced	Number of robins released	Forested predator-control area (ha)[a]	Peninsula	Rat tracking rate (95% CI)[b]	Standardised habitat ratio[c]	Connectivity Index	Mammalian predators present
Ark in the Park	April 2005	53	1100	no	0.05 (0.02-0.11)	0.34	0.97	yes
Boundary Stream	April 1998	28	800	no	0.01 (0-0.04)	-0.48	0.68	yes
Bushy Park	August 2001	28	87	no	*0.13 (0.01-0.52)*	-1.08	0.15	yes
Cape Kidnappers	May 2007	35	280	yes	0.10 (0.07-0.15)	-0.98	0.10	yes
Glenfern	April 2005	27	230	yes	0.16 (0.10-0.23)	-0.51	0.54	yes
Hunua	May 2001	30	600	no	0.34 (0.23-0.48)	1.79	0.99	yes
Kakepuku	June 1999	30	198	no	*0.68 (0.18-0.98)*	-1.33	0.33	yes
Paengaroa	March 1999	40	101	no	0.27 (0.20-0.34)	-0.32	0.50	yes
Tawharanui	March 2007	25	240	yes	0 (0-0)	-0.60	0.17	no
Trounson	April 1997	21	445	no	0.01 (0-0.04)	0.15	0.71	yes
Waotu	May 2001	30	31	no	*0.54 (0.10-0.93)*	1.55	0.40	yes
Wenderholm	March 1999	21	60	yes	*0.37 (0.05-0.85)*	0.93	0.25	yes
Windy Hill	April 2004	30	267	no	0.27 (0.20-0.35)	1.68	0.64	yes
Zealandia	May 2001	40	225	no	0 (0-0)	0.08	0.91	no
Pukaha (proposed)	NA	NA	942	no	NA	NA	0.60	yes

[a] Area of forest managed to control introduced mammalian predators at time of reintroduction.

[b] Tracking tunnel rates estimated from observed data. Imputed values are shown in italics for sites where data were missing (estimated from the modelled relationship between return rates and tracking tunnel rates for the other sites).

[c] Standardised (mean 0, variance 1) area of accessible forest habitat within 2 km of perimeter of reintroduction site divided by the forested predator-control area.

excluded from our analysis. All birds were individually colour banded prior to release, and data on the number of birds released and post-release sightings of individuals were available from site managers, reports, field notebooks or theses (Pattemore 2003, Small 2004). Nine of the sites were systematically searched in the first September following release using robin lure tapes at regular distances to identify individuals present at the start of the breeding season. Less targeted monitoring was undertaken at five sites, where field staff recorded birds sighted as they carried out other work in the site. Intensity of post-release monitoring is likely to influence the probability of detecting individuals that establish, so we took this into account in our analysis. We expected detection probability to be close to 1 at intensively monitored sites, meaning return rates are equivalent to establishment probabilities, and test this by estimating detection probabilities at sites where this is possible.

We also compiled data on variables that were potentially useful predictors of return rates based on our knowledge of the species. These fell into three main categories: 1) Reintroduction site characteristics, which included the size of forested predator control area, presence/absence of mammalian predators (ship rats and stoats), rat tracking rate (an index of rat density), and three landscape variables potentially influencing robin emigration post-release; 2) Translocation process, which included monitoring intensity (moderate or high, as described above) and time (number of months) from release to the start of the first breeding season; and 3) Source site characteristics, including forest type (exotic or native) and presence/absence of mammalian predators.

Rat tracking rates are used throughout New Zealand to monitor effectiveness of rat control. Rat tracking data were collected at 10 of the reintroduction sites. Usually 10 to 25 tracking tunnels were placed at 50 m intervals along transects (1 - 14 transects per site for sites with rats present). Tunnels were set by baiting them with peanut butter, and ink pads and paper were placed inside to record the prints of a rat if it moved through a tunnel. The papers were usually collected the next day but at two sites the papers were left out for more than one night. We used data collected between the date of reintroduction and the start of the breeding season at each site to estimate the rat tracking rate, which is the nightly probability of a rat moving through a tunnel. Tunnels were set 1-3 times at each of the sites with rats present over this timeframe.

The first landscape variable was a binary measure of whether sites were on a peninsula. We considered that peninsularity could be important for establishment of reintroduced birds, as peninsular sites were found to adversely affect apparent survival of juvenile North Island robins at 10 reintroduction sites, probably due to higher dispersal rates (Parlato and Armstrong 2012 [Chapter 3]). The second landscape variable was a connectivity index based on maps of the land-cover within 2 km of site perimeters, which we manually digitised (5 m cell resolution)

from aerial photographs and satellite imagery using ArcGIS 9.3 (ESRI, Redlands, California) and Imagine 9.2 (ERDAS, Atlanta, Georgia). Vegetation was classified as mature native forest, mature exotic forest, native/exotic shrubland or pasture/bareland. We assigned permeability values to each cell, reflecting the extent to which the different vegetation types facilitated robin movements. Permeability values were based on an inverse scale of the resistance values estimated for dispersing juvenile robins by Richard and Armstrong (2010). They found that resistance increased progressively from mature native forest to pine plantations, shrubland and pasture, and inferred that robins did not cross pasture gaps > 110 m. Values of zero were therefore assigned to any woody vegetation that could only be reached by crossing > 110 m of pasture. The connectivity index (*C*) for each site was calculated as:

$$C = \frac{\sum_{c=1}^{N_c} P_c}{100(N_c)}$$

where P_c is the permeability value of each cell and N_c is the total number of cells within 2 km of the site perimeter. The third landscape variable was an alternative index of connectivity where we used the land-cover maps to calculate the area of mature forest within 2 km of site perimeters (again excluding areas only reachable by crossing >110 m of pasture). We then calculated the ratio of forest area outside the site to the site's forest area and standardised these ratios for the 14 sites. This standardised variable is hereafter termed "habitat ratio".

Modelling

Data were analysed using generalised linear models (logit link function, binomial error distribution) fitted in WinBUGS 1.4 (Spiegelhalter et al. 2003) using Markov Chain Monte Carlo (MCMC) methods. Alternative models were compared based on the Deviance Information Criterion (DIC). DIC is a Bayesian criterion for model comparison that can be interpreted similarly to AIC (Akaike's Information Criterion). DIC will be approximately equal to AIC in models with negligible prior information (Spiegelhalter et al. 2002). All models had uninformative priors and were run with two chains for 110,000 samples, with the first 10,000 samples discarded as burn-in. We visually checked for convergence using the Brooks-Gelman-Rubin and auto-correlation plots.

We initially created a full model that included an intercept and fixed effects of peninsula, site area (log transformed), mammalian predators at reintroduction site, time from release to breeding season, monitoring intensity, and source site effects of forest type and presence of mammalian predators (which we applied only to reintroduction sites with those predators present). We assessed whether DIC was reduced by sequentially substituting the peninsula

effect with connectivity (logit transformed), then substituting the connectivity and area effects with habitat ratio. After identifying the best landscape metric (that which provided the lowest DIC), we assessed whether DIC was further reduced by substituting rat tracking rate (logit transformed) for presence of mammalian predators at the reintroduction site. Effects identified as important from the best full model were then used to create a simplified model to estimate return rates at the 14 reintroduction sites and the proposed reintroduction site. We always included the effect of monitoring intensity to account for differential detection of established birds. We ran the simpler model with and without a random effect among sites to assess whether there were differences in return rates among sites caused by random variation or unknown factors. We assumed the random effect was normally distributed.

To estimate the rat tracking rate (*rat.nightly*) for each site, we first sampled the number of tunnels tracked from a binomial distribution where the sample size was the total number of tunnels set. Because tunnels were set for more than one night at two sites, we used the modelled probability of a rat passing through a tunnel over *t* nights (*rat.total*) to estimate the nightly rat tracking rate ($rat.nightly=1-(1-rat.total)^{1/t}$). For the four sites where tracking tunnel data were missing, we imputed rat tracking rates based on the relationship with return rate modelled from the other data.

Return rates of reintroduced robins are the product of both individual establishment probabilities and detection probabilities (sensu Cam et al. 2005). We expected detection probabilities of established birds would be close to 1 (return rate ≈ establishment probability) for sites with systematic searches post-release, as robins are relatively easy to find due to their inquisitive and friendly nature (Armstrong 2000). To check this assumption, we used the Cromack-Jolly-Seber model in MARK (White and Burnham 1999) to obtain monthly survival and re-sighting estimates using individual encounter histories (Lebreton et al. 1992) of birds released into intensively monitored sites. Zealandia was excluded from this analysis as we did not have individual sightings data. The encounter histories reflected four surveys, at the start (September) and toward the end (January) of the first two breeding seasons post-release. We used the survival and re-sighting estimates to calculate the probability of an individual being detected in at least one survey (p'), which is given by:

$$p' = 1 - ((1 - p_1)(1 - s_2p_2)(1 - s_2s_3p_3))$$

where s_2 and s_3 are survival probabilities for the second and third intervals (first breeding season and subsequent non-breeding season), and p_1, p_2, p_3 are re-sighting probabilities for the first three surveys, respectively.

Results

Comparison of landscape variables gave strong support for connectivity as the best predictor of return rate, lowering DIC by 12.9 and 10.2 relative to the peninsula and habitat ratio effects, respectively (Table 2.2). The DIC was further reduced when rat tracking rate was substituted for mammalian predator presence at the reintroduction site (ΔDIC = 9.8). Parameter estimates from the best full model (Table 2.3) suggest effects of connectivity and rat tracking rates at the reintroduction site, and forest type and mammalian predator presence at the source site, were all useful predictors of return rate (95% credible intervals did not incorporate zero). Including these four effects with monitoring intensity in a simpler model resulted in better predictive capability than the full model (DIC lowered by 1.6) (Table 2.2). Adding a random effect among sites did not further improve the model, and instead reduced model performance (DIC increased by 1.3).

Robin return rates were higher at sites with lower connectivity and rat tracking rates (Figure 2.1, Table 2.3). Sourcing founders from native forest with mammalian predators also resulted in higher return rates than sourcing birds from a predator-free site (Figure 2.1) or pine forest (Table 2.3). The effect of monitoring intensity was more ambiguous although, as expected, more intense monitoring was positively associated with return rate. Detection probabilities for established birds at intensively monitored sites were between 0.99 and 1 indicating that established robins had a high probability of being encountered. As such, we were able to estimate individual establishment probabilities from return rates modelled with high monitoring intensity. Including the effect of monitoring intensity also allowed us to account for lower detection of established individuals at the five sites that weren't intensively monitored, and directly compare modelled and observed return rates. In general, the model provided a very good fit to the data (Figure 2.2).

Sites varied greatly in their connectivity to the surrounding landscape (Table 2.1), and this had a strong influence on estimated establishment probabilities. The two most connected sites, Ark in the Park and Hunua, were estimated to have the lowest probabilities of establishment (0.32 (95% CI 0.21-0.45) and 0.35 (95% CI 0.21-0.50), respectively) whereas Tawharanui, a relatively isolated mammalian predator-free site, had the highest establishment probability (0.93, 95% CI 0.85-0.98). Nevertheless, the importance of rat tracking and source site characteristics was also apparent, with moderately connected Boundary Stream estimated to have similarly high establishment (0.90, 95% CI 0.80-0.97) to Tawharanui due to low rat tracking (1%, 95% CI 0-3%), and because birds were sourced from native forest with mammalian predators present.

Table 2.2 Comparison of establishment models fitted to data for North Island robins at 14 reintroduction sites.

Model[a]	pD[b]	DIC[c]	ΔDIC[d]
$\text{logit}(r) = \alpha + \beta_c \text{logit}(C) + \beta_{rt} \text{logit}(rat.nightly) + \beta_{ps} mps*mpr + \beta_{fs} pi + \beta_{mi} i$	7.23	72.58	0.0
$\text{logit}(r) = \alpha + \beta_c \text{logit}(C) + \beta_{rt} \text{logit}(rat.nightly) + \beta_{ps} mps*mpr + \beta_{fs} pi + \beta_{mi} i + \text{re}$	9.43	73.90	1.32
$\text{logit}(r) = \alpha + \beta_c \text{logit}(C) + \beta_{rt} \text{logit}(rat.nightly) + \beta_{ps} mps*mpr + \beta_{fs} pi + \beta_{mi} i + \beta_a area + \beta_t mths$	8.64	74.22	1.65
$\text{logit}(r) = \alpha + \beta_c \text{logit}(C) + \beta_{pr} mpr + \beta_{ps} mps*mpr + \beta_{fs} pi + \beta_{mi} i + \beta_a area + \beta_t mths$	8.09	84.07	11.49
$\text{logit}(r) = \alpha + \beta_r ratio + \beta_{pr} mpr + \beta_{ps} mps*mpr + \beta_{fs} pi + \beta_{mi} i + \beta_t mths$	7.07	94.29	21.71
$\text{logit}(r) = \alpha + \beta_{\text{pen}} n + \beta_{pr} mpr + \beta_{ps} mps*mpr + \beta_{fs} pi + \beta_{mi} i + \beta_a area + \beta_t mths$	8.11	97.00	24.43

[a] r, return rate (probability of reintroduced individuals establishing and being detected in the reintroduction site); α, intercept term for return rate; β_c, effect of connectivity index (C); β_{rt}, effect of nightly rat tracking rate (*rat.nightly*); $\beta_{ps,}$ effect of mammalian predator presence at source site if predators present at reintroduction site (*mps* = 1 if present at source site, *mps* = 0 if not present at source site; *mpr* = 1 if present at reintroduction site, *mpr* = 0 if not present at reintroduction site); $\beta_{fs,}$ effect of forest type at source site (*pi*=1 if pine forest, *pi* = 0 if native forest); $\beta_{mi,}$ effect of monitoring intensity (*i* = 0 if moderate intensity, *i* = 1 if high intensity); β_a, effect of site area; β_t, effect of time from release to start of breeding season (*mths* = number of months); β_{pr}, effect of mammalian predator presence at reintroduction site; β_{pen}, peninsula effect (*n* = 1 if non-peninsula, *n* = 0 if peninsula); β_r, effect of standardised habitat ratio; re, random effect among sites.

[b] effective number of parameters (mean of the posterior deviance minus the mean of the posterior distribution).

[c] Deviance Information Criterion, indicating the model's level of support.

[d] difference in DIC from that of the best model.

Table 2.3 Means and credible limits (CL) for parameters in best full model and simplified model (Table 2.2) of return rates for North Island robins at 14 reintroduction sites.

Full model						Simplified model				
Node[a]	Mean	SD	2.5% CL	Median	97.5% CL	Mean	SD	2.5% CL	Median	97.5% CL
α	0.18	1.62	-2.93	0.15	3.43	-0.76	0.36	-1.52	-0.75	-0.09
β_c	-0.34	0.10	-0.55	-0.34	-0.14	-0.36	0.08	-0.52	-0.36	-0.22
β_{rt}	-0.32	0.07	-0.48	-0.32	-0.19	-0.32	0.07	-0.47	-0.32	-0.20
β_{ps}	0.96	0.45	0.11	0.94	1.89	1.29	0.39	0.56	1.28	2.08
β_{fs}	-0.96	0.51	-2.01	-0.94	-0.01	-1.22	0.46	-2.15	-1.21	-0.35
β_{mi}	0.47	0.44	-0.40	0.47	1.32	0.28	0.28	-0.27	0.28	0.84
β_a	-0.03	0.28	-0.59	-0.02	0.50					
β_t	-0.21	0.15	-0.49	-0.21	0.09					

[a] α, intercept term; β_c, effect of connectivity (*C*); β_{rt}, effect of rat tracking rate (*rat.nightly*); $\beta_{ps,}$ effect of mammalian predator presence at source site if predators present at reintroduction site; β_{fs}, effect of forest type at source site (*pi* = 1 if pine forest, *pi* = 0 if native forest); β_{mi}, effect of monitoring intensity (*i* = 0 if moderate intensity, *i* = 1 if high intensity); β_a, effect of site area; β_t, effect of time from release to start of breeding season.

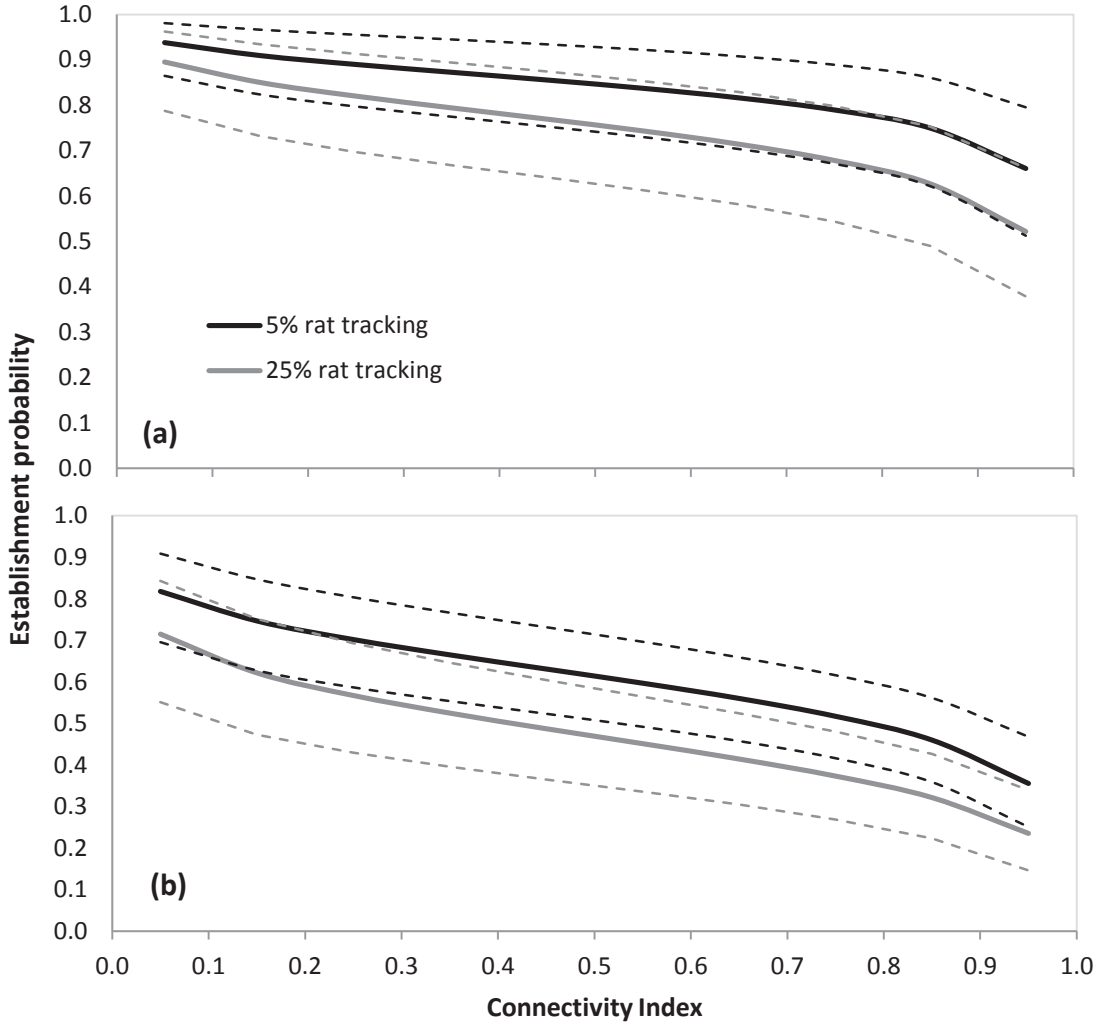


Figure 2.1 Modelled relationship between connectivity of reintroduction sites to surrounding forest and establishment probability (return rates with intensive post-release monitoring) for reintroduced North Island robins sourced from native forest with mammalian predators (a) or without mammalian predators (b). Black and grey lines are estimated probabilities at 5% and 25% rat tracking rates, respectively (dashed lines are 95% credible intervals).

Predictions for the proposed reintroduction site Pukaha were dependent on the level of predator control achieved and characteristics of the source site. Predicted establishment probabilities were similar if the founder population was sourced from pine forest with mammalian predators or native forest without mammalian predators. Our model predicted that reintroduced individuals captured from predator-free native forest would have 0.43 (95% CI 0.32-0.54) probability of establishing at Pukaha if rat tracking rates were 25%, or 0.45 (95% CI 0.31-0.59) probability if sourced from pine forest. This probability increased to 0.58 (95% CI 0.48-0.68) (0.59 when sourced from pine forest) if rat tracking rates were reduced to 5%, which might be expected with high intensity predator control. Sourcing founders from native forest with mammalian predators maximised predicted establishment probabilities for any level of rat

control. For instance, robins were estimated to have 0.73 (95% CI 0.60-0.84) or 0.83 (95% CI 0.72-0.92) probability of establishing at Pukaha with 25% or 5% rat tracking, respectively (Figure 2.2). These results in turn have implications for the initial population size at Pukaha. For example, if 40 robins were caught from mammal-free native forest and released into Pukaha when rat tracking rates were 25%, we would expect 17 (95% CI 13-22) to remain in the reintroduction area and survive to the start of the first breeding season. If the birds were instead sourced from native forest with mammalian predators, this initial population size is expected to be 29 (95% CI 24-34) at 25% rat tracking or 33 (95% CI 29-37) at 5% rat tracking.

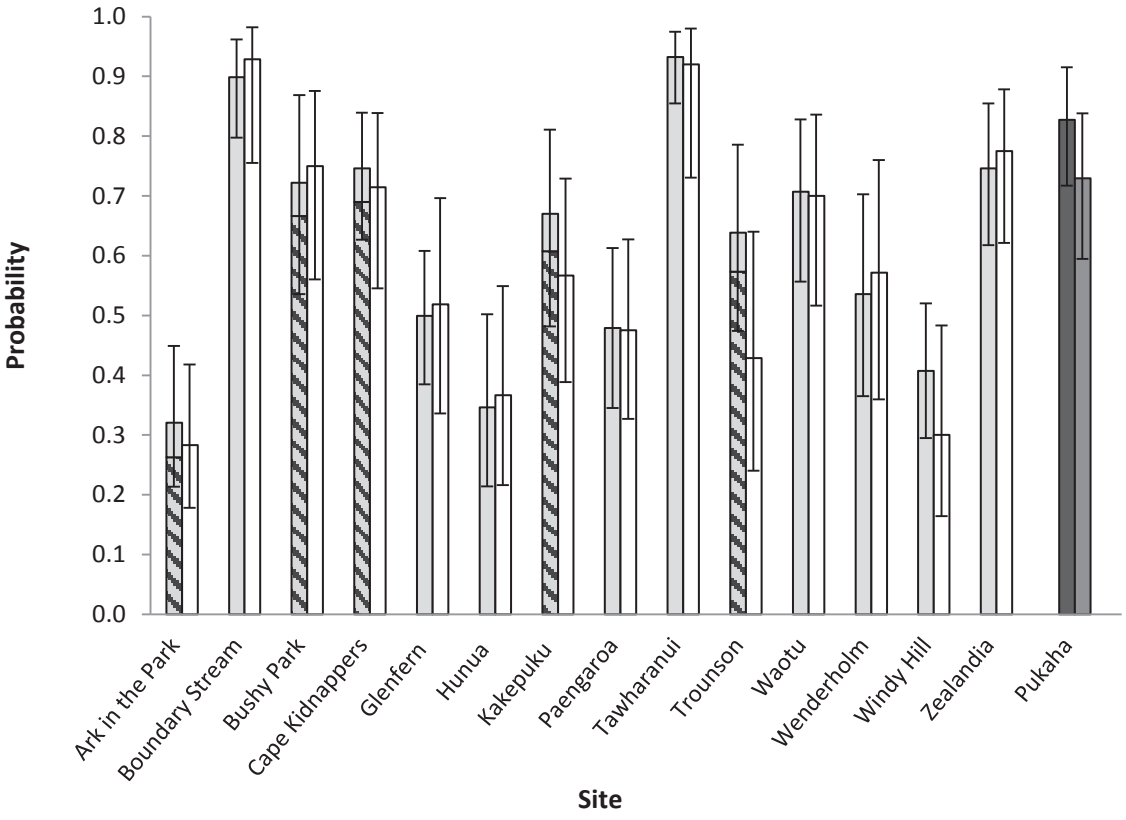


Figure 2.2 Observed return rates (white bars) and modelled establishment probabilities (light grey bars) for North Island robins at 14 reintroduction sites. Diagonal hatching represents modelled return rates for robins reintroduced to sites without intensive post-release monitoring. Dark grey and medium grey bars show predicted establishment probabilities for a proposed reintroduction site (Pukaha) at 5% and 25% rat tracking rates, respectively, assuming founders sourced from native forest with mammalian predators present.

Discussion

Maximising the probability of reintroduced individuals remaining in the target area and surviving to breed is an important consideration for any reintroduction. Only by understanding the key drivers of post-release establishment can we hope to identify effective management interventions and make useful predictions for future reintroductions. In recent years, there have been numerous calls for quantitative modelling to become part of reintroduction evaluations (Seddon et al. 2007, Armstrong and Reynolds 2012, Le Gouar et al. 2012, Osborne and Seddon 2012). The challenge is that reintroductions, by their very nature, often involve small data sets from distinct locations, so data from individual reintroduction attempts may be inadequate for thorough evaluation of factors affecting reintroduction success across a species' range (Jachowski et al. 2011). Species are increasingly being released into multiple sites as part of recovery programmes, providing a valuable opportunity to move beyond the inferences that can be derived from single-site studies. Our study demonstrates the benefits of integrating data from multiple reintroductions into a single model to identify important influences on establishment across sites. Our methods allowed us to make predictions of initial population size for a candidate reintroduction site while simultaneously quantifying uncertainty in those predictions. This approach also potentially allows unexplained variation among sites to be taken into account through inclusion of random effects, although no such variation was detected in this study.

Our results showed that landscape connectivity and rat tracking rates at the reintroduction site, and forest type and mammalian predator presence at the source site, were all important for post-release establishment of North Island robins. Lower establishment probabilities were associated with greater connectivity to surrounding forest, probably due to differential dispersal of robins out of sites. Post-release dispersal is increasingly being recognised as an important influence on establishment of reintroduced populations (Le Gouar et al. 2012); however, to date, there has been little consideration given to the biological implications of landscape structure in reintroduction biology (La Morgia et al. 2011). Identification of release sites where the surrounding landscape is more likely to inhibit dispersal out of the target area is essential to avoid dispersal-related failure of reintroductions (Le Gouar et al. 2012). Nevertheless, the effects of dispersal are not always detrimental. For example, if a reintroduced population can maintain positive population growth despite emigration or the habitat matrix outside the target area is of sufficient quality to allow dispersing individuals to survive and successfully breed, then there are unlikely to be negative consequences (Le Gouar et al. 2012). Understanding the implications of post-release dispersal is clearly important for improving reintroduction success. Our model enables us to predict individual establishment probabilities for a target area in

relation to the surrounding landscape, providing vital information for assessments of site suitability.

Rat tracking rate was negatively correlated with robin establishment, indicating that improvements in predator control at release sites will benefit reintroduced populations. This finding was somewhat unexpected, because although ship rats are known to prey on nesting female robins (Brown 1998), survival of adult males and non-breeding females in established populations is not markedly affected by rat densities (Armstrong et al. 2006b, Parlato and Armstrong 2012 [Chapter 3]). Translocation-induced stress is probably responsible for the relationship found here, given that reintroduced individuals are subject to a number of stressors as part of the translocation process (Teixeira et al. 2007, Dickens et al. 2009) and are especially vulnerable to predation immediately after release into a new location (Letty et al. 2007). This vulnerability can be particularly relevant if there are new predators at the release location (Dickens et al. 2010), and predator-naïve robins could be more susceptible to predation if they are unable to recognise predators as a potential threat. Previous studies have found that robins in mammal-free environments are less likely to recognise model mammalian predators than robins coexisting with such predators (Maloney and McLean 1995, Jamieson and Ludwig 2012), raising questions about the appropriateness of reintroducing naïve individuals to sites where mammalian predators are present (Jamieson and Ludwig 2012). Our results suggest predator experience may indeed be important for robin establishment in sites with mammalian predators, with founders sourced from sites with mammalian predators estimated to have a higher probability of establishing than individuals captured from mammal-free sites. The lower establishment rates associated with sourcing robins from exotic pine forest could also be linked to predation vulnerability, as rats are known to be generally less abundant in pine than native forest (King et al. 1996). In addition to predator exposure, prior habitat experience could influence post-release survival if robins sourced from pine forest were less able to forage effectively in unfamiliar native forest or were more stressed by release into native habitat than robins sourced from native forest; for example, leading to compromised foraging ability or predator evasion (Dickens et al. 2010). Robins sourced from pine forest may also have greater propensity to disperse out of reintroduction areas, as post-release movements of reintroduced individuals tend to be more extensive in unfamiliar release environments (Roe et al. 2010, Biggins et al. 2011). The importance of forest type and mammalian predator presence at the source site suggest choosing a source population from habitat that best matches the ecological characteristics of the reintroduction site can be important for reintroduction success (Letty et al. 2007, Rittenhouse et al. 2008). However, these factors need to be weighed against impact on source populations, as populations at mammal-free sites may be more resilient to harvesting than populations coexisting with mammalian predators.

The ultimate purpose of building models for reintroductions is to make predictions that can be used to inform management (Armstrong and Reynolds 2012). Our approach provides practical guidance for managers when determining appropriate management strategies. Model predictions for the proposed reintroduction site Pukaha indicated that sourcing robins from native forest with mammalian predators would attain the highest establishment rates for any level of rat control, giving a simple way to improve establishment probabilities. Predator control was also an important contributor to establishment (Figure 2.2) with an on-going influence on the long-term growth of the reintroduced population (Parlato and Armstrong 2012 [Chapter 3]). Estimated establishment probabilities can also guide decisions on the number of individuals to release. Despite the common focus on release group size in the literature, the relationship between the number of individuals released and initial population size at the first breeding season is often unknown, making it difficult to determine how many individuals should be released to meet programme objectives. For example, Tracy et al. (2011) developed a useful framework for deciding how many individuals to release to maintain a desired level of genetic diversity, but a key assumption was how many founders would remain to contribute to the gene pool. Our methods therefore move beyond the educated guesses about effective initial population size often necessary when planning reintroductions, and provide a quantitative basis for management decisions.

Our approach can easily be extended to other species; incorporating any factors considered potentially important for establishment (for example, age or body mass of founders). We do, however, caution against perfunctory inclusion of release group size as an explanatory variable due to potential confounds associated with the implicit, though probably unrealistic, assumption that numbers of individuals are chosen at random with respect to the probability of success (Armstrong and Wittmer 2011). Noting this, release group size can be an important determinant of establishment in its own right; for example, when Allee effects pose a non-trivial threat to the survival of reintroduced individuals (Armstrong and Reynolds 2012).

Factors influencing establishment of reintroduced populations are typically identified using data collected from single sites. Here we present an approach that integrates data from multiple reintroductions, providing confidence that identified relationships are general and allowing predictions to be made for a new population in a new situation. The resulting model gives useful guidance for managers at a number of levels, including source and release site selection, efficacy of management interventions and, ultimately, the number of individuals to release to achieve a desired initial population size. Nevertheless, taking steps to ensure successful establishment of a reintroduced population is only worthwhile if conditions at the release site are sufficient to allow long-term population growth and persistence. Establishment models should therefore be considered one of a suite of tools for assessing project feasibility. With the

value of modelling reintroduced populations becoming increasingly recognised, we expect to see greater emphasis on the development of quantitative models to inform management and guide future reintroductions. For species reintroduced to multiple sites, integrated models provide an ideal opportunity to develop understanding over time of the key drivers of reintroduction success.

Chapter 3

An integrated approach for predicting fates of reintroductions with demographic data from multiple populations

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Nesting female North Island robin (*Petroica longipes*) at Paengaroa Scenic Reserve

Abstract

We devised a novel approach to model reintroduced populations whereby demographic data collected from multiple sites are integrated into a Bayesian hierarchical model. Integrating data from multiple reintroductions allows more precise population-growth projections to be made, especially for populations for which data are sparse, and allows projections that account for random site-to-site variation to be made before new reintroductions are attempted. We used data from reintroductions of the North Island robin (*Petroica longipes*), an endemic New Zealand passerine, to 10 sites where introduced mammalian predators are controlled. A comparison of candidate models that we based on deviance information criterion showed that rat tracking rate (an index of rat density) was a useful predictor of robin fecundity and adult female survival, that landscape connectivity and a binary measure of whether sites were on a peninsula were useful predictors of apparent juvenile survival (probably due to differential dispersal away from reintroduction sites), and that there was unexplained random variation among sites in all demographic rates. We used the two best supported models to estimate the finite rate of increase (λ) for populations at each of the 10 sites, and for a proposed reintroduction site, under different levels of rat control. Only three of the reintroduction sites had λ distributions completely >1 under either model. At two sites, λ was expected to be >1 if rat tracking rates were <5%. At the other five reintroduction sites, λ was predicted to be close to 1, and it was unclear whether growth was expected. Predictions of λ for the proposed reintroduction site were less precise than for other sites because distributions incorporated the full range of site-to-site random variation in vital rates. Our methods can be applied to any species for which post-release data on demographic rates are available and potentially can be extended to model multiple species simultaneously.

Introduction

Although most of the reintroduction literature consists of descriptive accounts of reintroductions, there is increasing use of population modelling to analyse demographic data collected after reintroductions (Seddon et al. 2007). As with all population models, those constructed for reintroduced populations can be used to project future trends in abundance, estimate risk of extinction, and quantitatively compare potential effects of alternative management strategies (Beissinger and Westphal 1998). However, precision of predictions is limited by the data, so predictions may be relatively useless in the initial years after reintroduction. It is impossible to construct demographic models before reintroduction to a

given site unless data from other sites are used (e.g. South et al. 2000), and it is then necessary to consider likely variation in demographic rates among sites.

Two alternative approaches have been used to make predictions that can be used before reintroduction. First, species distribution models can be generated, typically by correlating current presence and absence of a species with spatially explicit data, and then these models are used to assess suitability of potential release sites (Schadt et al. 2002, Thatcher et al. 2006). Second, data on successes and failures of previous reintroductions can be used to model factors associated with probability of success (Griffith et al. 1989, Wolf et al. 1996, Wolf et al. 1998). These approaches can be useful to show trends in reintroduction outcomes over multiple species and extensive geographic areas. However, the inferences that can be derived from such studies are highly limited by the types of data available and are inevitably subject to confounding factors (Armstrong and Seddon 2008). The models also do not predict actual trends in population growth, which may be necessary for management purposes and are not easily integrated with post-release demographic data.

Currently lacking in the reintroduction literature is a framework for demographic modelling of populations that builds on results from other reintroduction programs. This approach makes it possible to use small data sets that on their own have little predictive power and to assess whether identified relationships are general rather than case specific (Johnson 2002). A major challenge is to model the general drivers of demographic rates while accounting for unexplained case-by-case variation in those rates.

The recent advent of Bayesian hierarchical modelling in population ecology (King et al. 2010) provides an opportunity to integrate data from multiple reintroduced populations into a single model while accounting for unexplained random variation in demographic rates among sites. Bayesian inference is a natural framework for modelling reintroductions because existing data can be used to obtain prior distributions of demographic rates before a proposed reintroduction takes place, and these distributions can then be updated as post-release monitoring data become available. More importantly, it is possible to fit Bayesian hierarchical models with multiple random effects, allowing random case-by-case variation in demographic rates to be accounted for.

We constructed Bayesian hierarchical models with data available from reintroductions of North Island robins (*Petroica longipes*) to 10 sites where introduced mammals are controlled and used the resulting models to project population growth at these sites and a proposed reintroduction site. This species was a logical starting point for developing an integrated model because data from multiple sites were available, we had prior knowledge of the species' population dynamics

and threats, and our projections would be used to guide ongoing management of existing populations and proposals for further reintroductions.

Methods

Species and reintroduction sites

The North Island robin is a 26-32 g insectivorous forest passerine endemic to New Zealand. Before European colonisation, its range included the entire North Island, but now the species is restricted to the central North Island and some offshore islands (Higgins and Peter 2002). Robins are limited by introduced ship rats (*Rattus rattus*) (e.g. Brown 1997, Armstrong et al. 2006a, Armstrong et al. 2006b) and may also be limited by other introduced mammals such as stoats (*Mustela erminea*). North Island robins are territorial and sedentary; they rarely leave a territory after establishing it. They typically breed in monogamous pairs, but unpaired females can successfully hatch and rear young without the assistance of a mate, although rate of success is lower than for paired females (Armstrong et al. 2006b). Nesting is usually from September to January, and juveniles usually disperse before establishing a territory. Robins breed in their first year, and the reproductive success of first-year birds is similar to that of older birds (Dimond and Armstrong 2007).

The 10 reintroductions we analysed took place between 1998 and 2007 (Table 3.1). All were to areas of mature native forest managed to control introduced predators, but birds could potentially disperse to adjacent unmanaged forest where they would be unlikely to return to the populations. Two sites were enclosed by predator-exclusion fences (fences to exclude all mammals except house mice [*Mus musculus*]); hence, rats were expected to be absent. The other sites had ongoing control programs to reduce rat densities. Eight of the sites were on the North Island, and the other two (Glenfern and Windy Hill) were on Great Barrier Island. We included data from the Great Barrier reintroductions because the forest was similar to the other sites (mature native forest) and the populations faced similar limitations from ship rats and dispersal. The proposed reintroduction site (Pukaha [Table 3.1]) also had mature native forest and a predator-control program.

Data collection

Raw data on robin fecundity and survival were available from field notebooks, reports, or a thesis (Pattemore 2003) for nine of the sites, and estimates (with SE) of demographic rates were obtained from a thesis (Small 2004) for the other site (Zealandia). Data were available from the

Table 3.1 Characteristics of North Island robin reintroduction sites and the years of data used to model demographic rates.

Site	Area (ha)[a]	Peninsula	Habitat ratio[b]	Standardised habitat ratio[c]	Year reintroduced	Years of data
Ark in the Park	1100	no	2.9	0.00	2005	4
Boundary Stream	800	no	1.6	-0.93	1998	2
Glenfern	230	yes	1.6	-0.93	2005	3
Hunua	600	no	5.3	1.72	2001	1
Paengaroa	101	no	1.9	-0.72	1999	5
Tawharanui[d]	588	yes	1.4	-1.07	2007	2
Waotu	31	no	4.9	1.43	2001	1
Wenderholm	60	yes	3.9	0.72	1999	10
Windy Hill	450	no	3.0	0.07	2004	6
Zealandia[d]	225	no	2.5	-0.29	2001	2
Pukaha	942	no	0.8	-1.50	NA	NA

[a] Area managed to control introduced mammalian predators.
[b] Area of accessible habitat within 2 km of perimeter of reintroduction site divided by area of the reintroduction site.
[c] Habitat ratios standardised so 10 reintroduction sites have mean 0 and variance 1.
[d] Sites with fencing to exclude all mammals except house mice.

start of the first breeding season after reintroduction and were collected for at least one year for all sites.

We compiled data with which to estimate three demographic rates: fecundity (number of fledglings per female per year), apparent juvenile survival (probability of fledgling remaining in the reintroduction site and surviving to the next breeding season), and annual adult survival (which was unlikely to be affected by dispersal). We assumed immigration was negligible because there were no other robin populations near any of the reintroduction sites, and it seemed unlikely that dispersers would return to the sites or any offspring from these dispersers would immigrate, although one such incident was recorded.

Because nesting was closely monitored, accurate data were available on numbers of young fledged for each breeding pair or female. Similarly, because birds were individually color banded and the sites were searched regularly, it was possible to create encounter histories (Lebreton et al. 1992) for estimating survival. The encounter histories reflected two surveys per year, at the start of the breeding season (September) and toward the end of the breeding season (January). Reintroductions always took place between March and June, and the released birds were considered to enter the population as adults when first sighted in a subsequent survey. This means the period of high mortality and dispersal that typically occurs immediately after translocation did not influence survival estimates. Birds fledged at the sites were considered to have entered the population at the end of the breeding season in which they fledged and to have reached adulthood if they were sighted during the survey at the start of the next breeding season.

We also compiled data on variables that were likely to be useful predictors of demographic rates: rat tracking rate, which is an index of rat density (Blackwell et al. 2002) used to monitor effectiveness of control; minimum daily temperature, which may reflect harsh weather; and two landscape variables, a connectivity index and a binary measure of whether sites were on a peninsula (intended to reflect ease of dispersal from the reintroduction site).

Rat tracking data were collected at nine of the sites each year since robins were reintroduced. Ten to 25 tunnels were usually placed along transects, spaced 50 m apart. Tunnels were baited with peanut butter, and ink pads and paper were placed inside to record a rat's tracks if it passed through a tunnel (Innes et al. 1995). We used the data to estimate the probability of a rat passing through a tunnel over one night (see below) and following standard usage (e.g. Blackwell et al. 2002) refer to this probability as the rat tracking rate. We divided the data into breeding season and non-breeding season and obtained separate estimates for both seasons for each site for each year. For the site where rat tracking data were not collected (Waotu), we modelled rat tracking rates as missing values.

We obtained minimum daily temperatures for each site from the New Zealand National Climate Database CliFlo (NIWA 2009-2010). We used these data to calculate average minimum daily temperature for both seasons at each site for each year since robins were reintroduced.

The first landscape variable was an index of connectivity that we based on land-cover maps, which were manually digitised (5-m resolution) from aerial photographs and satellite imagery (QuickBird) with ArcGIS 9.3 (ESRI, Redlands, California) and Imagine 9.2 (ERDAS, Atlanta, Georgia). Landscape connectivity represents the functional connection between habitat patches relative to the dispersal capabilities of a species (Tischendorf and Fahrig 2000). We calculated the area of mature forest within 2 km of the perimeter of the reintroduction site (i.e. the managed area where the population was intended to live), excluding areas that could only be reached by crossing >110 m of pasture. Such areas were excluded because 110 m is the maximum gap dispersing juvenile robins are estimated to cross (Richard and Armstrong 2010). We then calculated the ratio of forest area to the area of the reintroduction site and standardised these ratios for the 10 sites, meaning for an average site this standardised ratio was zero.[1] The second variable was a binary measure of whether sites were on a peninsula (Table 3.1). We suspected that dispersing juveniles may leave peninsular sites because they have a tendency to follow edges (Andrews 2007, Richard and Armstrong 2010).

Modelling

We used WinBUGS (version 1.4) to model the data; WinBUGS uses Markov chain Monte Carlo (MCMC) techniques (Spiegelhalter et al. 2003) to fit Bayesian hierarchical models. We initially separated analyses of the survival (adult and juvenile combined) and fecundity data and used the deviance information criterion (DIC) to compare candidate models (Spiegelhalter et al. 2002). All models had uninformative priors (normal distributions with mean 0 and precision 10^{-6} for main parameters, and uniform distributions from 0-100 for hyperparameters) and were run with an initial burn-in of 10,000 samples for two chains, followed by 100,000 samples after checking convergence. We checked convergence with the Brooks-Gelman-Rubin (BGR) diagnostic tool and by examining the chains and the autocorrelation plots.

After identifying the best models (models with the lowest DIC) for survival and fecundity, we combined the best models' codes into a single model to estimate the finite rate of increase (λ) of each population with all data modelled simultaneously. Because robins have no apparent age structure in survival or fecundity rates after their first year and the sex ratio of recruits is

[1] I also modelled the effect of an alternative connectivity index (*C*, see Chapter 2 for calculation) in my analysis. However, habitat ratio was found to be a better predictor of apparent juvenile survival than *C*. As such, the methods for calculating *C* and the details of this model comparison were excluded for the purposes of staying within the word limit required for publication.

approximately 1:1 (Dimond and Armstrong 2007), the finite rate of increase is

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

where s_a is annual adult survival probability for adult females, f is the mean number of fledglings per female per year, and s_j is the probability of a juvenile staying at the site and surviving to adulthood. For the 10 sites with data, the values of these parameters were influenced by estimated site-specific random effects and by the fixed effects included in the best models. In contrast, random effects for the proposed population at Pukaha were sampled from distributions on the basis of the estimated variation among sites.

Candidate models for both survival and fecundity were of a log-linear form (Tables 3.2 & 3.3). Our rationale was that survival of prey and "survival" of predator detection devices (i.e. tracking tunnels) are both expected to have a power relationship with predator density (Caughley 1977), meaning the relationship between robin survival (s) and rat tracking is expected to take the form

$$\ln(s) = \ln(\alpha) + \beta \ln(p),$$

where p is tunnel survival (the complement of rat tracking rate), α is the intercept (survival probability when there are zero rats), and β is the slope of the relationship (Armstrong et al. 2006b). The relationship between fecundity and rat tracking rate is expected to take the same form if fecundity is directly proportional to nest survival, and results of previous research show a log-linear fecundity model performs well in comparison with more complex nonlinear models (Armstrong et al. 2006b). For both survival and fecundity, we created alternative candidate models by adding both fixed and random effects to the basic log-linear model shown above. We assumed that random effects were normally distributed.

Our initial fecundity model (top line of Table 3.2) included a fixed effect of the female's pairing status (i.e. lone or paired), the intercept and slope shown above, and a random effect for the individual female and the site. Thus, we estimated five parameters. We included the random female effect to ensure robustness of the results to pseudoreplication resulting from some females occurring in multiple years. We then assessed whether the DIC was reduced by removing any of these effects or by substituting mean temperature during the breeding season for the random site effect.

Our initial survival model (bottom line of Table 3.3) included random site effects and the intercept and slope shown above, and we applied these three types of effect separately to adult males, adult females, and juveniles. For adult females, we applied the three effects separately for the breeding and non-breeding season because females are more vulnerable to predation

while nesting. This meant 12 different parameters were estimated. We then sequentially assessed whether the DIC was reduced by having a single intercept and random effect for adults (i.e. removing seasonal and sex differences) and by removing effects of rat tracking on juveniles, adults, and non-breeding females. We then assessed whether the DIC was further reduced by adding the temperature effect (applied separately to adults and juveniles) and the peninsula and connectivity effects (which we applied only to juvenile survival).

When modelling fecundity, we sampled the raw data on numbers of fledglings for each female each year from Poisson distributions with unknown means calculated on the basis of the effects included in the model. When modelling survival, the survival data consisted of the estimated survival probabilities for each age class, sex, and season for each site and year and their associated standard errors. We used the Cormack-Jolly-Seber live recaptures model in MARK (White and Burnham 1999) with MCMC estimation to obtain these estimates and standard errors from the raw encounter histories. In our WinBUGS code, the estimates were sampled from lognormal distributions with unknown means, which we calculated on the basis of the effects included in the model and variances corresponding to the standard errors. This method allowed uncertainty in the survival estimates to be accounted for in the models. It would also have been possible to directly model the raw encounter histories within WinBUGS by incorporating code for fitting live recapture models, and this would be the ideal approach to account fully for the uncertainty and covariances among the parameter estimates. However, writing code for fitting live recapture models (Schofield et al. 2009) is complex in comparison with obtaining estimates with MARK. We therefore preferred to use a more accessible approach, and a benefit of our approach is that it can be used for meta-analyses for which the raw data are not available.

We modelled rat tracking rates simultaneously with the other data, which allowed us to account for uncertainty in these rates. For each season for each site each year, the number of tunnels through which rats passed was sampled from a binomial distribution in which the sample size was the total number of tunnels set and the rat tracking rate (1- p) was unknown. We used these unknown rates as predictors of survival and fecundity (Tables 3.2 & 3.3). Because tracking data were missing for some periods at some sites and entirely missing for Waotu, the rat tracking rates for these periods were imputed on the basis of the relationship with survival and fecundity modelled from the other data.

Results

Survival and fecundity

The best fecundity model included rat tracking rate during the breeding season, female pairing status, and random effects of site and female, and had strong support (ΔDIC > 3.7) compared with other models (Table 3.2). The DIC increased substantially (ΔDIC = 21.4) when female pairing status was removed from the model and increased when random variation among sites or individual females was removed (ΔDIC = 5.0 & 3.7 respectively) or when mean annual temperature was substituted for the random site effect (ΔDIC = 8.7). In the best model, an average paired female at an average site had 3.64 fledglings with no rats present (α*f*, Table 3.4 & Figure 3.1a) and <2 fledglings when rat tracking was >50% as would occur typically without control (Figure 3.1a). Unpaired females were estimated to fledge about one-third as many young as paired females (Figure 3.1a). However, we did not include pairing status in the model when estimating λ, meaning the λ estimates reflect the fact that females occasionally outnumbered males at some sites.

Table 3.2 Comparison of fecundity models fitted to data for North Island robins at 10 reintroduction sites.

Model[a]	pD[b]	DIC[c]	ΔDIC[d]	*w*[e]
ln(*f*) = ln(α*f*) + β*f*1ln(*p*) + β*f*2*u* + re.site + re.fem	52.2	998.9	0.0	0.80
ln(*f*) = ln(α*f*) + β*f*1ln(*p*) + β*f*2*u* + re.site	33.0	1002.6	3.7	0.13
ln(*f*) = ln(α*f*) + β*f*1ln(*p*) + β*f*2*u* + re.fem	57.0	1003.9	5.0	0.07
ln(*f*) = ln(α*f*) + β*f*1ln(*p*) + β*f*2*u* + β*f*3*t* + re.fem	51.6	1007.6	8.7	0.01
ln(*f*) = ln(α*f*) + β*f*1ln(*p*) + re.site + re.fem	57.9	1020.3	21.4	0.00
ln(*f*) = ln(α*f*) + β*f*1ln(*p*)	25.1	1044.8	45.9	0.00

[a] α*f*, intercept term for mean number of fledglings per female; β*f*1, effect of tunnel survival (*p*); β*f*2, effect of being an unpaired female (*u* = 0 if paired, *u* = 1 if unpaired); β*f*3, effect of average minimum daily temperature (*t*); re.site, random effect of site; re.fem, random effect of individual female.

[b] Effective number of parameters (mean of the posterior deviance minus the mean of the posterior distribution).

[c] Deviance information criterion, where lower DIC means the higher predictive value.

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

[e] Relative support for the model, assuming support is proportional to $e^{-\Delta DIC/2}$ (Spiegelhalter et al. 2002).

The best survival model (Table 3.3) included an effect of rat tracking rate on survival of adult females over the breeding season, but not on survival of non-breeding females, adult males, or juveniles. It also included random variation among sites in both adult and juvenile survival. Apparent juvenile survival was lower for peninsular sites and among non-peninsular sites was lower at sites with a higher connectivity index. Including the peninsula effect improved the model (ΔDIC = 3.7), but the predictive value of the connectivity index was ambiguous (ΔDIC = 0.4). Thus, there were two survival models with similar support (Table 3.3).

Table 3.3 Comparison of survival models fitted to data for North Island robins at 10 reintroduction sites.

Model[a]	pD[b]	DIC[b]	ΔDIC[b]	w[b]
$\ln(s) = \ln(\alpha s_a) + \beta s1gb\ln(p) + \beta s2an + \beta s3anr + \text{re.site}_a$	75.6	335.9	0.0	0.43
$\ln(s) = \ln(\alpha s_a) + \beta s1gb\ln(p) + \beta s2an + \text{re.site}_a$	73.3	336.3	0.4	0.35
$\ln(s) = \ln(\alpha s_a) + \beta s1gb\ln(p) + \text{re.site}_a$	77.5	340.0	4.1	0.06
$\ln(s) = \ln(\alpha s_a) + \beta s1gb\ln(p) + \beta s4_a t + \text{re.site}_a$	78.4	340.8	4.9	0.04
$\ln(s) = \ln(\alpha s_a) + \beta s1_a g\ln(p) + \text{re.site}_a$	77.3	340.5	4.6	0.04
$\ln(s) = \ln(\alpha s_a) + \beta s1gb\ln(p) + \beta s2an + \beta s3anr + \text{re.site(juvenile)}$	69.8	340.5	4.6	0.04
$\ln(s) = \ln(\alpha s_a) + \beta s1_{agb}\ln(p) + \text{re.site}_a$	79.5	341.5	5.6	0.03
$\ln(s) = \ln(\alpha s_a) + \beta s1gb\ln(p) + \beta s2an + \beta s3anr + \text{re.site(adult)}$	73.9	342.9	7.0	0.01
$\ln(s) = \ln(\alpha s_{agb}) + \beta s1_{agb}\ln(p) + \text{re.site}_{agb}$	81.8	348.4	12.5	0.00

[a] αs, intercept term for probability of an adult surviving 1 year or a juvenile surviving from fledging to adulthood and remaining in the site; $\beta s1$, effect of tunnel survival (p); $\beta s2$, peninsula effect (n = 1 if not on a peninsula; n = 0 if on a peninsula); $\beta s3$, effect of standardised habitat ratio (Table 3.1); $\beta s4$, effect of average minimum temperature (t); a, age (a = 1 if juvenile, a = 0 if adult); g, sex (g = 1 if female, g = 0 if male); b, season (b = 1 if breeding season, b = 0 if non-breeding season); r = standardised habitat ratio; re.site, random effect of site. Subscripts denote variation among groups (e.g. αs_a specifies separate intercepts among ages and αs_{ags} specifies separate intercepts among ages, between sexes, and between seasons.

[b] As for Table 3.2.

The annual probability of survival for an adult male, or adult female in the absence of rats, was estimated at 0.77 (αs adult, Table 3.4). Because rat tracking rate and adult female survival were correlated only in the breeding interval, which was one-third of the year, the predicted annual survival probability of an average female was

$$\ln(s) = \frac{1}{3}\left[\ln(\alpha s) + \beta s1 \ln(p)\right] + \frac{2}{3}\ln(\alpha s),$$

with the effect of tracking tunnel survival ($\beta s1$) estimated at 0.32 (Table 3.4). Thus, there is a fairly gradual relationship between female survival and rat tracking rate with mean annual survival still 0.72 at 50% rat tracking (Figure 3.1b).

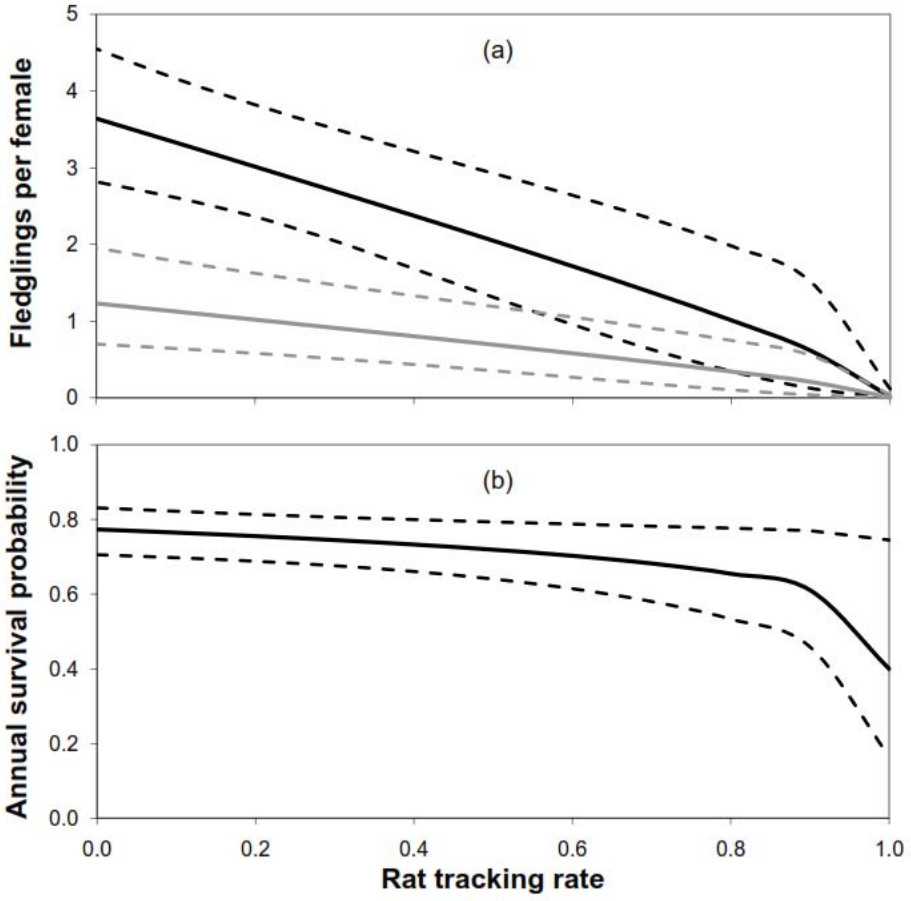


Figure 3.1 Best models (lowest DIC) of the relationships between rat tracking rate (probability of one or more rats passing through a baited tunnel over 1 night) and (a) mean number of young fledged per year if the female is paired (black) or unpaired (gray) and (b) annual survival probability of adult females on the basis of data from North Island robins reintroduced to 10 sites (dashed lines, 95% credible intervals).

Apparent juvenile survival was estimated at 0.15 (α*s* juvenile, Table 3.4) at peninsular sites, and the mean was 0.37 (95% CI 0.25-0.50) for non-peninsular sites. When the estimated connectivity effect (β*s*3, Table 3.4) was applied to the non-peninsular sites (standardised habitat ratios in Table 3.1), the predicted apparent juvenile survival probabilities ranged from 0.14 at the most connected site (Hunua) to 0.64 at the least connected site (Boundary Stream).

Table 3.4 Means and credible limits (CL) for parameters in best models of fecundity (Table 3.2) and survival (Table 3.3) of North Island robins at 10 reintroduction sites.

Node*	Mean	SD	2.5% CL	Median	97.5% CL
α*f*	3.64	0.44	2.81	3.62	4.55
α*s* (adult)	0.77	0.03	0.70	0.77	0.83
α*s* (juvenile)	0.15	0.05	0.08	0.15	0.26
β*f*1	0.85	0.29	0.37	0.82	1.49
β*f*2	-1.11	0.24	-1.60	-1.10	-0.66
β*s*1	0.32	0.17	0.02	0.31	0.68
β*s*2	0.91	0.34	0.18	0.92	1.56
β*s*3	-0.58	0.25	-1.09	-0.58	-0.10
σf_{fem}	0.21	0.08	0.04	0.21	0.37
σf_{site}	0.29	0.13	0.10	0.27	0.60
σs_{site} (adult)	0.09	0.05	0.01	0.09	0.21
σs_{site} (juvenile)	0.27	0.16	0.06	0.23	0.66

*α*f*, intercept term for mean number of fledglings per female; α*s*, intercept term for probability of an adult surviving 1 year (adult survival) or a juvenile surviving from fledging to adulthood and remaining in the reintroduction site (apparent juvenile survival); β*f*1, effect of tunnel survival (*p*) on fecundity; β*f*2, effect of being an unpaired female (*u*) on fecundity; β*s*1, effect of tunnel survival on survival of adult females in the breeding season; β*s*2, peninsula effect (*n* = 1 if not on a peninsula, *n* = 0 if on a peninsula) on apparent juvenile survival; β*s*3, effect of standardised habitat ratio (Table 3.1) on apparent juvenile survival; σf_{site}, standard deviation for random effect of reintroduction site on fecundity; σf_{fem}, standard deviation for random effect of individual female on fecundity; σs_{site}, standard deviation for random effect of reintroduction site on adult survival or apparent juvenile survival.

Population growth

Because it was unclear which was the best survival model, we estimated λ using models with and without the connectivity effect included. Model choice had little effect (<3%) on estimates for seven of the 10 reintroduction sites, but had stronger effects on sites with the highest and lowest connectivity (Figure 3.2). In particular, the estimated λ for Hunua and Waotu increased about 50% and 25% respectively when the connectivity effect was removed.

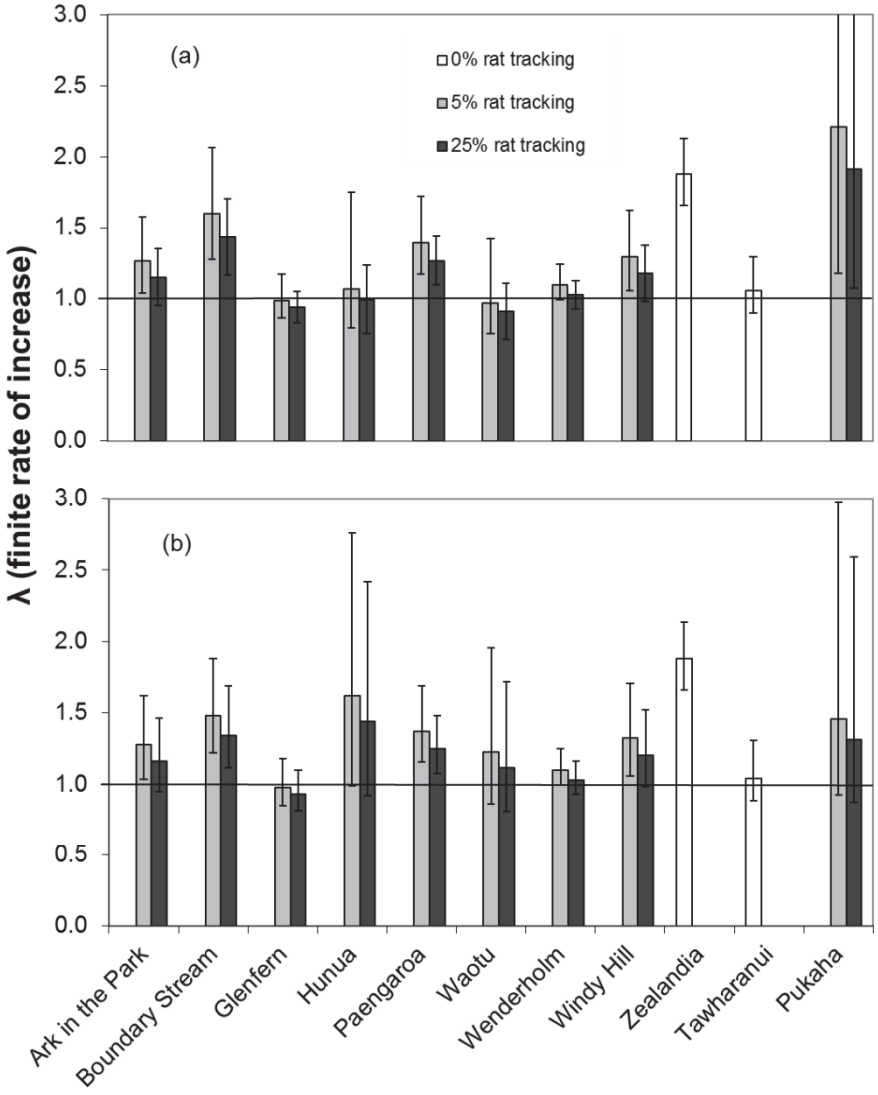


Figure 3.2 Estimated (95% credible interval) finite rates of increase (λ) for 10 reintroduced North Island robin populations and one proposed reintroduction site (Pukaha) at different rat tracking rates for (a) the best model and (b) an alternative model with similar support (ΔDIC = 0.4; Table 3.3) in which juvenile survival is not affected by connectivity to surrounding habitat. Estimates for sites with ongoing predator control are given for a 25% rat tracking rate (typical of low-intensity control) and a 5% rat tracking rate (typical of high-intensity control). Sites with 0% rat tracking rate have predator-exclusion fences.

Only three of the reintroduction sites had λ distributions that were ≥1 in either model, meaning the prediction of positive growth was robust to uncertainty in parameter estimation and model choice for these sites. Two of these, Boundary Stream and Zealandia, were the only sites where robins are currently abundant, and the population at the other site, Paengaroa, was growing until rat control was discontinued after three years. At two sites, Ark in the Park and Windy Hill, λ was estimated to be >1 when rat tracking rates were 5%. At the other five reintroduction sites, λ was predicted to be close to 1, and it was unclear whether growth was expected. These five sites include the three peninsular sites (Glenfern, Wenderholm, Tawharanui), where the populations have persisted at low abundance, and the two most connected sites (Hunua, Waotu), where the populations appear to be extinct.

Model predictions for the proposed reintroduction to Pukaha were less precise than for the others (Figure 3.2) because the distributions for λ incorporated the full range of random variation among sites in fecundity, adult survival, and juvenile survival (σf_{site} and σs_{site}, Table 3.4). The results for this site were particularly sensitive to model choice because Pukaha has lower connectivity than any other site (Table 3.1). With the connectivity effect included, the median λ for Pukaha was >1.9 with either 5% or 25% rat tracking rates; the 95% credible intervals did not include 1 (Figure 3.2a). With the connectivity effect excluded, the median λ values for Pukaha were in the middle of the predicted values for the seven non-peninsular reintroduction sites, and the 95% credible intervals encompassed the full range of credible intervals for those seven sites (Figure 3.2b).

Discussion

Our results illustrate how integrating data from multiple reintroduced populations into one model can greatly improve the information available. We were not surprised that rat tracking rate was a useful predictor of fecundity and adult female survival in North Island robins. It is known that ship rats prey on nesting females, eggs, and chicks (Brown 1997, Powlesland et al. 1999), and the relationship had been modelled previously with data from Paengaroa, one of the 10 reintroduction sites (Armstrong et al. 2006b). However, it was useful to quantify these relationships across multiple sites and to simultaneously quantify the residual variation among sites with hierarchical modelling.

The residual variation among sites in estimated population growth rates was large relative to the estimated effect of rat control (Figure 3.2), meaning there was variation among sites in management requirements. For example, although Ark in the Park and Windy Hill may need to have a rat tracking rate <5% to ensure a high probability of their robin populations growing,

low-intensity control appears adequate to make $\lambda > 1$for Boundary Stream. At Pukaha, where the rat tracking rate has often been >5% despite ongoing control, managers may now decide to proceed with the proposed robin reintroduction knowing there appears to be a high probability of population growth with a 25% rat tracking rate.

Our modelling approach also makes it possible to predict site suitability in terms of the landscape surrounding the site. In locations where predators are controlled, populations will be driven to extinction if dispersal out of the reintroduction site exceeds recruitment (Basse and McLennan 2003). Post-release dispersal is a well-recognised problem in reintroductions and is usually addressed through release strategies designed to minimise immediate dispersal, although these strategies are often ineffective (Armstrong and Seddon 2008). However, the problem of ongoing dispersal is less appreciated.

The variation among reintroduction sites in population growth rates mainly reflects differences in apparent juvenile survival, although the strength of this relationship depends on model choice. For the best model (Figure 3.2a), estimates of apparent juvenile survival ranged from 0.13 to 0.17 among the five marginal sites ($\lambda \leq 1.1$) and from 0.34 to 0.58 among the other five sites ($\lambda \geq 1.3$). We suspect these differences mainly reflect differential dispersal because the five marginal sites were either on peninsulas, where we expected juveniles to disperse along forest edges, or sites with high connectivity to habitat outside the site. Although the predictive value of the connectivity index is ambiguous, connectivity should not be considered unimportant because the estimated effect size was large. We believe sites may be marginal for North Island robin populations if they are on peninsulas or are well connected to habitat outside the site, regardless of the intensity of predator control within those sites.

Our modelling approach also supports adaptive management (Walters 1986) across multiple projects, meaning management actions would be chosen not only to maximise the probability of current reintroduction succeeding, but also to garner information for future reintroductions. For example, there is currently ambiguity about the best model for apparent juvenile survival (relating to the predictive value of the connectivity index). The greatest resolution will come from sites such as Pukaha, for which predictions from the two models were disparate due to its low connectivity relative to other sites. More controversially, if the objective is to better understand the importance of connectivity, it may be sensible to attempt further reintroductions to other well-connected sites even though they may have a low probability of success. Such decisions depend on a range of factors, such as resources available at different sites, potential effects on source populations, and the overall objectives of the introduction, and might ideally be considered in a structured decision framework (Nicol & Chades 2011).

The modelling approach we developed can be applied to any situation in which data are available from multiple populations. The most obvious extension is to project actual population dynamics rather than simply estimating the finite rate of population increase. Depending on the time frame and situation, this may involve incorporating demographic stochasticity (e.g. effects of sex ratio), environmental stochasticity, inbreeding depression, and density dependence, which may include Allee effects (Deredec and Courchamp 2007) and negative density dependence. Such modelling is done routinely with threatened populations, including one of the 10 reintroduced populations we analysed here (Armstrong et al. 2006a) and other reintroduced populations (Seddon et al. 2007). However, we focused on finite rate of population increase because $\lambda > 1$ is the most fundamental requirement for reintroduction success. After determining that λ may be >1, it makes sense to assess the population's viability considering demographic stochasticity in the short term and environmental stochasticity and inbreeding depression in the longer term.

We examined a somewhat ideal scenario: multiple reintroductions of one species have taken place, the biology of the species and its threats are well understood, and methods used to collect data on demographic rates have been consistent. However, it is also possible to apply models to inconsistent and fragmented data in a Bayesian framework. For example, it is possible to integrate demographic and abundance data (Brooks et al. 2004), and it would have been fairly easy for us to incorporate reintroduction sites where abundance had been estimated but no demographic data were collected. It is also possible to model various types of missing data in a Bayesian framework (Nakagawa and Freckleton 2008).

We emphasise that including standard errors around estimates is vital for allowing uncertainty to be incorporated in a model. When reporting standard errors, it is also important to distinguish process variation (e.g. spatial or temporal variation) from sampling variation when possible (White 2000). For example, in our results (Table 3.4), it is important to distinguish variation among sites in apparent juvenile survival from the standard error in the estimated mean.

Making data available in raw form could maximise analytical power and flexibility, although it would make the data less accessible and more difficult to incorporate into meta-analyses. It would be useful to assess the benefits gained from using raw data in comparison with meta-analyses conducted with estimates and standard errors. For example, it would be useful to compare our approach for modelling survival data in MARK with projections obtained with the ideal approach of directly modelling the raw encounter history data in WinBUGS. The most challenging extension would be to integrate data for multiple species, but this would be useful for two reasons. First, there will often be data from too few populations of any species to

estimate among-site variation in parameters. Second, it usually is necessary to consider multiple species when considering management options at any site.

Currently, models used in reintroduction projects are generally either species distribution models that are built with presence-absence data before reintroduction takes place or demographic analyses carried out with post-release monitoring data after reintroduction has occurred (Seddon et al. 2007). Our method bridges this dichotomy by creating initial demographic models with data available before release that can be updated as post-release monitoring data become available. We suggest monitoring information be made widely available and these data be used to construct demographic models to inform management decisions. In this way, reintroduction biologists can move beyond case studies and create a means by which information can be synthesised across programs.

Supporting Information

The WinBUGS code for our statistical model is available online

http://onlinelibrary.wiley.com.ezproxy.massey.ac.nz/doi/10.1111/j.1523-1739.2011.01794.x/suppinfo

Chapter 4

Traits influencing vulnerability to predation

in New Zealand's endemic forest birds



Ship rat (*Rattus rattus*) approaching a New Zealand pigeon (*Hemiphaga novaeseelandiae*) nest

Photo: Nga Manu Images

Abstract

Understanding how vulnerable endemic taxa are to predation is clearly important for conservation management. In New Zealand, predation by introduced mammals such as rats and mustelids are widely recognised as the primary factor responsible for declines of New Zealand fauna. The aim of our study was to evaluate the vulnerability of New Zealand's surviving endemic forest bird species to impacts of introduced mammalian predators, and identify key life history attributes underlying this vulnerability. We measured range contraction following the introduction of exotic mammalian predators for twenty five endemic forest bird species using information on both pre-human and current distributions. We used Bayesian modelling techniques to analyse whether variation in range contraction was associated with life history traits potentially influencing species' predation vulnerability, while accounting for phylogenetic relatedness. Our results showed that the degree of range contraction varied greatly among species, with some species remaining in available forest habitat throughout most of their pre-human range, and others having disappeared completely from the main islands. Cavity nesting was the key trait associated with more extensive range decline, indicating that cavity nesting species are more vulnerable to predation than species that nest in more open sites. Some families experienced disproportionately greater range contraction than others, with range contraction most extensive for families Callaeidae (New Zealand wattlebirds) and Notiomystidae (hihi).

Introduction

Like many oceanic islands, New Zealand's long history of geographic isolation has resulted in a unique avifauna that evolved in the absence of mammalian predators. Since human arrival approximately 1000 years ago (Wilmshurst and Higham 2004), the New Zealand avifauna has undergone a major period of extinctions, losing 40-50% of species during this time (Holdaway 1989). It is generally agreed that these losses were caused by some combination of human hunting, habitat loss, competition for food, and predation by invasive introduced mammals such as rats (*Rattus* spp.) and mustelids (*Mustela* spp.). The species that remain face ongoing threats of habitat destruction, predation and competition for food (Holdaway 1989), and many of these taxa have either small or declining populations (Innes et al. 2010).

Assigning causal factors for population declines is challenging because their impacts often interact. For example, deforestation and food competition may both alter bird foraging behaviour, leading to increased predation (Innes et al. 2010). Nevertheless, identifying the major factor(s) causing declines has been the focus of extensive research, leading to general

acceptance that predation by introduced mammals is the primary factor responsible for both historic and current declines of New Zealand birds (King 1984, Holdaway 1989, Innes et al. 2010).

This vulnerability to predation-driven population decline is supported by the numerous studies demonstrating significant predation on extant New Zealand birds (e.g. Sanders and Maloney 2002, Robertson et al. 2011, Starling-Windhof et al. 2011). However, extant species differ in their vulnerability to predation, as evidenced by the rapid disappearance of some taxa from the mainland (North and South Islands) following the arrival of mammalian predators. These species (e.g. hihi, *Notiomystis cincta*) only avoided extinction by surviving on offshore island refuges free of ship rats (*Rattus rattus*) and mustelids, whereas other species (e.g. grey warbler, *Gerygone igata*) have remained relatively widespread and common on the mainland to the present day. Understanding how vulnerable endemic taxa are to predation is clearly important for conservation management, and is becoming increasingly pertinent with species previously extinct on the mainland now being considered for reintroduction to mainland sites with mammalian predators present at a range of densities (e.g. Armstrong and Davidson 2006, Richardson 2009).

Predation usually affects prey species by limiting survival and/or fecundity (Coté and Sutherland 1997), leading to a reduced capacity for population increase. Range contraction can be an important indicator of vulnerability to predation because the ultimate impact of predation is usually to limit prey species' ranges (Holt et al. 2011). Population density is normally highest towards the centre of a species' range and declines toward the boundaries, reflecting changes in the intrinsic rate of population increase (Guo et al. 2005). Range contraction therefore occurs if deterministic processes such as predation cause mortality rates to increase, so the intrinsic rate of population increase falls below zero near the edge of the range (Holt et al. 2005). If the intrinsic rate of increase falls and remains below zero throughout a species range, then the species will inevitably decline to extinction.

While predation is likely to be the main cause of range contraction in New Zealand's endemic birds, there may be a suite of factors contributing to declines of bird populations on New Zealand's mainland. Disease (Taylor et al. 2005), low genetic diversity (Jamieson et al. 2008) and competition for food (Beggs and Wilson 1991) have all been suggested to contribute to population declines, although there is no evidence that any of these factors have been the primary cause of decline of any New Zealand forest bird species (Innes et al. 2010). Deforestation has had a devastating impact on the amount of available forest habitat, with over 70% of original forest lost since human arrival (Ewers et al. 2006), in turn leading to the disappearance of most forest bird species from this modified landscape and many of the

remaining forest fragments. Although area requirements can be an important limiting factor for forest birds (for example, loss of genetic diversity in small populations can lead to increased extinction risk (Jamieson et al. 2008)), management can allow species that disappeared from the mainland to persist in relatively small forest areas if predators are absent (e.g. on 220 ha Tiritiri Matangi Island). Furthermore, all forest birds are continuing to decline inside the largest remaining forest tracts, together suggesting that area requirements are not a major driver of declines in existing forest (Innes et al. 2010). By far the most compelling evidence exists for predation by introduced mammals as the primary driver of extant forest bird declines and distributional changes since human arrival in New Zealand (Worthy and Holdaway 2002).

Predation by exotic predators has contributed to the decline of many island bird populations (Heath et al. 2008), and numerous studies have investigated life history traits that pre-dispose island endemics to extinction (e.g. Cassey 2001, Duncan and Blackburn 2004, Boyer 2008, Bromham et al. 2012). The aim of this study was to estimate the relative vulnerabilities of New Zealand's surviving endemic forest bird species to the impacts of introduced mammalian predators, and identify key life-history attributes underlying this variation. This firstly involved estimating distributional changes using information on both pre-human and current distributions to quantify species' vulnerability to predation. We then analysed whether variation in distributional changes was associated with life history traits potentially influencing species' predation vulnerability, while accounting for effects of phylogeny.

Methods

Distributional changes

We compiled data on pre-human and current distributions of twenty five extant terrestrial forest bird species endemic to New Zealand's mainland (North and South Islands) (Table 4.1). Forest birds were defined as obligate forest dwellers, i.e. species dependent on forest communities throughout their range and life-cycle (sensu Innes and Hay 1990). Our study focused on forest birds because mature native forest habitat could be clearly identified, allowing us to estimate range contraction over remaining forest areas. Available habitat for non-forest birds was difficult to ascertain due to extensive habitat modification, making it impossible to determine the extent of range contraction attributable to predation in un-forested areas. Species for which forest was not their primary habitat or forest was not used year-round (e.g. takahe, *Porphyrio hochstetteri*) were therefore excluded from our analysis.

Data on current distributions of these twenty five species were obtained from the Ornithological Society of New Zealand. These data were based on a survey of the distribution of New Zealand birds for the period 1999-2004 (Robertson et al. 2007), and consisted of grid square (10 x 10 km) references where each taxon had been recorded as present over that time.

We obtained information about species' pre-human distributions from a range of publications, including Lovegrove (1992), O'Donnell (1996), Wilson et al (1998), Worthy & Holdaway (2002), Heather & Robertson (2005) and Department of Conservation species recovery plans (http://www.doc.govt.nz). Expert judgement was sought if historical distributions could not be ascertained from published information.

We then measured mainland distributional changes for the twenty five endemic forest bird species using information on both pre-human and current distributions. The range of human-induced impacts potentially contributing to range contraction made it impossible to directly quantify the relationship between predation and distributional changes. However, we assumed that variation in distributional changes was primarily associated with predation by introduced mammals in light of the substantial evidence for predation as the primary cause of past and present declines. To control for forest loss, we analysed distributional changes across only those grid squares that currently include all or part of contiguous mature native forest tracts of at least 200 ha. Areas of mature native forest greater than 200 ha were identified using the LCDB2 database (downloaded from http://koordinates.com/layer/1072-land-cover-database-version-2-lcdb2/) in ArcGIS10. The LCDB2 database is a classification of land cover and land use for mainland New Zealand and surrounding near shore islands (Ministry for the Environment 2004).

1755 grid squares contained all or part of a contiguous native forest tract greater than 200 ha (810 in the North Island, 945 in the South Island). For most species, information on historical distributions of bird species indicated they were found throughout native forest in pre-human times, and for those species we assumed they would have historically been found in all forested grid squares on the island(s) where they occurred (i.e. 810, 945 or 1755 for species endemic to the North Island, South Island or both islands, respectively). Where available evidence indicated historical distributions were more restricted (e.g. great spotted kiwi, *Apteryx haastii* [L. Shepherd and A. Tennyson pers. comm.]), we assessed distributional changes across forested grid squares within those historic ranges. For the three species of brown kiwi (*Apteryx australis, A. mantelli, A. rowi*), species-specific historical distributions are poorly known because the species have only been resolved recently through genetic analysis (Shepherd and Lambert 2008, L. Shepherd pers. comm.) Therefore, the three species were treated as one taxon "brown kiwi" for the purpose of our analysis.

To evaluate distributional changes for each species we calculated the proportion of grid squares occupied in pre-human times that were still naturally occupied between 1999 and 2004. This required removing species records that were the consequence of translocation (http://rsg-oceania.squarespace.com/nz/). The proportion of historical range still occupied (*p.hr*) for each taxon is:

$$p.hr = \frac{N_{cr}}{N_{hr}}$$

where N_{cr} is the number of grid squares where the species was recorded between 1999 and 2004 (excluding records due to translocations) and N_{hr} is the number of grid squares occupied before human arrival in New Zealand. There is potential for N_{cr} (and therefore *p.hr*) to be underestimated if a species present in a grid was not detected. However, the surveyed grid squares encompassed a large area (100 km^2), which minimised the likelihood of non-detection events. The broad scale of our analysis also minimised any potential bias on *p.hr* arising from occasional non-detection events, providing confidence that *p.hr* is a reliable measure of range contraction on New Zealand's mainland.

Explanatory variables

We compiled data on species traits that could potentially affect range contraction due to vulnerability to introduced predators: body size, flightlessness, ground foraging, nest height, nesting period, incubating sex, cavity nesting, productivity (number of clutches and clutch size), and generation length. These trait data were primarily sourced from Heather & Robertson (2005). Where a range of values was provided, such as for clutch size, we used the midpoint between the minimum and maximum. Little information was available for the orange-fronted parakeet (*Cyanoramphus malherbi*), so this species was excluded from further analyses.

Flightlessness and large body size have both been associated with high extinction risk in New Zealand bird species (Cassey 2001, Bromham et al. 2012). We therefore categorised birds as either flightless or able to fly (including poor fliers), and included average adult female body weight (g) in our analysis. We also included a measure of sexual size dimorphism, calculated as the ratio of average weight of the heavier sex to the average weight of the lighter sex, as some studies have suggested that sexual selection can result in a greater likelihood of population extinction (Morrow and Pitcher 2003).

Nest predation is a known cause of bird population declines (Smith et al. 2011), so the amount of time spent nesting could influence how vulnerable species are to predation. We therefore included nesting period as a factor in our analysis, calculated as the total number of days from

start of incubation to fledging. Predation of nesting females in particular has been associated with population declines of New Zealand birds (Wilson et al. 1998, Parlato and Armstrong 2012 [Chapter 3]) but for some species males undertake all (or part) of nest incubation, potentially reducing predation pressure on females. We therefore categorised species based on whether incubation was carried out by males or females. Cavity nesting is another factor identified as increasing species' vulnerability to predation, primarily because incubating adults are unable to escape (O'Donnell 1996b). We therefore recorded whether species primarily nested in cavities (including burrows) or more open sites. We classified grey warblers as nesting in more open sites because although they build an enclosed nest, the nest hangs from a twig at the top rather than being located within a cavity. Ground nesting has also been associated with increased predation vulnerability (Duncan and Blackburn 2004, Van Turnhout et al. 2010), so species were categorised according to whether or not they usually nest on the ground.

Similarly, ground foraging could also increase species' risk of predation by increasing exposure to introduced predators compared to species that primarily forage in the canopy. We therefore categorised species according to whether they commonly use the forest floor to forage. In the face of predation, the resilience of a species may be enhanced by higher productivity (Holdaway 1999), so we also included data on average number of clutches and average clutch size, as well as generation time (average female age at first breeding).

Modelling

Given the number of variables potentially associated with range contraction, we initially examined these variables for multicollinearity. Multicollinearity occurs when two or more explanatory variables are highly correlated, and can cause large variability in the estimation of parameters (El-Fallah and El-Sallam 2011). Variables with a correlation coefficient (r) ≥ 0.7 were considered highly correlated, and no more than one of these variables were fit to the data simultaneously. Highly correlated variables were flightlessness, female weight, ground nesting, nesting period and generation length.

The data (*p.hr*) were logit transformed after adding 0.01 to enable transformation of zero values (the analysis was also repeated using constants of 0.001 and 0.0001, giving similar results). We used generalised linear models fitted in WinBUGS (version 1.4) using Markov chain Monte Carlo (MCMC) techniques (Spiegelhalter et al. 2003). Candidate models were compared using the Deviance Information Criterion (DIC). All models had uninformative priors (normal distributions with mean 0 and precision 10^{-6} for main parameters, and uniform distributions from 0 to 100 for hyperparameters) and two chains were run for 100,000 samples with the first

10,000 samples discarded as burn-in. Convergence was checked with the Brooks-Gelman-Rubin (BGR) diagnostic tool and by examining the chains.

We initially created a set of candidate full models (Set 1, Table 4.2) that included an intercept and fixed effects of ground foraging, cavity nesting, incubating sex, productivity, weight ratio and β_i, where β_i is one of the five correlated variables (flightlessness, female weight (log transformed), ground nesting, nesting period, generation length); giving five alternative full models. To fit these models, each transformed *p.hr* value was treated as sampled from a univariate normal distribution, with a mean (μ) and precision (τ_{err}), where μ was determined by the fixed effects in the model. We sequentially substituted each of the correlated variables and assessed which of the five models had the lowest DIC. Because closely related lineages will share life-history traits affecting their vulnerability to predation, it is important to control for potential confounding effects of relatedness (Bromham et al. 2012). Lack of independence can be explicitly accounted for with appropriate random effects (Williams et al. 2002). We therefore accounted for phylogenetic non-independence among species by adding a random effect of family to each model. The random effect was assumed to be normally distributed with mean 0 and precision (τ_{fam}). However, including the random effect of family in full models led to convergence problems, so random effects could not be used for full model comparison.

As an alternative to incorporating random effects of family, we also took into account more complex phylogenetic relationships among species by constructing a variance-covariance matrix using Lanfear and Bromham's (2011) phylogeny of New Zealand birds, where the variance is the branch length from the root to the tip, and the covariance is the branch length from the root to the most recent common ancestor (de Villemereuil et al. 2012). Although cladograms do not provide absolute branch lengths (i.e. they do not represent time), the branch lengths are internally consistent and provide a useful measure of evolutionary relationships among species. We created an alternative set of models (Set 2, Table 4.2) where similarity among species was modelled using the variance-covariance matrix (Σ) reflecting the species' phylogenetic relationships. To fit the models, each *p.hr* value was sampled from a multivariate normal distribution, with a mean (μ) and multi-dimensional precision (T) that was obtained by multiplying the inverse of the variance-covariance matrix (Σ^{-1}) with the residual precision (τ_{err}) (de Villemereuil et al. 2012).

After finding the best full model (model with the lowest DIC), we then simplified the model by removing all effects with credible intervals that included zero. We ran this simpler model with and without the random effect of family, and DIC values were used to identify the best model.

Results

The proportion of historical range still occupied across currently forested grid squares on New Zealand's mainland varied greatly among species (Table 4.1). Some species have undergone little range contraction, whereas others have gone extinct on the mainland (*p.hr* ranged from 0 to 0.92).

Table 4.1 Range contraction from pre-human to present day for twenty five forest bird species endemic to New Zealand's mainland (North and South Islands). The three species of brown kiwi have been grouped into one brown kiwi taxon.

Family	Species	Endemic to[a]	Proportion of forested mainland range still occupied[b]
Acanthisittidae	Rifleman (*Acanthisitta chloris*)	NI, SI	0.34
Acanthizidae	Grey warbler (*Gerygone igata*)	NI, SI	0.92
Apterygidae	Little spotted kiwi (*Apteryx owenii*)	NI, SI	0
	Brown kiwi, all species (*Apteryx australis, A. mantelli, A.rowi*)	NI, SI	0.11
	Great spotted kiwi (*Apteryx haastii*)	SI	0.21
Callaeidae	South Island saddleback (*Philesturnus carunculatus*)	SI	0
	North Island saddleback (*Philesturnus rufusater*)	NI	0
	North Island kokako (*Callaeas wilsoni*)	NI	0.02
Columbidae	New Zealand pigeon (*Hemiphaga novaeseelandiae*)	NI, SI	0.70
Meliphagidae	Tui (*Prosthemadera novaeseelandiae*)	NI, SI	0.73
	Bellbird (*Anthornis melanura*)	NI, SI	0.80
Nestoridae	Kaka (*Nestor meridionalis*)	NI, SI	0.26
Notiomystidae	Hihi (*Notiomystis cincta*)	NI	0
Pachycephalidae	Mohua (*Mohoua ochrocephala*)	SI	0.10
	Whitehead (*Mohoua albicilla*)	NI	0.44
	Brown creeper (*Mohoua novaeseelandiae*)	SI	0.59
Petroicidae	North Island robin (*Petroica longipes*)	NI	0.28
	South Island robin (*Petroica australis*)	SI	0.37
	Tomtit (*Petroica macrocephala*)	NI, SI	0.70
Psittacidae	Orange fronted parakeet (*Cyanoramphus malherbi*)	NI, SI	0.002
	Red crowned parakeet (*Cyanoramphus novaezelandiae*)	NI, SI	0.02
	Yellow crowned parakeet (*Cyanoramphus auriceps*)	NI, SI	0.12
Strigopidae	Kakapo (*Strigops habroptilus*)	NI, SI	0

[a]NI = North Island, SI = South Island.

[b]Proportion of 10 x 10 km grid squares occupied out of those containing all or part of a contiguous native forest tract >200 ha. Current occupancy is based on recorded presence between 1999 and 2004 (Robertson et al. 2007), excluding occupancy of grid squares due to translocation.

Full models that excluded the phylogenetic matrix (Set 1, Table 4.2) were better supported, lowering DIC by at least 8.6 relative to models that included the matrix (Set 2, Table 4.2). Parameter estimates from the best full model indicated that cavity nesting was the only trait that was clearly associated with proportionate range contraction (95% Credible Interval (CI) did not include zero). This inference was further supported by examining parameter estimates of all candidate full models, i.e. cavity nesting was always the only trait with a clear effect.

Including the effect of cavity nesting in a simplified model (i.e. model with all other explanatory variables removed) resulted in slightly better predictive capability than the best full model (DIC lowered by 0.94). Adding the random effect of family to this simplified model provided a substantial further improvement (ΔDIC=10.68), resulting in the lowest DIC and the best model overall (Table 4.2). Under the best model, the proportion of historical range still occupied is estimated by:

$$\text{logit}(p.hr) = \alpha + \beta_{cn} cn + \text{re}_{fam}$$

where *cn* is cavity nesting (1= cavity nesting, 0 = non-cavity nesting), α is the intercept, β_{cn} is the slope of the relationship, and re_{fam} is the random effect of family. Distributional changes were strongly linked to cavity nesting habits, with cavity nesting species experiencing more extensive range declines than species nesting in more open sites (Table 4.3). The substantial model improvement associated with including the family random effect indicated that distributional changes are not independent of phylogeny. After accounting for the effect of cavity nesting, species in families Callaeidae (kokako, North and South Island saddleback) and Notiomystidae (hihi) experienced the greatest range contraction, whereas families Acanthizidae (grey warbler) and Acanthisittidae (rifleman) experienced the least (Table 4.3).

Table 4.2 Comparison of vulnerability models fitted to data on distributional changes for twenty four New Zealand forest bird species, ranked from best to worst. Models in Set 2 include an inverse variance-covariance matrix based on species' phylogenetic relatedness.

	Model[a]	*pD*[b]	DIC[c]	ΔDIC[d]
	$\text{logit}(p.hr) = \alpha + \beta_{cn}cn + \text{re}_{fam}$	10.799	80.433	0
	$\text{logit}(p.hr) = \alpha + \beta_{cn}cn$	3.111	91.114	10.68
Set 1	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{nh}nh$	8.462	92.057	11.624
No matrix	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{fl}fl$	8.487	92.582	12.149
	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{fw}\log(fw)$	8.487	92.783	12.35
	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{gl}age$	8.486	93.694	13.261
	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{np}np$	8.487	93.856	13.423
	$\text{logit}(p.hr) = \alpha + \beta_{cn}cn$	3.014	99.787	19.354
	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{fl}fl$	8.333	100.685	20.252
Set 2	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{nh}nh$	8.325	102.915	22.482
Matrix	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{fw}\log(fw)$	8.412	105.606	25.173
	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{np}np$	8.304	105.84	25.407
	$\text{logit}(p.hr) = \alpha + \beta_{gf}gf + \beta_{cn}cn + \beta_{is}sex + \beta_{pr}nc*ne + \beta_{wr}wr + \beta_{gl}age$	8.344	106.575	26.142

[a] *p.hr*, proportion of forested mainland range still occupied; α, intercept term; β_{cn}, effect of cavity nesting (*cn* = 1 if primarily nest in cavities or burrows, *cn* = 0 if do not primarily nest in cavities or burrows); β_{gf}, effect of ground foraging (*gf* = 1 if use forest floor to forage, *gf* = 0 if do not forage on forest floor); β_{is}, effect of incubating sex (*sex* = 1 if male, *sex* = 0 if female); β_{pr}, effect of productivity (mean number of clutches per breeding season (*nc*) x mean number of eggs per clutch (*ne*)); β_{wr}, effect of weight ratio (*wr*, heavier sex : lighter sex); β_{nh}, effect of nest height (*nh* = 1 if nest above the ground, *nh* = 0 if nest on the ground); β_{fl}, effect of flightlessness (*fl* = 1 if flightless, *fl* = 0 if able to fly); β_{fw}, effect of female weight (*fw*), β_{gl}, effect of generation length (*age*, age at first breeding); β_{np}, effect of nesting period (*np*), re_{fam}, random effect among taxonomic families.

[b] effective number of parameters (mean of the posterior deviance minus the mean of the posterior distribution).

[c] Deviance Information Criterion, indicating the model's level of support.

[d] difference in DIC from that of the best model.

Table 4.3 Means and credible limits (CL) for parameters in best model (top model in Table 4.2) fitted to data on distributional changes for twenty four New Zealand forest bird species

Node[a]	Mean	SD	2.5% CL	Median	97.5% CL
α	0.090	0.699	-1.344	0.103	1.438
β_{cn}	-2.640	0.819	-4.255	-2.640	-1.033
$re_{Acanthizidae}$	1.389	1.177	-0.603	1.320	3.841
$re_{Acanthisittidae}$	1.000	1.020	-0.830	0.945	3.115
$re_{Nestoridae}$	0.800	0.985	-1.017	0.741	2.855
$re_{Meliphagidae}$	0.797	0.920	-0.874	0.742	2.732
$re_{Columbidae}$	0.468	0.993	-1.402	0.395	2.559
$re_{Pachycephalidae}$	0.118	0.746	-1.369	0.100	1.628
$re_{Apterygidae}$	-0.097	0.786	-1.735	-0.067	1.426
$re_{Psittacidae}$	-0.142	0.838	-1.885	-0.105	1.485
$re_{Petroicidae}$	-0.159	0.805	-1.784	-0.144	1.468
$re_{Strigopidae}$	-1.162	1.112	-3.498	-1.087	0.748
$re_{Notiomystidae}$	-1.163	1.112	-3.505	-1.091	0.753
$re_{Callaeidae}$	-1.878	0.978	-3.744	-1.918	0.012

[a] α, intercept term; β_{cn}, effect of cavity nesting (*cn* = 1 if primarily nest in cavities or burrows, *cn* = 0 if do not primarily nest in cavities or burrows); re_{fam}, random effect of family (*fam)* on proportion of historical range still occupied.

Discussion

With global biodiversity declining at a startling rate (Butchart et al. 2010), understanding the key factors causing population declines is crucial for developing effective species recovery strategies. Oceanic islands are highly susceptible to invasion of continental mammalian predators, with *Rattus* species having reached 82% of the world's islands or island groups (Brockie et al. 1988). Island avifaunas that evolved with few or no mammalian predators are well recognised for their vulnerability to predation (Boyer 2010), and introduction of

mammalian predators has been a predominant cause of bird extinctions on oceanic islands worldwide (Blackburn et al. 2004).

In New Zealand, predation by introduced mammals has been identified as the primary cause of decline in extant forest bird species (Innes et al. 2010). Mainland range contraction associated with these declines in forested areas >200 ha were found to vary greatly among species, with some species remaining in available forest habitat throughout most of their pre-human range, and others disappearing completely from the main islands. Because any measure of range contraction is dependent on the scale of resolution used, the full extent of range contraction in forested areas is likely to have been underestimated for the twenty species still present on the mainland because the relatively broad scale presence/absence data used to estimate distributional changes did not capture species' actual area of occupancy. Predator control has also been implemented in many forested areas on New Zealand's mainland in recent years (Saunders and Norton 2001), and this in turn may have reduced the amount of range contraction that would have otherwise been observed in the absence of this predator management.

Cavity nesting was the key attribute associated with more extensive range contraction, indicating that cavity nesting species are more vulnerable to predation than species that nest in more open sites. The vulnerability to predation of cavity nesting species is well recognised (e.g. Elliott 1996, Lovegrove 1996a, O'Donnell 1996b), arising primarily because incubating adults are confined, making them less able to escape or defend themselves against nest predators. The association between cavity nesting and range contraction in mainland forest could also be associated with past habitat modification within existing forest areas. Selective logging of large mature trees would have reduced availability of suitable nest sites (e.g. Spurr 1987), potentially increasing competition for nest sites among cavity nesting species. However, there is no evidence to suggest that interspecific competition for nest sites has been the major cause of declines (Innes et al. 2010), and predation has been found to constrain some cavity nesting species at levels below that at which nest sites would be limiting (Elliott et al. 1996).

The importance of cavity nesting identified in our analysis differs from the results of other studies examining correlates with geographical distribution or extinction threat for extant New Zealand land birds. For example, ground nesting and smaller average clutch sizes have been associated with current extinction threat (Bromham et al. 2012), and distributions of endemic species were found to be significantly correlated with incubation time, body size and habitat generalism (Cassey 2001). However, these studies included non-forest birds in their analyses, so the discrepancy from our results is not necessarily unexpected. Further, they did not consider cavity nesting as an explanatory variable. If we remove cavity nesting from our model, similarities with these past results emerge, with ground nesting and longer nesting periods both

associated with more extensive range declines (β_{nh} = 4.91, 95% CI = 1.22,8.61; β_{np} = -0.06, 95% CI = -0.11,-0.003, respectively).

Our results indicate that the vulnerability to predation of extant New Zealand forest bird species is not independent of species relatedness, with some families experiencing disproportionately greater range contraction than others, even after the effect of cavity nesting is accounted for. Range contraction was most extensive for families Callaeidae (kokako, North and South Island saddleback) and Notiomystidae (hihi), followed by Strigopidae (kakapo) and Petroicidae (tomtit, North and South Island robins). One possible explanation for why these families inhabit disproportionately less of their historical range is their limited dispersal ability. Saddlebacks and kakapo, in particular, are noted for being poor dispersers (e.g. Spurr 1981, Lovegrove 1996b); while movements of robins and kokako are inhibited by gaps in forest cover (Molles et al. 2008, Richard and Armstrong 2010). The dispersal abilities of hihi and tomtit are not well known, although there are examples of tomtits dispersing long distances, including an individual that crossed at least 3.5 km of open water (Parker et al. 2004), perhaps helping to explain why tomtits still occupy a far greater proportion of their historic range than the other species (Table 4.1). Dispersal can inflate the size of a species' range if individuals are able to recolonise areas from which they previously disappeared or if recurrent immigration from source populations can maintain populations at sites with negative population growth (sink habitats) (Holt et al. 2005). Nevertheless, the emigration of individuals from source patches can in turn increase local extinction risk (Hanski 1998) so the implications of dispersal are far from straightforward. Information on the dispersal capability of most species in our analysis was limited or lacking. Gaining more knowledge about species' propensity to disperse would enable further investigation into how dispersal affects the resilience of endemic forest birds to predation and other threats.

Similarly, there are a number of other factors that we consider warrant further research to improve our understanding of their influence on prey species' vulnerability. For example, some non-endemic cavity nesting species in New Zealand (such as morepork owls, *Ninox novaeseelandiae*) are widespread throughout most remaining forested areas, indicating they possess other attributes making them less susceptible to predation. Behavioural characteristics such as nest site defence may be important for reducing predation on eggs, chicks and brooding adults. Bird odours are rarely considered (Hagelin and Jones 2007) but are likely to affect how conspicuous species are to mammalian predators. We did not include these variables in our current analysis due to inconsistent (nest defence) and limited (bird odour) available data, but our model could easily be updated if more data become available in the future. Also linked to vulnerability of prey species are the hunting strategies used by predators, for example, the extent

to which different predator species use visual, auditory and/or olfactory cues, which in turn will have further implications for how perceptible bird species are to their predators.

Introduced predatory mammals have had a devastating effect on island avifauna worldwide (Blackburn et al. 2005), and New Zealand is no exception. Understanding how vulnerable endemic taxa are to predation, and the underlying reasons for this vulnerability, is important for effective conservation management in these ecosystems. We present a novel approach for estimating the impacts of introduced mammalian predators on New Zealand's surviving endemic forest bird species. The model we developed provides valuable insight into life history traits influencing species' vulnerability to predation, while accounting for effects of phylogeny, and is a useful framework that can be readily adapted to other systems or updated as more data become available in the future.

Chapter 5

A multi-species approach for predicting reintroduction outcomes



North Island saddleback (*Philesturnus rufusater*). Photo: Paul Gibson

Abstract

Predicting reintroduction outcomes before populations are released is inherently challenging. It becomes even more difficult when the species being considered for reintroduction no longer co-exists with the identified threats in any location. However, data from other projects and species can potentially be used to make predictions under these circumstances. I present an integrated Bayesian modelling approach for predicting growth of a reintroduced population at a range of predator densities when the candidate species for reintroduction has never been observed in the presence of that predator. North Island saddlebacks were extirpated from mainland New Zealand following the arrival of exotic mammalian predators but are now being considered for reintroduction to mainland sites with intensive predator control, creating an ideal opportunity to develop this approach. I initially construct a model using data from multiple North Island saddleback (*Philesturnus rufusater*) reintroductions to predator-free sites, and predict population growth at a new predator-free site while accounting for random variation in vital rates among sites. I then predict population growth at different rat tracking rates (an index of rat density) by incorporating a previously modelled relationship between rat tracking and vital rates of reintroduced North Island robins (*Petroica longipes*). I adjust the strength of the relationship to account for the greater vulnerability of saddlebacks to predation using information on historical declines of both species. Model predictions indicate that a saddleback population reintroduced to a new site free of mammalian predators would be expected to grow (assuming no emigration). My results also suggest that saddlebacks could be successfully reintroduced to mainland sites with very low rat densities. The model I developed can be updated if population data in the presence of predators become available through mainland reintroductions in the future, and the updated model can in turn guide further reintroductions. This study therefore represents an initial step towards improving our understanding of how highly vulnerable species will fare in new situations with key threats present, providing a useful foundation on which knowledge can be built.

Introduction

Reintroduction is a frequently used conservation tool undertaken to re-establish species within their historical ranges, (Seddon et al. 2007, IUCN/SSC 2013). A prerequisite for any successful reintroduction is that the factors responsible for original extirpation must be identified and reversed (Kleiman 1989, Veitch 1994). Management at reintroduction sites therefore usually involves measures to eliminate or control the factors responsible for species extirpation, thereby enabling population persistence. However, assessing the intensity of management necessary for

a reintroduced population to persist is often difficult before release, given there are usually no data available for the species at the site (Armstrong and Seddon 2008). Recent advances in population modelling through the use of hierarchical models (King et al. 2010) have made it possible to make more informed *a priori* assessments for candidate reintroduction sites, whereby data collected from other reintroduction sites are used to fit models with random effects. This allows random variation among sites to be accounted for when evaluating what is required for a reintroduced population to persist (Parlato and Armstrong 2012 [Chapter 3]).

However, an even greater challenge is presented if the species being considered for reintroduction no longer co-exists with the identified threats in any location, making it impossible to use data from other sites to make inferences about the level of management necessary to allow persistence. This situation has arisen in New Zealand, where a number of species disappeared from the mainland (North and South Islands) following the arrival of exotic mammalian predators, but survived on mammal-free offshore islands (Worthy and Holdaway 2002, Innes et al. 2010). Some of these species have since been successfully reintroduced to mainland sites surrounded by predator-proof fencing (e.g. tuatara (*Sphenodon punctatus*), little spotted kiwi (*Apteryx owenii*), North Island saddleback (*Philesturnus rufusater*)), suggesting that future reintroductions to similar predator-free sites will be successful. In recent years, intensive predator control has also been implemented at numerous unfenced mainland sites (Saunders and Norton 2001), increasing the potential for reintroducing mainland extirpated species to those locations. However, these reintroductions are inherently risky given ongoing reinvasion by predators (Armstrong and Davidson 2006) and the lack of available information about the amount of predation by exotic mammals that mainland populations can withstand. There have been two reintroductions of mainland extirpated species to unfenced sites on New Zealand's mainland to date, with saddlebacks reintroduced to Boundary Stream Mainland Island in 2004 (Sullivan 2006) and hihi (*Notiomystis cincta*) reintroduced to Ark in the Park in 2007 (Richardson 2009). Both of these populations are now extinct.

It is therefore important that reliable models are developed to predict the level of predator control necessary for mainland populations to persist (Armstrong and Davidson 2006). An initial attempt to develop a prior model for mainland reintroductions was made by Armstrong & Davidson (2006) who made predictions for the saddleback reintroduction to Boundary Stream Mainland Island in 2004. However, projections of saddleback population growth in the presence of predators were dependent on guesses of how vulnerable saddlebacks are to predation. In addition, model projections were based on data from individual case studies, so case-by-case variation could not be accounted for.

This study aims to build on the concepts used by Armstrong & Davidson (2006) to develop a framework for modelling outcomes of mainland reintroductions. Here I present an integrated Bayesian modelling approach for predicting growth of reintroduced populations at a range of predator densities using post-release information from multiple sites and species. Saddlebacks were considered an ideal species for developing my approach because they were extirpated from the New Zealand mainland following the arrival of exotic mammalian predators, data from multiple reintroductions to predator-free sites were available, and they have previously been considered for reintroduction to unfenced mainland sites. I initially construct a model using published vital rate estimates from multiple saddleback reintroductions to predator-free sites to predict population growth at a new predator-free site, while accounting for unexplained variation among sites. I then predict population growth at different rat tracking rates (an index of rat density) by incorporating a previously modelled relationship between rat tracking and vital rates of reintroduced North Island robins (*Petroica longipes*). I adjust the strength of the relationship to account for the greater vulnerability of saddlebacks to predation using information on historical declines of both species. I then further extend the model to incorporate site-specific effects on vital rates, enabling conditions at particular candidate reintroduction sites to be accounted for. The resulting model is used to predict growth of a saddleback population reintroduced to Boundary Stream Mainland Island at a range of rat tracking rates.

Methods

Study species

The North Island saddleback is a medium size (c. 25 cm) endemic New Zealand passerine species, formerly found throughout North Island forests. North Island saddlebacks and South Island saddlebacks (*P. carunculatus*) both declined during the 1800s after European settlement, and these declines are attributed to the introduction of mammalian predators, particularly rats and stoats. North Island saddlebacks persisted on the mainland until after 1860, but had almost disappeared by 1890 (Williams 1976) and by 1900 only survived on offshore Hen Island (Lovegrove 1996a). This extinction has been primarily attributed to ship rats (*Rattus rattus*), which spread through the North Island after 1860 (Lovegrove 1996a). North Island saddlebacks were already rare by the time mustelids were introduced in the 1880s (King 1995).

North Island robins are a small (c. 18 cm) forest-dwelling passerine endemic to New Zealand. Similarly to saddlebacks, the North Island robin and South Island robin (*P. australis*) were both formerly widespread but declined following the introduction of mammalian predators. Natural populations are now restricted to native forest remnants and exotic plantations in the central

North Island, as well as some offshore islands (Higgins and Peter 2002). Robin populations are limited by ship rats (e.g. Brown 1997, Armstrong et al. 2006a, Parlato and Armstrong 2012 [Chapter 3]), and may also be limited by other introduced mammals such as stoats. North Island robins are usually the first species reintroduced to unfenced mainland sites and have been identified as a useful species for evaluating the effectiveness of predator control before reintroductions of more vulnerable species are contemplated (Armstrong 2000, Ewen and Armstrong 2007).

Saddlebacks and robins are both territorial species that form monogamous pairs. Nesting is usually from September to January for robins and October to February for saddlebacks, but the saddleback breeding season can extend from August to May at some sites (Heather and Robertson 2005). For both species, incubation and brooding is done solely by females, and pairs can raise up to four broods of 1-4 chicks in a season (Heather and Robertson 2005). Offspring breed in their first year at around 9 months of age (Armstrong et al. 2002). Saddlebacks nest in cavities, often close to the ground, whereas robins build a cup-shaped nest usually 1-11 m off the ground (Heather and Robertson 2005).

Data

I used published estimates of survival and fecundity for three reintroduced saddleback populations (Gedir et al. 2013) to develop a model for predicting outcomes of saddleback reintroductions to mainland sites with mammalian predators present. All three previous reintroduction sites were free of ship rats, cats and stoats, so data were lacking on how saddleback vital rates would change in the presence of these predators. Tiritiri Matangi Island is a 220 ha island (off the north-east coast of the North Island) where 24 saddlebacks were released in 1984, Mokoia Island is a 135 ha island (in Lake Rotorua) where 36 saddlebacks were released in 1992, and Bushy Park is an 87 ha mainland reserve (in the central North Island) where 34 saddlebacks were released in 2006. Bushy Park is enclosed by a predator-proof fence that was built in 2005. The survival and fecundity estimates used were based on 8, 5 and 3 years of monitoring data from Tiritiri Matangi, Mokoia and Bushy Park, respectively (Gedir et al. 2013).

I used a previously modelled relationship between the finite rate of increase (λ) of North Island robins and rat tracking rates based on data from 10 robin reintroductions to mainland sites (Parlato and Armstrong 2012 [Chapter 3]) to infer the relationship between predator levels and saddleback population growth. Rat tracking rate is the estimated probability that a baited tunnel will be passed through by one or more rats in 24 hours, and is used throughout New Zealand to monitor the effectiveness of rat control (see Parlato and Armstrong 2012 [Chapter 3]). Data on how robin λ changes as a function of predator control is a useful surrogate for inferring that

relationship for saddlebacks because both species are vulnerable to rats and stoats, and they share similar behavioural traits such as ground foraging and females alone carrying out incubation and brooding (Armstrong and Davidson 2006). Although predation by introduced mammals is considered the primary cause of saddleback (Hooson and Jamieson 2003) and robin (e.g. Brown 1997) declines in North Island forests, these species clearly differ in their vulnerability to the impacts of mammalian predators – saddlebacks disappeared within 40 years after ship rats arrived whereas robins have persisted for more than 150. To account for this, I used information on historical declines to estimate the relative vulnerability of saddlebacks (v) and used this parameter to adjust the strength of the rat tracking effect on saddleback λ (*sensu* Armstrong and Davidson 2006) (see modelling section below).

Modelling

Fecundity and survival in the absence of rats

I used WinBUGS 1.4 (Spiegelhalter et al. 2003) to develop a model for predicting saddleback population growth at a range of rat densities. This firstly involved using survival and fecundity estimates from the three rat-free sites to generate distributions for mean fecundity and annual survival probability for a new rat-free site, while accounting for unexplained site-to-site variation in vital rates. I always used uninformative priors (mean 0, precision 10^{-6}) unless otherwise specified. Models were run with two chains for 100,000 samples with the first 10,000 samples discarded as burn-in. Convergence was checked using the Brooks-Gelmin-Rubin (BGR) diagnostic tool and by visually examining the chains. I initially generated site-specific distributions for mean fecundity and survival probability for each site on log and logit scales, respectively, using means (μ) and precisions (τ) estimated by Gedir et al. (2013). Survival and fecundity models included fixed effects of age (juveniles or adults for survival; first year or older for fecundity, with effects constrained to be positive), following the model structure used by Gedir et al. (2013). I did not include effects of density on survival or fecundity because reintroduced populations are initially at low densities and density dependence will not be important until the most fundamental requirement for reintroduction success has been met, i.e., that the population grows. Site-specific survival and fecundity estimates were then used to estimate mean survival and fecundity across sites. I included site random effects to account for random variation in vital rates among sites, which I assumed were normally distributed, with mean 0 and standard deviation (SD) drawn from a uniform distribution. The uniform distribution was constrained to be between 0 and 1 because upper 95% credible limits (CL) for SDs estimating variation among sites based on robin data were never higher than 0.6, and some constraint was necessary because there were only three sites.

Population growth

Mean survival and fecundity estimates among sites were then used to estimate λ for a saddleback population reintroduced to a new rat-free site. Saddleback fecundity differs between first-year and older females (lower for first-year birds) (Armstrong et al 2002, Gedir et al 2013) so I calculated λ from the Leslie matrix:

$$\begin{bmatrix} 0.5s_j f_1 & 0.5s_j f_{2+} \\ s_a & s_a \end{bmatrix}$$

where s_j is the probability that a fledgling will survive 9 months to the breeding season, 0.5 is the probability that a surviving fledgling will be female (Armstrong et al. 2002), f_1 is the mean number of fledglings per first-year female, f_{2+} is the mean number of fledglings per older female, and s_a is the probability of an adult female surviving one year. λ is the dominant eigenvalue of the matrix (Akçakaya et al. 1999) and was obtained using the EigVal function from the PopTools add-in in Microsoft Excel. To account for uncertainty in parameter estimates, I obtained multiple values of λ using the "coda" output in WinBUGs for 1000 samples taken after model convergence to estimate λ standard deviation.

I then modelled the effect of rat tracking rates on saddleback λ (λ_s), based on the estimated effects of rat tracking on robin λ (λ_r). The model took a log-linear form because fecundity and survival of prey (used to estimate λ) and tracking tunnel "survival" (complement of rat tracking rate) are all expected to have a power relationship with predator density (Armstrong et al. 2006b, Parlato and Armstrong 2012 [Chapter 3]). However, differences between the effects of tunnel survival on survival and fecundity can break down the linearity of the relationship. Linearity was tested by allowing the effects of tunnel survival on fecundity and survival to differ based on the relative effects of tunnel survival on robin vital rates (Parlato and Armstrong 2012 [Chapter 3]) as it is impossible to estimate these effects for saddlebacks in the absence of data. The relationship between the natural logarithms of λ_s and tunnel survival remained approximately linear so the log-linear relationship was considered reasonable. The relationship between λ_s and tunnel survival therefore took the form:

$$\ln(\lambda_s) = \ln(\alpha_s) + v\beta_{ts}\ln(p) \qquad \text{Eqn. 1}$$

where α_s is the intercept (finite rate of population increase for saddlebacks when there are no rats), p is tunnel survival, β_{ts} is the effect of tunnel survival on robin population growth, and v is a parameter accounting for differences in vulnerability between saddlebacks and robins (sensu Armstrong and Davidson 2006).

β_{ts} was estimated using outputs from the model developed by Parlato & Armstrong (2012 [Chapter 3]), which allowed λ_r to be estimated for an average reintroduction site at a range of *p* values. I estimated the effect of tunnel survival on λ_r using the model:

$$\ln(\lambda_r) = \ln(\alpha_r) + \beta_{ts}\ln(p) \qquad \text{Eqn. 2}$$

where α_r is the intercept (finite rate of increase for robins when there are no rats) and β_{ts} is the effect of tunnel survival (*p*) on λ_r.

Site-specific predictions

In addition to predicting growth of a saddleback population reintroduced to a random new site, I also made site-specific predictions for Boundary Stream Mainland Island (Boundary Stream), a reserve considered for saddleback reintroduction in the past, and where North Island robins had previously been reintroduced. This allowed me to incorporate site-specific effects on robin survival and fecundity into saddleback population growth projections, as saddleback vital rates might be expected to respond similarly due to shared life history traits (e.g. both species are primarily insectivorous).

Boundary Stream is an 800 ha forest reserve in the North Island's Hawke's Bay. Intensive predator management has been in place since 1996, with poison bait stations at 150 m intervals throughout the reserve (100 m around perimeter) as well as traps to control cats and mustelids (Department of Conservation 1999). This intensive management meant Boundary Stream was considered suitable for reintroduction of threatened species (Sullivan 2006), leading to the release of 28 North Island robins in 1998. Parlato & Armstrong (2012 [Chapter 3]) modelled survival and fecundity data from the Boundary Stream robin population as well as data collected from 9 other robin reintroduction sites, allowing random site effects on vital rates to be estimated (i.e. variation among sites due to unknown factors). I therefore added the Boundary Stream site effects estimated for robin survival and fecundity to models that estimated mean saddleback survival and fecundity among sites. I did not include a site effect on juvenile saddleback survival, as the estimated site effect for juvenile robins accounted for differences in emigration probability associated with connectivity to other forest. It was unknown whether juvenile saddlebacks would be similarly affected by connectivity given that saddlebacks have poor dispersal capabilities (Hooson and Jamieson 2003) due to being capable of only a few metres of sustained flight (Merton 1975).

Mean saddleback survival and fecundity estimates that incorporated site-specific effects were then used to calculate λ_s at a range of rat tracking rates for a saddleback population reintroduced to Boundary Stream.

Vulnerability to predation (v)

Equations 1 and 2 use natural logarithms of λ and *p* to give a linear relationship for the effect of rat tracking on the finite rate of population increase, with the strength of the relationship determined by the effect of tunnel survival on λ_r ($ß_{ts}$) and the relative vulnerability of saddlebacks and robins to rat predation (*v*, Equation 1). Estimation of *v* therefore requires some understanding of the relative effect of rats on saddleback population growth compared to robin population growth. In the absence of data on how saddleback vital rates are affected by ship rats, I developed an approach using information on historical declines following arrival of ship rats on the North Island to evaluate the relative effect of rats on population growth of saddlebacks and robins. For notational efficiency, I refer to the intrinsic population growth rate in continuous time (*r*), which is the equivalent of ln(λ) in discrete time.

Whether a population grows or declines is dependent on its intrinsic growth rate. In the absence of stochasticity, a population will grow if $r > 0$ ($\lambda > 1$), remain stable if $r = 0$ ($\lambda = 1$), or decline if $r < 0$ ($\lambda < 1$), as shown by the exponential population growth equation:

$$N_t = N_0 e^{rt} \qquad \text{Eqn. 3}$$

where N_0 is the initial population size, N_t is the population size at time *t*, and *r* is the intrinsic growth rate (Akçakaya et al. 1999). Environmental conditions can influence the rate of population growth, meaning that if an environmental change (such as the introduction of a new predator) causes *r* to fall below zero, then the population in question will decline. In a closed system with no immigration or emigration, the rate of decline is dependent on the extent to which births and deaths are affected by the environmental change, with faster declines occurring when births and deaths are lower and higher, respectively. The population growth rate is also expected to depend on density (Akçakaya et al. 1999). However, I did not include density dependence in my models because negative density dependence will have little influence on initial population growth and is usually reasonable to ignore (e.g. Converse et al. 2013). Positive density dependence is also unlikely to significantly affect population growth of robins and saddlebacks because their biology is such that any Allee effects (Deredec and Courchamp 2007, Armstrong and Wittmer 2011) are expected to be trivial (for example, they do not exhibit group defence strategies or experience reduced foraging efficiency at low densities). Where the effects of density dependence are so weak that they can be ignored, *r* becomes r_{max}, where r_{max} is the average (maximum) growth rate at low population densities (Akçakaya et al. 1999). I therefore refer to r_{max} rather than *r* when estimating population growth rates for saddlebacks and robins.

To quantify the relative impact introduced mammals have had on saddlebacks and robins, I estimated r_{max} for both species following predator arrival on the mainland. Transformation of Equation 3 gives:

$$r_{max} = \ln(N_t/N_0)/t \qquad \text{Eqn. 4}$$

Solving this equation therefore typically requires knowledge of initial population size (N_0) and population size at time t (N_t). However, data on the historical and current abundance of North Island saddlebacks and robins are lacking, with the exception that saddlebacks were extinct on the North Island by 1900. Nevertheless, there is extensive evidence that distribution and abundance are correlated (Krebs 2009), so changes in the size of species' geographic ranges is a useful proxy for changes in abundance in the absence of better information. I therefore used information on the proportion of historical range (*p.hr*) occupied by each species t years after the arrival of ship rats, and assumed that *p.hr* was a reasonable proxy for N_t/N_0 ; i.e. that declines in the abundance of each species were correlated with the extent of range contraction they experienced. Therefore, r_{max} in the presence of rats (r'_{max}) was calculated as:

$$r'_{max} = \ln(p.hr)/t \qquad \text{Eqn. 5}$$

Since it was known that saddlebacks were no longer present on the North Island 40 years after the spread of ship rats, the values of *p.hr* and t were taken to be 0 and 40, respectively. Robin *p.hr* was obtained from Chapter 4 where range contraction following the introduction of mammalian predators was measured for 25 endemic forest bird species, including robins, using information on pre-human and current distributions. t was taken to be 140 because the distributional data used to estimate *p.hr* for robins was collected between 1999 and 2004, approximately 140 years after ship rats spread throughout the North Island.

The above equations assume exponential growth or decline of populations. This assumption is reasonable for North Island saddlebacks given their rapid decline to extinction on the mainland. However, an alternative model for North Island robins is that they have now reached approximate equilibrium rather than experiencing an ongoing decline to extinction. I therefore calculated an alternative r'_{max} for robins assuming they are currently at equilibrium. For a population to be at equilibrium rather than declining to extinction, r_{max} must be greater than 0, i.e. the population has positive growth at low density. Assuming a constant per capita predation rate (sensu Schaefer 1957), under the equilibrium model the proportional reduction in range experienced by robins after the arrival of ship rats will be approximately proportional to the reduction in r_{max} that has occurred:

$$r'_{max} = p.hr \times r_{max} \qquad \text{Eqn. 6}$$

where r'_{max} is the maximum growth rate with ship rats present, and r_{max} is the maximum growth rate in the absence of rats. This Type I functional response (sensu Holling 1959) was considered most realistic because robins probably form a minor component of predators' diet in New Zealand forests, so per capita predation rate is unlikely to be affected by prey density.

As noted above, estimating the relative vulnerability to predation of saddlebacks and robins requires some understanding of the relative impact ship rats have had on both species' population growth. I therefore calculated v by estimating the reduction in r_{max} caused by ship rats for each species ($r_{max} - r'_{max}$), and taking the ratio of these differences:

$$v = (r_{max_s} - r'_{max_s}) / (r_{max_r} - r'_{max_r}) \qquad \text{Eqn. 7}$$

where r'_{max_s} and r_{max_s} are r_{max} values for saddlebacks with and without ship rats present, r'_{max_r} and r_{max_r} are the respective r_{max} values for robins, and v is the relative reduction in r_{max} for saddlebacks and robins following ship rat arrival. Estimates of r_{max} were based on modelled estimates of population growth ($\ln(\lambda)$) for saddlebacks and robins at zero rat tracking for an average reintroduction site (i.e. $r_{max} = \ln(\alpha)$, see Eqn.s 1 and 2).

Because I estimated r'_{max} for robins under two alternative models (i.e. ongoing exponential decline (Eqn. 5) or currently at equilibrium (Eqn. 6)), v was calculated under both scenarios using the alternative estimates of r'_{max_r}. I also considered two alternative scenarios for saddleback decline. In addition to calculating r'_{max_s} based on a decline to extinction over 40 years, I also considered the possibility that saddleback populations exposed to ship rats may have declined to extinction within a shorter timeframe, given that ship rats would have been spreading throughout the North Island over that period, and are unlikely to have reached all regions simultaneously. I therefore also estimated r'_{max_s} assuming local populations declined to extinction within 10 years of ship rats establishing in the area (i.e. $t = 10$ in Eqn. 5 above). Consequently, v was estimated under four alternative scenarios that differed based on the speed of saddleback decline and/or robin population dynamics.

Results

Fecundity and survival in the absence of rats

Modelling mean saddleback fecundity and survival among multiple sites enabled vital rate predictions to be made for a saddleback population reintroduced to a new rat-free site while accounting for unexplained site-to site variation. Estimated intercepts and age effects for mean saddleback fecundity and survival had high uncertainty (Table 5.1), which was unsurprising

given the distributions incorporated uncertainty associated with each of the three site-specific estimates. Adult saddlebacks were predicted to have an annual survival probability of 0.83 (95% CI = 0.53-0.98), with juveniles estimated to have a 0.80 (0.46-0.96) probability of surviving 9 months to the breeding season. Mean annual fecundity was estimated to be 1.41 (0.59-3.36) fledglings for first-year females and 3.96 (1.53-10.39) fledglings for older females.

Table 5.1 Means and credible limits (CL) for parameters in saddleback fecundity[a] and survival[b] models developed using published vital rate estimates from three reintroduction sites (Gedir et al. 2013).

Node[c]	Mean	SD	2.5% CL	97.5% CL
α_f	0.34	0.22	-0.12	0.80
α_{sv}	1.04	0.49	0.12	2.07
β_{af}	1.04	0.21	0.59	1.5
β_{as}	0.90	0.44	0.11	1.81
σ_f	0.24	0.23	0.01	0.86
σ_s	0.65	0.24	0.10	0.98

[a] $\ln(f) = \alpha_f + \beta_{af}\, a + re_{site}$, where f = mean fecundity, a = age (0 = yearling, 1 = year 2^+), and re_{site} = site random effect

[b] $\text{logit}(s) = \alpha_{sv} + \beta_{as} a + re_{site}$, where s = annual survival probability, a = age (0 = juvenile, 1 =adult), and re_{site} = site random effect

[c] α_f, intercept term for mean number of fledglings per first-year female; α_{sv}, intercept term for mean annual juvenile survival probability; β_{af}, effect of age (year 2^+ females) on fecundity; β_{as}, effect of age (adult) on annual survival probability; σ_f standard deviation for random effect of reintroduction site on fecundity; σ_s standard deviation for random effect of reintroduction site on survival.

Vulnerability to predation

In the absence of rats, saddlebacks were estimated to have a higher rate of population growth (r_{max_s} = 0.619) than robins (r_{max_r} = 0.346) at an average site. Estimation of r_{max} in the presence of ship rats showed both species were negatively affected by the arrival of ship rats, but to different extents. When robins were assumed to be experiencing an ongoing exponential decline, r'_{max_r} was -0.009 (Δr_{max_r} = 0.355), whereas r'_{max_r} = 0.10 under the alternative scenario where robins are currently at equilibrium (Δr_{max_r} = 0.24). Unsurprisingly, saddleback r_{max} was more strongly affected by ship rat presence. Under the 40-year extinction model r'_{max_s} was -0.17 (Δr_{max_s} = 0.79), and under the 10-year extinction model r'_{max_s} = -0.69 ($\Delta\ r_{max_s}$ = 1.31). The relative vulnerability (v) of saddlebacks ranged from 2.45 to 5.84 depending on the current

status of robins (exponentially declining or at equilibrium) and the speed of saddleback decline following ship rat arrival (Table 5.2).

Population growth

λ_s estimates indicated that a saddleback population reintroduced to a new site would be expected to grow in the absence of rats (λ_s = 1.80, 95% CI = 1.07-3.05, Figure 5.1). λ_s was negatively affected by rat presence (β_{ts} = 0.29, 95% CI = 0.19-0.39, Table 5.2), with population growth slowing and becoming negative as rat densities increased (Figure 5.1).

Table 5.2 Means and credible limits (CL) for parameters in saddleback population growth models*.

Node*	Mean	SD	2.5% CL	97.5% CL
α_s	1.87	0.51	1.07	3.04
β_{ts}	0.29	0.04	0.19	0.39
v_{exp_40}	2.45	0.93	1.26	4.89
v_{equ_40}	3.52	1.38	1.78	7.15
v_{exp_10}	4.07	1.43	2.30	7.90
v_{equ_10}	5.84	2.13	3.25	11.58

* $\ln(\lambda_s) = \ln(\alpha_s) + v\beta_{ts}\ln(p)$ where: λ_s, finite rate of population increase for saddlebacks; α_s, intercept (finite rate of increase in the absence of rats at a new random site); β_{ts}, effect of tracking tunnel survival (p, complement of rat tracking rate) on robin population growth; and v, parameter accounting for differences in vulnerability between saddlebacks and robins where: a) robins are exponentially declining and saddlebacks became extinct on the mainland within 40 years of ship rat arrival (v_{exp_40}), b) robins have reached equilibrium and saddlebacks became extinct within 40 years (v_{equ_40}), c) robins are exponentially declining and saddlebacks were locally extirpated within 10 years of ship rat establishment in an area (v_{exp_10}), and d) robins have reached equilibrium and saddlebacks were locally extirpated within 10 years (v_{equ_10}).

The amount of predation a saddleback population could sustain was dependent on the relative vulnerability of saddlebacks compared to robins (Figure 5.1, Table 5.2). Predictions of λ_s across the full range of vulnerabilities considered showed that rat tracking rates needed to be kept at low ($\leq$ 3-8%) levels for there to be high certainty of saddleback population growth. Under the most optimistic scenario where saddlebacks were estimated to be approximately 2.5 times as

vulnerable to rat predation than robins (v_{exp_40}), the λ_s distribution was ≥ 1 at rat tracking rates ≤ 8%, meaning the prediction of positive growth was robust to uncertainty in parameter estimation at tracking rates ≤ 8%. When saddlebacks were instead considered to be almost 6 times more vulnerable than robins (v_{equ_10}), λ_s was predicted to be ≥ 1 if tracking rates were ≤ 3% (Figure 5.1). The uncertainty associated with λ_s estimates meant it was unclear whether growth could be expected at higher tracking rates, despite mean λ estimates ≥ 1 occurring with tracking rates up to 29% (v_{equ_10}) and 56% (v_{exp_40}).

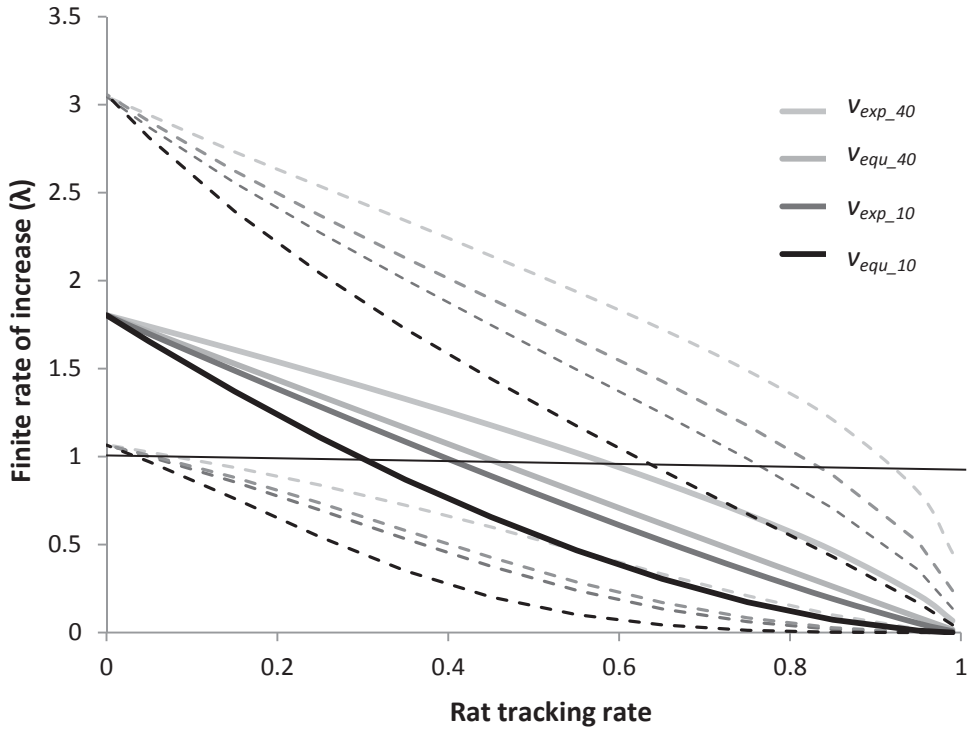


Figure 5.1. Relationship between rat tracking rate and finite rate of increase (λ) estimates for a saddleback population reintroduced to a new site, based on previously modelled effect of rat tracking on robin λ (Parlato et al. 2012 [Chapter 3]) adjusted to account for the greater vulnerability of saddlebacks (*v*). Alternative values of *v* were determined by the speed of saddleback extirpation following ship rat arrival (10 or 40 years, v_{10} or v_{40}) and the current status of North Island robins (exponentially declining or at equilibrium, v_{exp} or v_{equ}). Dotted lines are 95% credible intervals. Horizontal line shows λ = 1.

Site-specific predictions

Incorporating site-specific effects into population growth projections indicated rat levels at Boundary Stream needed to be reduced to lower levels than were estimated for a random site. This was due to the estimated site-specific effect on fecundity, which was negative for the Boundary Stream robin population (-0.15, SD=0.19), and had stronger influence than the positive site effect on adult survival (0.06, SD=0.06).

Although the mean λ_s for Boundary Stream remained ≥ 1 up to tracking rates of at least 28% across the range of vulnerabilities considered, uncertainty around parameter estimates meant rat levels needed to be much lower to achieve more robust predictions of population growth. Under the most optimistic scenario ($v \approx 2.5$), the 95% credible intervals for λ_s did not include 1 at rat tracking rates $\leq 5\%$. When predictions were based on saddlebacks having the highest relative vulnerability ($v \approx 5.8$), rat tracking needed to be $\leq 1\%$, for the prediction of positive growth to be robust to parameter uncertainty.

Discussion

Any attempt to understand an ecological process or to manage an ecological system requires a model (McCallum 2000). Models are essential for making informed decisions about reintroductions, as there is no other basis for predicting how reintroduced populations will respond to potential management actions (Armstrong and Reynolds 2012, Nichols and Armstrong 2012, Converse et al. 2013). While such models can be intuitive descriptions of the system involved, development of explicit quantitative models improves our capacity to predict the response of populations to management. Quantitative population models are increasingly being used to guide reintroduction programmes but, despite this, decisions about reintroductions have remained largely intuitive (Armstrong and Reynolds 2012, Nichols and Armstrong 2012), making them prone to unreliable knowledge (Romesburg 1981). While development of good models in no way guarantees reintroduction success, they allow managers to make rational decisions by taking considered risks rather than a "release and see" approach necessitated by the absence of quantitative predictions.

Reintroductions of extirpated species back to unfenced areas on New Zealand's mainland are an exciting prospect for New Zealand conservation, but have been unsuccessful to date. Past attempts have necessarily relied on intuitive decisions, as there were no models available to evaluate the level of management required for populations to grow in the presence of predators.

Making inferences about species when data are lacking is a well-recognised challenge in conservation biology, and has led to the development of surrogate-species concepts such as indicator species (Morrison 1986) where data from other species are used to make inferences about a species (or group of species) of interest. However, these approaches are limited by their assumption that the surrogate species will be a reliable indicator of population response in the target species, which may not be valid given that species often respond differently to threatening processes (Verner 1984, Landres et al. 1988, Lindenmayer et al. 2002). The relationship between species and their indicators is likely to depend on the extent to which shared ecological drivers impact on populations (Hoare et al. 2013) so extrapolating from one species to another is difficult unless the relative response of populations can be estimated. This study has built on the idea of using data from other species to estimate population parameters for a species of interest (Landres et al. 1988) by developing a more sensitive framework that accounts for differential species responses to key ecological drivers when modelling population growth.

The modelling approach I have presented enables predictions of population growth to be made at a range of predator densities when the candidate species for reintroduction (the North Island saddleback in this case) has never been observed in the presence of that predator. My results indicate that a saddleback population reintroduced to a new site free of mammalian predators would be expected to grow, assuming there is no emigration and the site has similar native (broadleaf-dominated) forest to the three sites I used to develop the model. While obviously dependent on habitat availability to a certain extent (for example, a population of 30 saddlebacks released into a 5 ha site could not reasonably be expected to increase in number), this finding is highly encouraging for the success of future saddleback reintroductions to mammal-free sites.

My results also suggest that saddlebacks could be successfully reintroduced to unfenced mainland sites with very low rat densities. Predictions for a new random site indicated that rat tracking rates would need to be $\leq$ 3-8% to achieve high certainty of saddleback population growth. A number of North Island reserves with intensive rat control are now achieving tracking rates below this range, raising the prospect of future saddleback reintroductions. Predictions of mean population growth indicated that saddleback populations could potentially withstand higher tracking rates, although there was less certainty of population increase. Given the financial and ethical implications of reintroduction failure, practitioners are unlikely to reintroduce highly threatened species to any site where conditions do not provide high certainty of population growth. Furthermore, rats are not the only factor affecting saddleback populations so it is important to interpret these results within a broader context. Food supply and the presence of other predators, particularly stoats, will also influence population growth and will vary among sites. However, such effects are currently difficult to quantify because data are

lacking. Data from closely related species may provide some insight into whether a particular site will have a positive or negative influence on population growth due to unexplained variation caused by such factors. North Island robins have previously been identified as a useful species for assessing habitat before reintroductions of more vulnerable species are contemplated (Armstrong 2000). I therefore attempted to account for some unexplained site-to-site variation by incorporating previously modelled site-specific effects on North Island robin vital rates into predictions of population growth for saddlebacks reintroduced to Boundary Stream Mainland Island. This in turn suggested that rat tracking rates would need to be ≤1-5% at Boundary Stream for there to be high certainty of population increase.

Rat tracking was approximately 1% at Boundary Stream after 37 saddlebacks were reintroduced in 2004 but, despite this, there were only nine birds known to be alive one month after translocation and the population was functionally extinct (no females) within four months. This rapid decline may have been the result of rat and/or stoat predation. It may also have been, in part, due to a period of bad weather immediately after the birds were released, with some deaths known to have been caused by aspergillosis (Sullivan 2006), a fungal disease that can be associated with stresses such as translocation or poor weather conditions (Wobeser 1997). It is therefore difficult to use this case study to evaluate how reliable the model predictions were. A useful extension of my model would be to project population dynamics, as this would allow additional uncertainty associated with environmental and demographic stochasticity to be incorporated. However, for this study I focused on the finite rate of population increase because $\lambda > 1$ is the most fundamental requirement for reintroduction success (Armstrong and Reynolds 2012).

The intensity of management necessary to achieve high certainty of saddleback population growth was dependent on the relative vulnerability to predation (v) of saddlebacks compared to robins. Accurate estimation of v is clearly important for reliable predictions, but this is highly challenging when population data in the presence of predators are lacking. I therefore developed an approach for estimating v using information on historical declines of saddlebacks and robins following the arrival of ship rats on the North Island. Historical data can provide valuable insight into the vulnerabilities of mainland extirpated species because the relative effects of new predators should be apparent in times of extinction if prey responses to predation pressure were rapid enough (Holdaway 1999).

Nevertheless, using historical data to estimate v does have some limitations. First, it is impossible to ascertain which of the four scenarios considered most closely reflects reality, and this increases uncertainty around the level of management necessary to achieve a high probability of population growth (e.g. for a random site, required rat tracking rates ranged from

≤ 3% to ≤ 8%). Second, the estimates of range contraction used to estimate *v* assumed both species were found throughout North Island forests at the time of ship rat arrival (i.e. their pre-human historical range, Chapter 4). However, Norway and Pacific rats (*Rattus norvegicus* and *Rattus exulans*) were already present on the mainland when ship rats arrived. These species are known nest predators of saddlebacks and robins, with Norway rats also known to affect survival of adult birds (Lovegrove 1996a, Masuda and Jamieson 2013), though both species are considered a lesser threat than ship rats (Atkinson 1973). Consequently, range contraction of saddlebacks and robins may have commenced before ship rat arrival, but the extent of any such change is unknown. Third, stoats as well as rats are likely to have contributed to robin range contraction, and possibly expedited North Island saddleback extinction on the mainland, but the effects of those predators are currently impossible to separate. Fourth, predator control has been implemented in many forested areas on the North Island in recent years (Saunders and Norton 2001), and this may have reduced the amount of range contraction that robins would have experienced in the absence of predator management. While it is important to acknowledge these potential biases on *v*, information on historical declines nevertheless provided valuable insight into the relative vulnerabilities of saddlebacks and robins. My approach has provided the first opportunity to move beyond purely hypothetical *v* values (e.g. Armstrong and Davidson 2006) and thereby quantify the effect of rats on saddleback population growth prior to reintroduction. The *v* values estimated in this study can be updated if population data in the presence of predators become available through mainland reintroductions in the future, and could potentially be extended to allow estimation of *v* for different vital rates and to apply to stoats as well as rats.

The extent to which stoats influence saddleback population growth remains a key unknown. Saddlebacks nest in cavities and are poor fliers, making them highly susceptible to stoat predation. Because saddlebacks were already rare by the time stoats arrived on the North Island in the late 1800s, it was not possible to quantify the relative vulnerability of saddlebacks to stoat predation using historical data, as it was for rats. I was therefore unable to explicitly account for stoat predation when developing the model, so predictions are likely to be most relevant to sites where predator control has reduced stoats to very low levels or stoats are absent (e.g. Great Barrier Island), and might be optimistic otherwise. Gaining a better understanding of how both stoats and rats affect saddleback vital rates is essential for making robust predictions for mainland reintroductions, and will only be possible if appropriate data become available in the future. Opportunities to collect such data may arise as a consequence of rat or stoat invasions to existing saddleback habitat or through saddleback reintroductions to sites with rats and/or stoats present. Unfortunately the rapid demise of the saddleback population at Boundary Stream provided little opportunity to gather data on saddleback vital rates in the presence of these

predators. Although there have been no further attempts to reintroduce saddlebacks to unfenced mainland sites, saddlebacks have recently been reintroduced to two fenced mainland sites (Cape Sanctuary and Tawharanui) with low or occasional presence of rats and/or stoats, providing a unique opportunity to collect data from populations coexisting with these predators. The Bayesian modelling approach I have used provides an ideal framework for incorporating these data into future predictions because it allows existing population growth distributions to be readily updated as new data become available.

In addition to controlling or eliminating the factors responsible for original extirpation, the problem of ongoing dispersal out of target areas is becoming increasingly recognised as an important consideration for reintroduction programmes (e.g. Tweed et al. 2003, Stamps and Swaisgood 2007, Le Gouar et al. 2012, Parlato and Armstrong 2012 [Chapter 3]). Dispersal and mortality can have similar implications because individuals who disperse and settle away from the reintroduction area will not contribute demographically or genetically to the population (Le Gouar et al. 2012). The tendency of individuals to disperse is affected by the habitat matrix surrounding the reintroduction site (La Morgia et al. 2011) and landscape connectivity has been identified as an important factor influencing growth of reintroduced populations (Parlato and Armstrong 2012 [Chapter 3]). Because species differ in their dispersal behaviour and ability (e.g. gap crossing ability, Creegan and Osborne 2005), the functional connectivity of landscape surrounding reintroduction sites (i.e. how surrounding landscape influences species movements) will be species-specific (Tischendorf and Fahrig 2000). Saddlebacks are considered to be poor dispersers (Hooson and Jamieson 2003), but because most reintroductions have been to offshore islands surrounded by ocean, little is known about their propensity to disperse on the mainland. My model assumes no emigration (or that emigration does not have an important influence on apparent survival probabilities), which might be reasonable given saddlebacks' limited flight ability. However, saddleback dispersal out of the target area has been recorded for two fenced mainland reintroduction sites (Zealandia (Raewyn Empson *pers comm.*) and Orokonui Ecosanctuary (Masuda and Jamieson 2012)), and population growth will have been overestimated if dispersal frequently occurs at mainland sites. Gaining a better understanding of saddleback movements in fragmented mainland habitat will enable landscape effects to be incorporated into model predictions and, consequently, assessments of site suitability (sensu Parlato and Armstrong 2012 [Chapter 3]).

Predicting reintroduction outcomes before populations are released is inherently challenging, and becomes even more difficult when the species being considered for reintroduction no longer co-exists with the identified threats in any location. I have developed a modelling approach that integrates data from multiple species and sites to predict population growth of mainland-extirpated species reintroduced to sites with mammalian predators present. Data arising from

such reintroductions in the future can be used to update the model I have presented, and the updated model can in turn guide further reintroductions. This iterative process is a cornerstone of Bayesian analyses, making them a natural framework for modelling reintroductions (McCarthy et al. 2012). This study therefore represents an initial step towards improving our understanding of how highly vulnerable species will fare in new situations with key predators present, providing a useful foundation on which knowledge can be built.

Chapter 6

General Discussion

With reintroduction increasingly being used to redress the detrimental effects of human activities on species and ecosystems, we, as a conservation community, have a responsibility to take whatever steps we can to improve the success of existing and future reintroductions. It is widely recognised that analysis of factors influencing reintroduction outcomes is essential to improve success rates (Sarrazin and Barbault 1996, Ewen and Armstrong 2007, Sutherland et al. 2010, Le Gouar et al. 2012). For how else can we hope to assess habitat suitability, identify optimal release techniques or evaluate the efficacy of alternative management actions? Quantitative models clearly have enormous potential for helping us better understand the key factors affecting reintroduction outcomes. There has been growing recognition of the value of quantitative modelling for reintroductions, and this has been reflected in the literature, with most (> 80%) papers modelling reintroduced or translocated populations published since 2000 (Armstrong and Reynolds 2012). However, the majority of these studies have used single-population models to predict the growth, persistence or spread of existing reintroduced populations, with relatively few studies focused on making predictions for future reintroductions (Armstrong and Reynolds 2012).

While this strong emphasis on case studies contributes greatly to our knowledge of local species and systems (Armstrong and Seddon 2008), extrapolating results to make predictions for other sites could be unreliable because factors influencing reintroduced populations in other parts of a species' range may not be apparent in results from a single location (Jachowski et al. 2011). Although some attempts have been made to evaluate factors influencing reintroduction outcomes across multiple populations, these have tended to focus solely on evaluation of success rates (e.g. Jachowski et al. 2011, Matějů et al. 2012, White et al. 2012). While these studies can be useful to show trends in reintroduction outcomes across multiple sites, they can produce misleading results in the absence of good data (Armstrong and Seddon 2008). For example, results may be subject to confound (e.g. founder group sizes are unlikely to be chosen at random with respect to the chances of success, Armstrong & Wittmer 2011). Furthermore, there is no widely accepted definition of reintroduction "success" and the dynamic nature of populations means a reintroduction can only be considered successful at a particular point in time (Seddon 1999). Analyses of binary data are also limited in the inferences that can be made. For example, it is impossible to distinguish driven from stochastic extinction, and it is much more informative to know the expected population growth rate for a given situation (e.g. if a population is declining, managers are in a better position to make effective decisions if population growth under different management strategies can be estimated). Because all factors affect reintroduced populations by acting on survival and reproductive rates (Sarrazin and Barbault 1996), analyses of demographic data improve our capacity to identify important influences on reintroduction outcomes (Converse et al. 2013). It is impossible to construct

demographic models before reintroduction unless data from other sites are used, and it is then necessary to account for likely site-to-site variation. However, until now, no attempt has been made to integrate demographic data from multiple reintroduced populations into a single model that can be used to make predictions for current and future reintroductions.

My study presents a novel approach that allows data from multiple reintroduced populations to be modelled simultaneously, thereby enhancing predictive capability and enabling effective management to improve reintroduction outcomes. I have shown how this multi-population approach can be used to identify the general drivers of population establishment (Chapter 2), vital rates and growth (Chapter 3) and to account for unexplained site-to-site variation when making predictions for new sites.

My results from Chapter 2 showed that landscape connectivity and rat tracking rates at the reintroduction site, and forest type and mammalian predator presence at the source site, were all important for post-release establishment of North Island robins. These four fixed effects predominantly explained the variation in establishment among sites, and no random site-to-site variation was detected. Connectivity to surrounding forest and rat tracking rates at the reintroduction site were both negatively associated with the probability of reintroduced individuals remaining in the target area and surviving to breed. My results also suggested that choosing a source population from habitat that best matches the ecological characteristics of the reintroduction site can be important for success (sensu Letty et al. 2007, Rittenhouse et al. 2008), as robins sourced from native forest had higher establishment than those from exotic pine forest, and robin establishment in sites with mammalian predators present was higher when founders were sourced from sites with these predators than when sourced from mammal-free sites. Model predictions for the proposed reintroduction site, Pukaha, indicated that while predator control was important for robin establishment, sourcing birds from native forest with mammalian predators would attain the highest establishment rates for any level of rat control; thereby providing a relatively simple and inexpensive way to improve establishment probabilities. This analysis showed how integrating establishment data from multiple sites into a single model can provide useful guidance for managers at a number of levels, including source and release site selection, effectiveness of management interventions, and numbers of individuals to release to achieve desired initial population sizes. Nevertheless, taking steps to ensure the successful establishment of a reintroduced population is only worthwhile if conditions at the release site are sufficient to allow long-term growth and persistence, and this was explored in Chapter 3.

In Chapter 3, I constructed survival and fecundity models using vital rate data from multiple reintroduced robin populations, and used the best supported models to estimate population growth (λ, finite rate of increase) for existing populations and for the proposed reintroduction to Pukaha at different levels of predator control. My results showed that rat tracking rates were an important influence on both fecundity and adult female survival, that landscape connectivity and whether or not sites were located on a peninsula were important for apparent juvenile survival, and that there was unexplained random variation among sites in all demographic rates. Because the predictive value of the connectivity index for juvenile survival was ambiguous, λ was estimated using models with and without the connectivity effect included. Only three sites had a high certainty of population growth (λ distributions completely >1) under either model at both 5% and 25% rat tracking rates. At two sites, populations were expected to grow if rat tracking rates were <5%, and at the other five sites λ was estimated to be close to 1 and it wasn't clear whether growth would occur. Predictions for Pukaha were particularly sensitive to model choice because Pukaha had the lowest connectivity index of all sites. With the connectivity effect included, there was a high certainty of population growth at both 5% and 25% rat tracking. With the connectivity effect excluded, the λ distribution encompassed the full range of 95% credible intervals for the seven nonpeninsular sites (Pukaha is not on a peninsula) and it was unclear whether a reintroduced population would grow.

My findings in Chapters 2 and 3 suggest rat tracking rates and the surrounding landscape at reintroduction sites are important for both the establishment *and* persistence of reintroduced robin populations. It was not surprising that rat tracking was a useful predictor of fecundity and adult female survival in robins, as it is known that ship rats prey on nesting females, eggs, and chicks (Brown 1997, Powlesland et al. 1999). However, the finding that establishment probabilities were negatively associated with rat tracking rates was somewhat unexpected because robin survival in established populations was previously not found to be affected by rat densities outside the breeding season (Armstrong et al. 2006b, Chapter 3). This result could suggest that robins become more susceptible to predation as a result of translocation-induced stress (sensu Teixeira et al. 2007) although other recent research has also suggested that rat control affects survival of non-translocated robins outside the breeding season (Armstrong et al. 2014). These results show that improvements in predator control at reintroduction sites will benefit reintroduced populations, both initially and in the longer-term. However, the intensity of management necessary to achieve desired objectives will be site-specific. The unexplained random variation among sites in estimated population growth rates was large relative to the variation explained by rat control, meaning that other factors not included in my analysis were also having an important impact on population growth. As a consequence, some sites needed to

reduce rat tracking to <5% to achieve a high probability of population growth, whereas lower intensity control appeared adequate for others.

Moreover, my findings in Chapter 3 suggest sites may be marginal for North Island robin populations if they are on peninsulas or are well connected to habitat outside the site, regardless of the intensity of predator control within those sites. These landscape effects were probably due to differential dispersal of robins out of sites. While post-release dispersal is a well-recognised problem in reintroductions, the implications of ongoing dispersal on population persistence are less appreciated. On one hand, dispersal can be crucial to allow access to resources (e.g. Schadt et al 2002) and to restore meta-populations (e.g. La Morgia et al. 2011) so its effects are not always detrimental. On the other hand, populations will be driven to extinction if dispersal out of the reintroduction area exceeds recruitment (even at sites where key threats are controlled or eliminated, Base & McLennan 2003). Identifying sites where the surrounding landscape is more likely to inhibit dispersal out of the target area is therefore essential to avoid dispersal-related failure of reintroductions (Le Gouar et al. 2012).

The importance of landscape structure and how it inhibits or facilitates dispersal may differ between the establishment and persistence phases of a reintroduction programme. Post-release dispersal can be a result of the stress and disorientation of the release, rather than being a process of active habitat selection (Osborne and Seddon 2012). Consequently, founders might move through the landscape differently to juveniles undertaking long directed dispersal movements or established individuals undertaking routine movements associated with resource exploitation (sensu Van Dyck and Baguette 2005). My results suggest the dispersal behaviour of recently-released robins may differ from that of dispersing juveniles, given that sites located on a peninsula had lower apparent juvenile survival but did not have lower establishment probability of founders. In fragmented landscapes, dispersing juvenile robins tend to move through forest until they reach the edge (Richard 2007), and this could have increased juveniles' tendency to disperse out of peninsula sites area along coastal boundaries compared to recently-released birds whose movements might be more erratic (e.g. Bradley et al. 2011) due to post-translocation stress. These findings reiterate the need to distinguish influences on establishment and persistence (Sarrazin 2007, Armstrong and Seddon 2008), and highlight that improving our knowledge of dispersal behaviour will help to identify factors affecting dispersal propensity throughout the phases of a reintroduction and evaluate their influence on reintroduction outcomes.

A natural, though challenging, extension to integrating data from multiple populations is to integrate data from multiple species (Chapter 5), and this could be useful for several reasons.

First, when assessing management options at any site, it is usually necessary to consider the consequences of those actions on other species. Second, if existing data for the candidate reintroduction species are too few to evaluate the demographic consequences of alternative management actions then data from other species can potentially be used to infer those relationships. Third, site-specific effects on demographic rates estimated from other species at the proposed reintroduction site can be incorporated into assessments of site suitability for the candidate species. Evaluating multiple species' responses to management actions is an important component of effective conservation management (Lindenmayer and Likens 2011), but is far from straight forward because species often differ in their response to the control or removal of a shared threat (Lindenmayer et al. 2002, Hoare et al. 2013). Understanding differential species responses to key ecological drivers is therefore necessary for making reliable inferences about the efficacy of management interventions for multiple species, and it was this problem I attempted to tackle in Chapters 4 and 5.

Invasive species are considered to be one of the leading causes of biodiversity loss worldwide (Wilcove et al. 1998). In New Zealand, predation by introduced mammals such as rats and mustelids are widely recognised as the primary factor responsible for declines of New Zealand fauna (King 1984, Holdaway 1989, Innes et al. 2010). Consequently, much of the conservation effort in New Zealand is associated with the control or eradication of introduced mammals (Atkinson 2001, Clout 2001). Nevertheless, species clearly differ in their vulnerability to predation, so gaining a better understanding of the relative vulnerabilities of endemic taxa to predation and what factors promote this vulnerability (sensu Krushelnycky and Gillespie 2010) will contribute to the effective management of those species and the threats they face. In Chapter 4, I measured range contraction to estimate the relative vulnerabilities of New Zealand's surviving endemic forest bird species to the impacts of introduced mammalian predators, and identified a key life history attribute underlying this variation. My results suggest that New Zealand forest bird species differ greatly in how vulnerable they are to predation by introduced mammalian predators, with some species remaining in available habitat throughout most of their pre-human range, and others having disappeared completely from the mainland (proportion of historical range still occupied ranged from 0-0.92). Cavity nesting was the trait associated with more extensive range contraction, indicating that cavity nesting species are more vulnerable to predation than species that nest in more open sites. The vulnerability to predation of cavity nesting species is well recognised (e.g. Elliott 1996, Lovegrove 1996a, O'Donnell 1996b) so this finding was not particularly surprising. Nevertheless, other studies examining correlates with geographical distribution or extinction threat for extant New Zealand land birds (Cassey 2001, Bromham et al. 2012) have not included cavity nesting as an explanatory variable so my results provide new insight into the over-riding influence of nesting

habits on predation vulnerability of surviving New Zealand forest bird species. My analysis also suggested that vulnerability to predation is not independent of phylogeny, with some families experiencing disproportionately greater range contraction than others. This indicates there may be some phylogenetic association of other traits that make certain families more vulnerable to predation. After accounting for the effect of cavity nesting, range contraction was most extensive for families Callaeidae (New Zealand wattlebirds) and Notiomystidae (hihi).

Some of the most vulnerable extant forest bird species that were extirpated from the mainland following the arrival of mammalian predators (Table 4.1, Chapter 4) are now being considered for reintroduction to unfenced mainland sites with mammalian predators present at a range of densities (e.g. Armstrong and Davidson 2006, Richardson 2009). The failure of all such reintroductions to date highlights the need for reliable models to evaluate whether predator control at candidate release sites is sufficient for populations to grow. This is clearly challenging when the species being considered for reintroduction no longer co-exists with the mammalian predators responsible for their original extirpation in any location, making it impossible to use data from other sites to predict the amount of predation reintroduced populations can withstand. Data from other species can potentially be used to infer the effect of predator levels on population growth. However, it is then necessary to account for differential population responses among species. In Chapter 5, I developed a multi-species approach to predict growth of a reintroduced population at a range of predator densities when the candidate species for reintroduction has never been observed in the presence of those predators. Population growth of North Island saddlebacks at different rat densities was predicted using the estimated effects of rat tracking on robin population growth (Chapter 3), with the strength of the relationship adjusted to account for the greater vulnerability of saddlebacks to rat predation (estimated using results from Chapter 4). My results suggested that saddlebacks could be successfully reintroduced to unfenced mainland sites with very low rat densities, improving the outlook for future mainland reintroductions. However, the extent to which stoats influence saddleback population growth remains a key unknown. Stoats are highly effective hunters (Hutching 2004) that range over large areas (Gillies et al. 2007), so it is possible that saddleback populations will be unable to persist at sites with even very low stoat densities. Gaining a better understanding of how both stoats and rats affect saddleback vital rates is essential for making robust predictions for mainland reintroductions, and will only be possible if appropriate data become available in the future. Nevertheless, managers are often faced with making decisions for novel reintroductions when data are lacking, particularly for very rare species (e.g. those restricted to captivity or with few remnant wild populations). In this situation, using more common closely related species as surrogates for endangered species can potentially help to improve knowledge of likely outcomes before translocations take place (Letty et al. 2007). Using data from North

Island robins allowed me to not only estimate the effects of rat tracking on saddleback population growth, but also to incorporate site-specific random effects on demographic rates into predictions. I am unaware of any previous attempt to do this, and the validity of using data from another species to assess relatively "good" or "bad" sites due to unknown factors has not been tested. Nevertheless, because species reintroductions are often carried out consecutively, the ability to use site effects estimated from other closely related species at the site has the potential to provide valuable insight into predictions for the candidate species. The framework I developed in Chapter 5 shows how data from another species can be used to improve our understanding of how highly vulnerable species will fare in new situations with key predators present, thereby enhancing predictive capability in the face of substantial uncertainty.

Developing this ability to integrate data from multiple populations and species to improve predictions is at the heart of my thesis; that is, how can we make the best use of the information that *is* available when predicting reintroduction outcomes? Uncertainty is a key component of many reintroductions (McCarthy et al. 2012, Converse et al. 2013) and it is often not feasible to delay acting until we have more data to inform decisions. Integrating data from multiple reintroductions not only allows more precise predictions to be made with existing data, but also allows understanding to increase over time as more data become available (Armstrong and Reynolds 2012). Bayesian inference therefore provided an ideal framework for developing my multi-population approach because existing data can be used to obtain prior distributions of population parameters before new reintroductions take place, and these distributions can be updated as post-release monitoring data become available. Models constructed in a Bayesian framework allow simultaneous analysis of diverse sources of data (Ogle 2009), making it possible to integrate data from multiple reintroduced populations (and species) into a single model with random effects, even when those data are inconsistent (e.g. establishment data collected at different monitoring intensities, Chapter 2). There is also potential to integrate different data types (Armstrong and Reynolds 2012), such as demographic and abundance data (Brooks et al. 2004), providing greater flexibility in the monitoring and data requirements for multi-population inference. This is important because monitoring can be variable across projects. It is unrealistic to expect all reintroductions to be closely monitored (Ewen and Armstrong 2007) so an ability to include inconsistent, missing or different types of data will allow predictions to more fully reflect the information available (Brooks et al. 2004, Nakagawa and Freckleton 2008).

Given there are many different types of data that can potentially be collected (Armstrong and Reynolds 2012), monitoring should be done strategically (Ewen and Armstrong 2007) and will ideally focus on reducing key uncertainties (Nichols and Armstrong 2012). Population

modelling can provide valuable insight into where important uncertainties lie and therefore guide where greater certainty would lead to better management (Moehrenschlager et al. 2013). Uncertainty about how reintroduced populations will respond to management arises because the model parameters (e.g. survival probabilities) are uncertain and because the choice of model can also be uncertain (McCarthy et al. 2012, Nichols and Armstrong 2012). For example, my results in Chapter 3 showed that predictions for a robin population reintroduced to Pukaha were less precise than for other sites and there was ambiguity about the best model for apparent juvenile survival (relating to the predictive value of the connectivity index). Monitoring rat tracking rates (during the breeding season only) and robin population vital rates at Pukaha post-release would reduce uncertainty around estimates of population growth for any level of rat control, and would also help resolve model choice for juvenile survival because Pukaha has low connectivity relative to the other sites.

The collection of targeted monitoring data can also contribute to adaptive management (Walters 1986) of reintroduced populations, whereby management decisions are reviewed recurrently on the basis of improved knowledge acquired through ongoing monitoring (Armstrong et al. 2007, McCarthy et al. 2012). Adaptive management aims to improve management performance in the face of uncertainty and so improve the quality of future decision-making (Converse et al. 2013). The multi-population approach I have presented supports passive adaptive management by demonstrating how monitoring can reduce uncertainty to guide future management, and also supports active adaptive management, where management actions are explicitly undertaken to improve learning (McCarthy et al. 2012). For example, if the objective is to better understand the importance of connectivity for robin population growth, reintroductions could be attempted to well-connected sites even though they may have a low probability of success. However, there are obvious welfare issues associated with such management decisions (e.g. Harrington et al. 2013). These issues are ideally considered as part of the adaptive management process where the benefits of improved knowledge are formally considered alongside welfare implications and other relevant considerations, such as financial constraints or impacts on source populations (Converse et al. 2013) in order to optimise the management objective (McCarthy et al. 2012).

As the frequency of reintroductions has increased in recent years, so too has the wealth of research undertaken to learn from those experiences and improve the outcomes of current and future programmes. Until recently, isolated case studies have dominated the reintroduction literature (Seddon et al. 2007) but there has been an emerging recognition (e.g. Seddon et al. 2007, Jachowski et al. 2011, Armstrong and Reynolds 2012, Parker et al. 2013) that meta-analyses using data from multiple reintroduced populations provide a valuable opportunity move beyond the inferences that can be derived from individual case studies. Analyses of

success rates among programmes are limited in their ability to provide useful information because results can be confounded (Armstrong and Seddon 2008), they do not predict trends in population growth, and they are not easily integrated with post-release data. Here I have presented a modelling framework that builds on results from multiple reintroduction programmes to improve predictions of population establishment and growth. This approach can potentially be applied to any species where demographic data are available from multiple populations. While the data requirements are somewhat more onerous than those for comparative analyses of success rates, even so they remain flexible. Depending on the accessible information, analyses can be conducted with raw data (Chapter 2), with estimates and standard errors (Chapter 5) or both data types can be modelled together (Chapter 3). I therefore join others (e.g. Sutherland et al. 2010, Parker et al. 2013) in recommending monitoring information and/or results be made widely available, ideally through publishing, reports or websites, and note the importance of including standard errors around estimates (of predicted vital rates and estimates of covariate effects) to allow uncertainty to be incorporated in models. In this way, we can move beyond case studies and create a means by which information can be integrated across programmes.

With the value of modelling reintroduced populations becoming increasingly recognised, there is likely to be greater emphasis on the development of quantitative models to inform management and guide future reintroductions. For species reintroduced to multiple sites, integrated models provide an ideal opportunity to develop understanding over time of the key drivers of reintroduction success.

Next steps

The research presented in this thesis represents my attempt at developing a basic framework for multi-population inference, in the hope that it might contribute to improving our ability to predict reintroduction outcomes and therefore improve reintroduction success. The obvious question at this point is; where to from here? As is often the case in modelling, the models I have presented here are far from perfect. Nevertheless, the very process of developing those models and considering their results helped to clarify my thinking about the issues reintroduction biologists face; and simultaneously re-iterated the complexity of the systems we are trying to understand. Throughout this thesis I have tried to "keep it simple", which was challenging at times, especially when it is so compelling to try to master this complexity in the quest for better knowledge. Keeping it simple helped me to focus on the factors that I considered were likely to be most influential on the populations I studied, but also highlighted important information gaps and where further work would make a useful contribution to

developing this approach. It is these opportunities for advancements that I touch on below, as well as where this approach might make a useful contribution in the future.

Can we explain some of the unexplained variation?

At the risk of compromising model simplicity somewhat, it would be useful to better understand the factors causing the high residual variation in robin population growth estimates among sites (Chapter 3). A large proportion of this unexplained variability was probably caused by factors that were not included in my analysis, and some of these could be useful predictors if measured. Two particularly obvious potential influences on robin population vital rates (and growth) are the effects of other predators (such as stoats, cats or moreporks) and effects of food supply. I did not include these covariates in my analyses as data were lacking for most sites (and were inconsistent if available) but there is certainly scope for incorporating these factors into future models if more data become available as part of ecosystem monitoring at robin reintroduction sites. There may also be benefit in investigating whether alternative indices for rat densities or landscape connectivity would better reflect the quantities they attempt to measure. For example, while rat tracking rates have been found to be a useful indicator of rat density within a single site (e.g. Brown et al. 1996), they may be more limited in their ability to measure relative density among sites if rats spend less time on the ground at some sites compared to others (e.g. due to vegetation structure) (Blackwell et al. 2002). Dispersal is clearly important for reintroductions, so improving our knowledge of how landscape facilitates or impedes dispersal of robins (or other target species) throughout the different phases of a reintroduction will greatly improve our ability to account for this when predicting reintroduction outcomes. Where possible, it would also be useful to distinguish mortality from dispersal (Tweed et al. 2003, Le Gouar et al. 2012) to evaluate their respective influences on reintroduced populations, improve survival estimates, and allow the implementation of appropriate strategies to reduce the loss of individuals through each process (e.g. Armstrong et al. 2013). These issues are just a few of many that could help explain variation in vital rates among sites and, as is often the case, it will be a matter of weighing up the value of the knowledge gained with the cost of gathering the necessary information.

Extending the multi-population approach

An obvious extension to the multi-population approach is to combine the establishment (Chapter 2) and vital rate (Chapter 3) models to project actual population dynamics. After determining that λ may be >1, it makes sense to assess a population's viability considering demographic stochasticity (e.g. effects of sex ratio) in the short term and environmental

stochasticity and inbreeding depression in the longer term. It may also be appropriate to incorporate density dependence, which could include Allee effects and positive density dependence. These projections could not only be used to estimate population viability under alternative management scenarios, but could also be used to inform other relevant management decisions, such as the minimum number of individuals needed for release to preserve a desired level of genetic diversity (e.g. Tracy et al. 2011).

Extending the multi-species approach

While the approach I presented in Chapter 5 has advanced our ability to predict species responses to a key threat when data are lacking; as with all models, the reliability of predictions can only be tested and improved with good data. Clearly, then, the first step for improving the existing model is to collect data on saddleback vital rates at varying rat densities and use these data to update population growth estimates. Moving beyond the existing model that only considers one fixed effect (rat tracking), it may also be relevant to incorporate additional covariates such as the effects of other predators, landscape or food supply. This will be relatively straightforward if the relevant data to estimate those effects are available. However, there is also potential to incorporate additional effects in the absence of such data. For example, it might be possible to estimate "*v*" values for other predators, allowing indices of two or more predator types to be considered. It might also be possible to incorporate landscape effects if dispersal data from another species with similar dispersal abilities are available (e.g. species with similar wing morphology, Dawideit et al. 2009). The ability to use data from other species to estimate key parameters for a species of interest is exciting in its possibilities but is also incredibly challenging given the immense uncertainties associated with making inferences in the absence of species-specific data. Only through exploring different ideas, creating models, making predictions, and testing the reliability of those predictions, will we learn the true potential of multi-species approaches for improving our understanding of how reintroduced populations will fare in novel situations.

Future applications

My thesis has focused on reintroductions – conservation translocations designed to restore populations within species' historical ranges. However, releases of species outside historical ranges for conservation purposes, termed conservation introductions (IUCN/SSC 2013), are increasingly being discussed in the literature (e.g. Hulme 2005, Schwartz et al. 2009, Vitt et al. 2009) as a tool for filling niches left unoccupied following extinction of native species (ecological replacement, e.g. Parker et al. 2010) or to protect species from human induced

threats in their natural range (assisted colonisation, e.g. Hoegh-Guldberg et al. 2008). Making reliable predictions about populations introduced into ecosystems outside their historic ranges will obviously be very challenging (Armstrong and Reynolds 2012) and any proposals to undertake such actions will require careful risk analysis, including a transparent evaluation of uncertainty (Schwartz et al. 2009). Many of the relevant issues are well beyond the scope of my research (ethical, legal, risks of impacts of introduced species, etc.). However, modelling data from multiple existing populations of the candidate species could potentially help to evaluate the suitability of new habitat that has become available through climate change, for example, and could contribute to existing frameworks for predicting suitable sites (e.g. ecophysiological approach, Mitchell et al. 2013). An integrated approach would also allow information to be synthesised across conservation introduction programs if/when they occur over time. Depending on the circumstances, a multi-species approach may also prove valuable for making predictions for conservation introductions. For example, introducing a species as an ecological replacement has some parallels with reintroducing a species like the saddleback to New Zealand's mainland – i.e. neither species has ever been observed in the presence of threats that exist at the new site. As such, there may be opportunity to use data from other species present in the new habitat, both to identify likely threats and to evaluate their implications for successful introduction of replacement species.

Models of demographic data from multiple populations could also be usefully integrated into other modelling approaches used for reintroduced populations. For example, it might be possible to integrate demographic data with binary (success/failure) data from sites where demographic rates have not been monitored, to make optimal use of available information. Species distribution modelling to predict suitable habitat for reintroductions (e.g. Schadt et al. 2002, Hirzel et al. 2004) is a relatively new area, with the potential for demographic data to be used in model predictions (e.g. Macdonald et al. 2000). Integrating demographic data with species distribution data could conceivably address some of the key challenges that currently exist for distribution modelling, such as identifying which variables are useful for defining site suitability (Osborne and Seddon 2012). Given that demographic rates are the only direct measure of habitat quality (Armstrong 2005), combining species distribution modelling with demographic modelling of multiple populations could prove a powerful tool for assessing optimal habitat throughout a species' range and identifying suitable sites for future reintroductions.

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Appendix

Statements of contribution to Doctoral thesis containing publications

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Elizabeth Parlato

Name/Title of Principal Supervisor: Professor Doug Armstrong

Name of Published Research Output and full reference:

Predicting post-release establishment using data from multiple reintroductions.

Parlato, E. H. and D. P. Armstrong. 2013. Predicting post-release establishment using data from multiple reintroductions. Biological Conservation 160:97-104.

In which Chapter is the Published Work: 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  The candidate compiled the data, performed all analyses and wrote the first draft of the manuscript for review by the co-author. The candidate made revisions to the submitted manuscript as part of the peer-review process for publication.

Elizabeth Parlato — Candidate's Signature — 14/05/2014 — Date

Doug P. Armstrong — Principal Supervisor's signature — 14/5/2014 — Date

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STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Elizabeth Parlato

Name/Title of Principal Supervisor: Professor Doug Armstrong

Name of Published Research Output and full reference:

An integrated approach for predicting fates of reintroductions with demographic data from multiple populations.

Parlato, E. H. and D. P. Armstrong. 2012. An integrated approach for predicting fates of reintroductions with demographic data from multiple populations. Conservation Biology 26:97-106.

In which Chapter is the Published Work: 3

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  The candidate compiled the data, performed all analyses and wrote the first draft of the manuscript for review by the co-author. The candidate made revisions to the submitted manuscript as part of the peer-review process for publication.

Elizabeth Parlato — Candidate's Signature — 14/05/2014 — Date

Doug P. Armstrong — Principal Supervisor's signature — 14/05/2014 — Date