The Effect of a Translocation on a Source Population Using North Island Robins as a Case Study.

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Errata Sheet

Corrections and amendments to pages 7, 30, 50, 53 and 75.

Page 7: "There are approximately 2-3 birds/ha with about 2 pairs/ha". The line should read only: *There are approximately 2-3 birds/ha.*

Page 30: "Based on 500 bootstrap data sets, the global model $\{\phi(a^*y + s^*y + p), p(a^*y + s^*y + p)\}$ appears to fit the data ($P = 0.14$)". *The value of $P = 0.14$ means that, under the assumptions of the model, the probability of a deviance as large or greater than the observed value (269.716, Table 2.2) is approximately 0.14. This is well above an α level of 5% (0.05), so it is reasonable to assume that the data set meets the assumptions of the model.*

Page 50: Paragraph 3. For adult survival the β value should read $\beta = 3.92$. For juvenile survival the formula should read $\beta = 4.07 - 0.87P$.

Page 53, Table 3.1: The row "Intercept (β value) for juvenile survival" should read as follows:

Parameter	**Worst value (Lower 95% confidence interval)**	**Predicted values**	**Best values (Upper 95% confidence interval)**
Intercept (β value) for juvenile survival	2.95	4.07	5.19

Page 75: Methods, first sentence. Reference to Appendix C should be *D*.

Abstract

This thesis aims to assess the effects of a translocation on a source population. In 1999, 21 North Island robins (*Petroica australis longipes*) were translocated from Tiritiri Matangi Island (Hauraki Gulf) to Wenderholm Regional Park (north of Auckland). Previous research on Tiritiri Matangi Island suggested that the population was limited to about 60 birds by the available habitat. There was high (about 75%) juvenile mortality each year, and the number of juveniles surviving closely matched the number of adults dying. It was therefore hypothesised that juvenile survivorship was density dependent, and that a portion of the population could thus be removed each year with little impact. The translocation was designed as an experimental reduction in density to test this hypothesis.

Survival was modelled using by mark-recapture analysis, and suggested that density dependence was present in the Tiritiri Matangi population. Survival of juvenile robins was correlated with the number of pairs present in the population during the breeding season they were produced. Population viability analysis (PVA) suggested that the Tiritiri Matangi robin population was not affected detrimentally by the removal of 21 birds for translocation, with a 0% probability of extinction within the next 20 years. The PVA indicated around 3 years was required for the population to recover to an equilibrium of around 65 birds. A sensitivity analysis suggested that even if all the parameters are overestimated, the probability of extinction of the Tiritiri Matangi population within 20 years was still low (1.3% for a worst-case scenario).

PVA indicated that the Wenderholm population had a high probability of extinction, but this may be an artefact of the translocation. This PVA was based on only one year of data, and therefore had a high degree of uncertainty. It nevertheless suggested that juvenile recruitment was a key factor limiting population survival; hence the viability of the population could be improved by identifying and managing threats to juvenile survival.

I investigated the viability of different harvesting regimes for the Tiritiri Matangi population. Annual, biennial and triennial harvesting indicated around 100, 90 and 80 birds respectively, could be removed over 6 years resulting in a 5% probability of extinction within 20 years. The model indicated that harvesting the population to as few as 4 pairs was possible, and would result in an extinction probability of 0% within 100 years. This would take about 10 years to recover from.

Acknowledgements

In writing this thesis I have been very lucky to have so many people give me advice, support and the benefit of their knowledge. Without these people I would never have got so far as I have. I just want to start by apologising if I miss you off this list. It's not intentional and I will probably be kicking myself the minute this gets to the binders and I realise all the people who have helped in their own little ways.

I want to start by saying a big thank you to my supervisor, Dr Doug Armstrong. He has taught me a lot, which is an amazing gift. I am grateful for all his support, for explaining things to me more than once, with infinite patience and for only offering to kill me once. He has been amazing through all aspects of my thesis and I consider myself lucky to have had his help.

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On Tiritiri Matangi Island I wish to thank the Department of Conservation (DoC) staff, Barbara and Ray Walter, Jason Taylor and Shaun Dunning. Their help and friendship made my fieldwork so much easier, enjoyable and memorable. They have variously taught me to drive, leant me their height where I was lacking, and taught me the joys of climbing a ladder that was vertical, attached only to the ground. Along with fellow students Rosalie Stamp and Ruby Jones and the many Supporters of Tiritiri Matangi volunteers, my experiences and confidence were greatly enhanced. Thank you!

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Finally, I would like to thank my family and friends that let me stay with them over the last three years, drove me to field sites and believed that one day I'd enter the "real world". Dad, Mum and Robert, who have given me a friendly ear and reminded me that I could come home any time I wanted, as long as at some point I brought a finished thesis with me. Well, just as I promised I am bringing it.

Thanks to everyone who has made this research, not only possible, but an experience that I will never forget!

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Introduction

Translocating birds from established areas to initiate new populations, or augment small populations, is an important conservation management tool in New Zealand (Armstrong & McLean 1995). While translocated populations are often studied, the potential effects on source populations have been almost entirely ignored. McCarthy (1994) expressed the cost of reintroduction efforts as the increased risk of extinction faced by the source population due to the removal of individuals. If a recovery takes a long time and/or the source is placed at risk of extinction, this cost may outweigh the potential conservation gains from the translocation.

To ensure rapid recovery from translocations with minimal risk of extinction, what factors do we need to consider? Burgman et al. (1993) suggested that questions relating to this could be answered with mathematical models. These models may include parameters such as survival, fecundity, minimum population size and reproduction (Burgman et al. 1993, Rosenburg et al. 1993). The study of life history parameters is becoming increasingly important in ecology, particularly in studies of population regulation (Lebreton et al. 1992).

In this thesis I look at the effects of a translocation on a source population of North Island robins (*Petroica australis longipes*). This translocation involved the removal of 21 robins, in March 1999, from Tiritiri Matangi Island in the Hauraki Gulf, for reintroduction to Wenderholm Regional Park north of Auckland (Fig. 1.1). I assess how the Tiritiri Matangi population reacts to this density perturbation in terms of population parameters and risk of extinction.

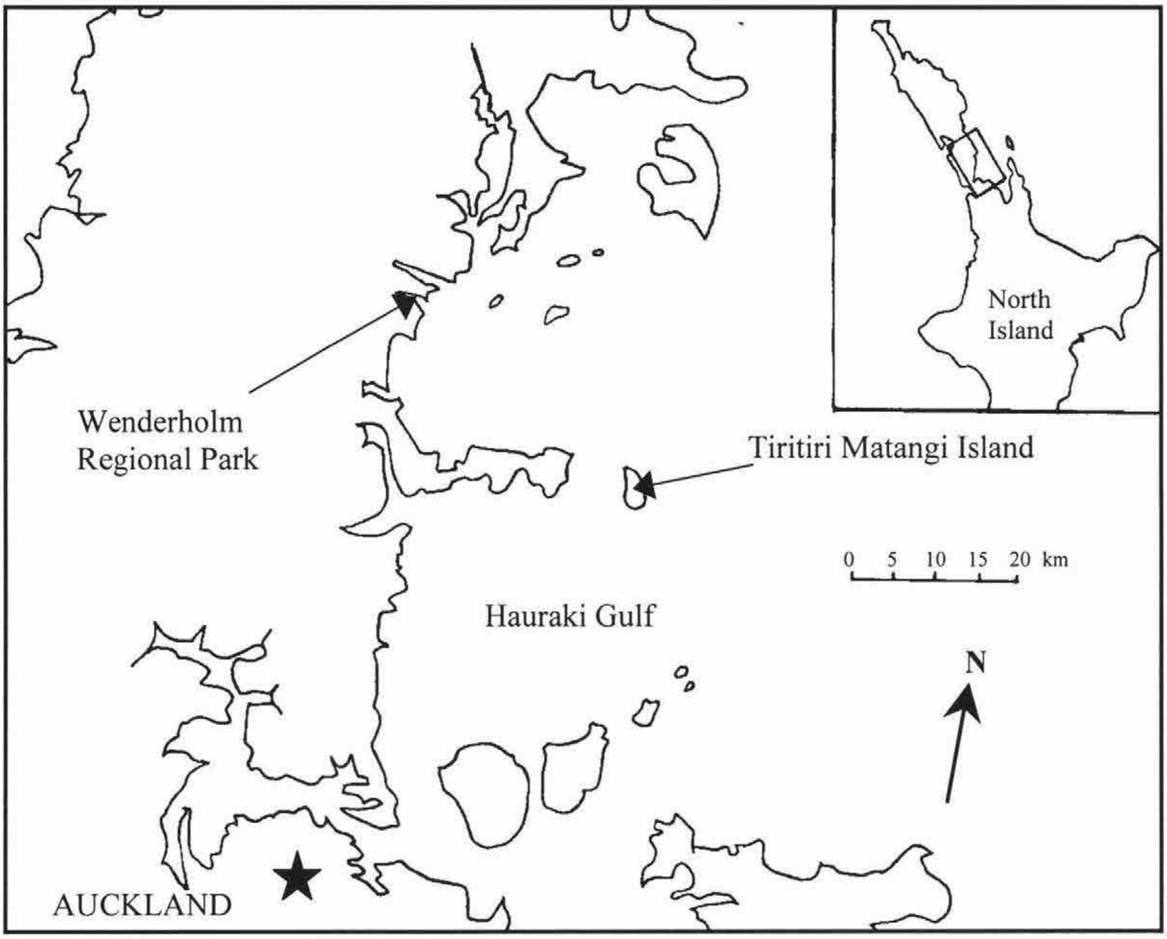

Fig 1.1. Map showing locations of Tiritiri Matangi Island and Wenderholm Regional Park, North Island, New Zealand.

TRANSLOCATIONS

"Translocation" is broadly defined as the intentional release of captive-reared and/or wild caught animals into the wild for the purpose of establishing a new population, re-establishing an extirpated population or augmenting a critically small population (Griffith et al. 1989). Griffith et al. (1989) estimated that 700 translocation programs are conducted annually in North America alone, and this has increased in the past two decades (Wolf et al. 1996).

In New Zealand, translocations have been conducted since at least the 1880s with Richard Henry's releases of endemic, flightless birds to offshore islands (Saunders 1994). The black robin (*Petroica traversi*) is probably one of the most well known cases of a reintroduction, where an entire species was relocated from Little Mangere Island to Mangere Island (Merton 1992). The reintroduction of New Zealand robins has been purported as a key component of ecological restoration by Armstrong (2000), and translocations of South Island robins (*Petroica australis australis*) have been used as an analogue for black robins (Merton 1992). There has been a rapid acceleration in the number of translocations in the last 30 years (Armstrong & McLean 1995). By June 1993, over 392 individual translocations of at least 50 taxa (the majority of which were birds) had been recorded in New Zealand (Saunders 1994). With over 700 offshore islands and the advent of mainland islands, New Zealand provides a rare opportunity to undertake a managed approach to translocations (Saunders 1994).

Guidelines for the design and practice of re-introductions are being produced in an attempt to move away from translocations as one-off management exercises (Kleiman 1989, Towns et al. 1990, IUCN 1998). If translocations are to be effective, it is important that those engaged in translocations monitor their projects scientifically, and then ensure that their results are available and preferably published (Stanley-Price 1991). We need to know how well translocations work, what factors are associated with success, and what factors allow greatest success. Therefore, a greater emphasis needs to be put on experimentation involved with re-introductions (Armstrong et al. 1994). An example of this can be seen in the first robin translocation to Tiritiri Matangi, which was designed as a test of familiarity (Armstrong 1995).

NORTH ISLAND ROBINS

The New Zealand robin or toutouwai (*Petroica australis* (Sparrm.), Fig. 1.2) is a passerine in the family Eopsaltriidae, which include the closely related Chatham Island black robin (*P. traversi* (Buller)) and the New Zealand tomtits (*P. macrocephala* (Gmelin)). The New Zealand robin is further divided into three subspecies, the North Island (*Petroica australis* *longipes* (Lesson)), the South Island (*P. australis australis* (Sparrm.)), and the Stewart Island (*P. australis rakiura* (Fleming)). The South Island subspecies is slightly larger than the North Island (Oliver 1974). Maloney & McLean (1995) noted that South Island robins on Motuara are 35-40g, and (Armstrong et al. 2000) noted that North Island robins on Tiritiri Matangi were 26-32g. There are subtle differences in plumage between North and South Island robins (Guthrie-Smith 1925). The North Island robin has a streaky appearance with a whitish belly whereas the South Island robin has a darker (smoky black) back and yellowish white belly. The Stewart Island robin is smaller than the South Island robin, with darker upper parts and white breast (Flack 1985).

Figure 1.2. North Island robin (*Petroica australis longipes*) feeding chick in nest. Photo: Tim Lovegrove.

Robins nest in a variety of sites – in hollow trees, against banks, adhered to the trunks of tree ferns, in forks or branches of live trees and nests are usually sheltered from above and on one side. The robin breeding season on Tiritiri Matangi stretches from September through mid-February (Armstrong et al. 2000), and is similar in other parts of the North

Island (Oliver 1974, Powlesland et al. 2000). During this time they lay up to three clutches with 2-3 eggs per clutch, but more clutches may be laid if unsuccessful (Brown 1997, Armstrong et al. 2000). Guthrie-Smith (1925) discovered one clutch with 5 eggs, but was unable to confirm their hatching. Robins are ground-feeding insectivorous birds that feed mainly on small invertebrates, including wetas, worms, grubs, caterpillars and spiders, but have been reported to occasionally take berries (Turbolt 1967, Martinson 1991). Robins on Tiritiri Matangi Island have also been observed killing and attempting to eat skinks (Doug Armstrong, pers. comm.; personal observation).

Robins are territorial birds and defend their territories diligently during the breeding season. Flack (1976) reported territories ranging from 0.2-0.6 ha on predator-free islands. This was also the size reported for robins on Inner Chetwood Island, Marlborough (Powlesland 1983). In coastal broadleaf forest on Kapiti Island (during the 1982-1986 period, when possums (*Trichosurus vulpecula*), Norway rats (*Rattus norvegicus*), kiore (*R. exulans*) and weka (*Gallirallus australis*) were all present), robin numbers ranged from 2.7 to 8.9 birds/ha (Lovegrove 1988). Robins have generally been thought to have quite limited powers of dispersal (Flack 1976), but there has been little evidence for this. Observations on Tiritiri Matangi Island show that while adults are generally sedentary, this is not be the case for juvenile and recently translocated birds (Armstrong 1995, Armstrong & Ewen in press). Several Stewart Island robins recently flew from their release site on Ulva Island back to their original site on Stewart Island 18 km away (Brent Beaven, pers. comm.). Newly translocated robins were observed leaving Motuara Island, flying nearly 1500 m (Tim Lovegrove, pers. comm.). A juvenile robin from Paengaroa Scenic reserve was recently found about 10 km away near Taihape (Liz Raeburn, pers. comm.).

Robins are patchily distributed on the main islands of New Zealand as well as being found on some offshore islands (Flack 1985). While robins are still found on the mainland, they have declined from most of their former range following European settlement. Buller (1888) announced that the robin had become one of the rarest of native birds, that it was seldom met with on the mainland, and that its doom was sealed (Fleming 1950). It appears that Buller may have been a little premature in his predictions of doom. The robin has been reasonably sensitive to European settlement and has disappeared from large areas in the North Island (Oliver 1974). However, robins do show some ability to adapt to civilization with some appearing in cultivated gardens (Martinson 1991) and in exotic pine plantations where there is a good understorey of exotic ferns and native shrub (Daff 1974, Oliver 1974). These include pine plantations in Waimarino forest (Raeburn 2001) and plantations in the Tokoroa and Otanewainuku districts and Mamaku Plateau, which were the source locations for robin reintroductions to Mokoia and Tiritiri Matangi Islands (Jansen 1993, Armstrong 1995). Robins are vulnerable to introduced predators like rats, mustelids, cats and occasionally possums (Brown 1997). Native predators include Moreporks (*Ninox novaeseelandiae*) and Australasian harriers (*Circus approximans*). Introduced predators and European settlement have frequently been identified as causes of decline, especially in the North Island (Bell 1986, Duncan et al. 1999, Armstrong 2000).

The current distribution now stretches in a band across the central North Island from Taranaki to the Bay of Plenty and Te Urewera National Park (Heather & Robertson 1996). In the South Island they are relatively common north of Arthur's Pass National Park, in Buller, Nelson and coastal Marlborough. South of Arthur's Pass they are patchily distributed, with strongholds in Okarito Forest, the eastern foothills of Fiordland, the Umbrella Mountains of northern Southland, and around Dunedin. The Stewart Island robin is moderately common on Stewart and some outlying islands (Heather & Robertson 1996).

Robin populations also survived on offshore islands (e.g. Little Barrier and Kapiti Islands). Robins were successfully reintroduced to Motuara and Allports Islands in 1973, and from 1983-1986 robins were reintroduced twice to Maud Island (unsuccessful both times), Moturoa Island (unsuccessful) and Moturua Island (successful) (Armstrong 2000). More recent 'range extensions' through translocations include Mokoia Island in Lake Rotorua in 1991 (Jansen 1993), Tiritiri Matangi Island in 1992 (Armstrong 1995) and to mainland islands such as Wenderholm Regional Park in 1999 (this study). For a full list of translocations up to 1999 see Table 1 in Armstrong (2000), and for more recent reintroductions see http://www.massey.ac.nz/~Darmstro/nz_projects.htm.

TIRITIRI MATANGI ISLAND

Tiritiri Matangi Island (36°36'S, 174°53'E), part of the Hauraki Gulf Maritime Park, is a 220 ha island situated 28 km northeast of Auckland, 4 km east of Whangaparoa Peninsula (Fig 1.1). The island has a gentle topography with slopes running down from a main ridge forming a mid-line approximately northwest southeast (Esler 1978). The highest point on the island is 91 m above sea level (Mitchell 1985). The climate on Tiritiri Matangi is relatively mild with moderate rainfall and temperatures ranging from a mean monthly minimum of 9.2°C in July to a mean monthly maximum of 22.6°C in February (Mitchell 1985). However, rainfall tends to be concentrated in autumn and winter with a tendency for drought in summer. The island's location means that it experiences the full force of northeasterly cyclonic storms (Mitchell 1985).

Tiritiri Matangi Island has had a long history of human activity, first by Maori (Kawerau and Ngati Paoa) and then by European farmers, with 92% of the island being pasture by the 1940s (Drey et al. 1982). Farming ceased in 1971, by which time the remaining vegetation had been reduced to a few small remnants in gullies (Cashmore 1995). In 1980, 206 ha of scenic reserve was designated a scientific reserve, with the remaining 16 ha being incorporated in 1985 (Mitchell 1985). Management has been intensive, including the planting programme, the introduction of pollinating and seed dispersing birds, and the removal of kiore (Hawley 1997). Planting on the island began in 1984 and finished in 1993. About 15 ha is made up of forest remnants ranging in size from 0.15 to 3.8 ha, with stands ranging in age from a few decades up to about 100 years. A further 100 ha is covered by replanted vegetation (Galbraith & Hayson 1994) with 14-28 ha of this suitable for robin territories (Fig 1.3). There are approximately 2-3 birds/ha with about 2 pairs/ha. Not all the island has been replanted. This is to ensure that a diversity of habitats is maintained and hence a greater diversity of animal life can be supported (Galbraith & Hayson 1994).

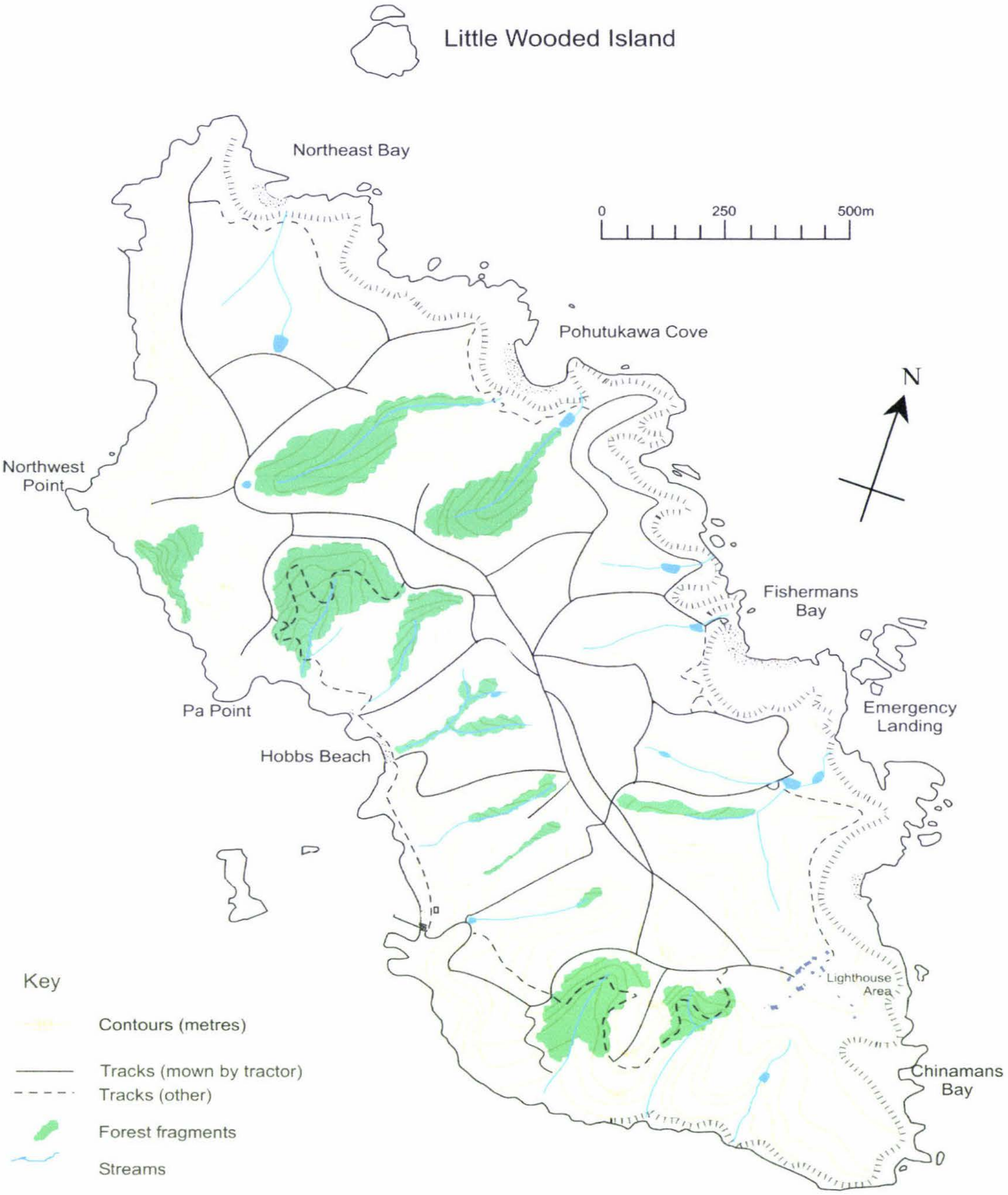

Fig 1.3. Tiritiri Matangi Island showing the main forest fragments where robins have held long-term territories, which correspond to the most mature patches. The remainder of the island is mostly regenerating planted vegetation or grassland.

The 1982 management plan for Tiritiri Matangi Island proposed the reintroduction of a number of species that could have once been present on the island (Drey et al. 1982). The New Zealand robin was the sixth bird species reintroduced to Tiritiri Matangi Island (Galbraith & Hayson 1994). There have been 9 other translocations of bird species including, red-crowned parakeets (*Cyanoramphus novaeseelandiae*), North Island saddlebacks (*Philesturnus carunculatus rufusater*), whiteheads (*Mohoua albicilla*), brown teal (*Anas aucklandica chlorotis*), South Island takahe (*Porphyrio mantelli hochstetteri*), little spotted kiwi (*Apteryx owenii*) (Galbraith & Hayson 1994), stitchbirds (*Notiomystus cincta*) (Ewen 1998) kokako (*Callaeas cinerea wilsoni*) (Jones 2000), and North Island fernbirds (*Bowdleria punctata vealeae*). Others planned include the tuatara (*Sphenodon punctatus*) (Ussher 1999). Flora species that have been translocated include species that may have been present if it weren't for human intervention and are important food sources for birds (Mitchell 1985, Hawley 1997).

WENDERHOLM REGIONAL PARK

Wenderholm Regional Park is a 134 ha peninsula 40 km north of Auckland (Fig. 1.1). It is the site of the longest-running mainland programme in the Auckland region. Wenderholm is the field base for the four northern regional parks (Shakespear, Wenderholm, Mahurangi and Tawharanui) and has the most northern parks staff based there. Wenderholm has 60 ha of mature coastal forest, which was expected to be enough to house a viable robin population (Lovegrove & Greene 1998). Wenderholm has several adjoining bush areas including Loch Amber, Waiwera Hill Scenic Reserve and privately owned forest and shrub lands between the Puhoi and Waiwera Rivers. Although robins are unlikely to breed very well in these peripheral areas they could act as reservoirs for surplus birds from Wenderholm itself (Lovegrove & Greene 1998).

A large proportion of Wenderholm Regional Park is managed intensively as a small mainland island. This management includes a poison grid, which operates between September and March each year. Due to the geography of the peninsula, reinvasion by rats is quite slow (Lovegrove & Greene 1998). Pest control also includes possums, mustelids and feral cats (Lovegrove et al. 2000). By 1998 restoration had reached the stage where bird reintroductions could be included as part of the restoration programme (Lovegrove et al. 2000).

OBJECTIVES OF THESIS

My thesis aims to assess the cost of the translocation of North Island robins (*Petroica australis longipes*) from Tiritiri Matangi Island to Wenderholm Regional Park. I have identified costs in terms of the probability of extinction following (McCarthy 1994). This involves looking at the established Wenderholm population as well as the Tiritiri Matangi population. In addition, I have investigated the feasibility, in terms of probability of extinction, of regular harvesting of robins from the Tiritiri Matangi population.

This has been carried out in steps:

Chapter 2: ***Density dependence and survival.***
I use mark recapture methods to investigate survival of the Tiritiri Matangi robins. Combining experimental manipulation of the island with analysis of survival, I investigate density dependence in the population. If survival is density dependent, we may expect that the population could be sustainably harvested for translocation.

Chapter 3: ***Population Viability Analysis.***
I use data from both robin populations (Tiritiri Matangi and Wenderholm) to estimate parameters required for simulation models of the populations. I then simulate both populations to estimate probabilities of extinctions and to assess the costs of the translocation to the Tiritiri Matangi robin population.

Chapter 4: ***Harvesting.***
I investigate the effects of different harvesting regimes using the simulation model for the Tiritiri Matangi robin population developed for chapter 2.

Chapter 5: ***Summary and Conclusions.***

I bring all three chapters of the thesis together and suggest management actions for the two robin populations. I discuss the broader implications of harvesting populations for translocations including the use of one source repeatedly for translocation

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Density Dependence and Juvenile Survival

INTRODUCTION

The notion of density "dependence" implies a reciprocal causal connection between population density and factors determining it (Royama 1977). This involves the idea that population numbers are regulated by one or more factors that act as negative-feedback loops on the population's growth rate (Murray 1999; Turchin 1999; Elkinton 2000). The regulating factors, such as predation, disease, or competition for food or other resources, act linearly or curvilinearly on birth and death rates (Murray 1999). Stubbs (1977) suggested that density dependent suppression of juvenile or adult survival is one way that a population can be regulated. She divided density dependent mortality into four categories according to where they occurred in the life cycle: (a) adult loss, (b) reduced fecundity, (c) parasitism and predation and (d) young and larval loss.

Debate over the influence of density dependence on population regulation (or even its existence) has been widespread in the last five decades (Cappuccino & Harrison 1996; Elkinton 2000). Turchin (1999) suggests it is broadly agreed on that density dependence is a necessary, but not sufficient, condition for population regulation. Recent debate has been over statistical methods for detecting density dependence. Existing methods rely largely on series of counts as well as variation in population size (Fox & Ridsdill-Smith 1996). Paradoxically, the most stable populations, in which density dependence is most marked, are also those in which density dependence are most difficult to demonstrate (Newton 1991).

Density dependent factors may have a stabilising effect on bird numbers, and are widely assumed to influence fluctuations in the size of local bird populations. Increasing population size decreases food and space availability, decreasing fecundity and/or survival (Saether et al. 1996; Tinbergen et al. 1985; Williams et al. 1993). Mortality outside the breeding season is often considered a major factor determining bird numbers in the subsequent breeding season (e.g. Tinbergen et al. 1985). Density dependent winter mortality could therefore constitute an important regulating mechanism (Saether et al. 1996).

Murray (1999) proposed that proponents of density dependence should do more than describe what a regulated population should look like. Turchin (1999) suggests that we should be more interested in asking, "Why do populations behave as they do?" and that we build mechanistic explanations for this. Density manipulations typically show clearer, and more powerful, evidence for regulation than do the more abundant census and life-table studies (Cappuccino & Harrison 1996; Massot et al. 1992; Murdoch 1970; Sinclair 1988). Cappuccino and Harrison (1996) go on to state that experiments can reveal the causal mechanisms of regulation more conclusively than non-experimental methods. Elkinton (2000) notes that a common problem withi manipulative experiments is the small scale (in comparison to the size of natural populations) they are carried out on, but that they almost always yield more information than studies of unmanipulated populations.

North Island robins were reintroduced to Tiritiri Matangi Island in 1992. Population surveys and nest monitoring were carried out from 1992 until 1998, and Armstrong and Ewen (in press) used these data to model the dynamics of the population. Under their best model juvenile survival was density dependent, whereas adult survival was constant and equal for males and females. This conclusion was based on the substantially lower juvenile survivorship in 1995/1996 and 1996/1997, once the population had levelled off, as compared to the three previous years. Armstrong and Ewen (in press) proposed that, "If survival and/or reproduction is suppressed at high density, the population can be sustainably harvested for translocation or other purposes with no cost to the source population".

In 1999, 21 robins were translocated from Tiritiri Matangi Island to Wenderholm Regional Park. The translocation was designed as an experimental reduction in density with the aim of testing Armstrong and Ewen's (in press) model. The aim of this chapter is to identify any density dependent response in juvenile survival. Reanalysis was carried out with Armstrong and Ewen's (in press) data plus data I collected for two subsequent years including 18 months after the translocation. This analysis was used to test their prediction that density dependent juvenile survival should increase after the population was reduced below carrying capacity.

METHODS

FIELD METHODS

Most North Island robins on Tiritiri Matangi Island are individually identified with a unique combination of a numbered, B-size, metal leg band and 1-3 coloured plastic leg bands. Banding began in 1992 when the 44 original birds were released onto Tiritiri Matangi Island (Armstrong 1995), and continued until the end of the 1996/1997 breeding season. I began banding again at the beginning of the 1998/1999 breeding season and continued until the beginning of the 2000/2001 season. No banding was carried out during the 1997/1998 breeding season, so birds produced that year, and survived to adulthood, were banded during the next breeding season.

All known pairs were monitored throughout each breeding season except 1997/1998. Nests were usually found during incubation or the nestling stage and nestlings were typically banded at 7-15 days of age. Some nests were never discovered or could not be accessed with a ladder. Fledglings from these nests were usually captured with a hand-net about 4 weeks after fledging, after they started to feed for themselves but before they left the natal territory. Juveniles that left their natal areas unbanded were caught with hand-net or claptrap and banded if discovered later. However, these birds were not used in the survival analysis.

I visited territories at least weekly during the 1998/1999 and 1999/2000 breeding seasons (November – February), and at least once every two months the rest of the year. Nests were usually found by feeding mealworms to males who would subsequently call the female off her nest to feed her (males rarely fed females on the nest). The female could then be followed back to the nest. When nestlings were already present in the nest both adults would usually take mealworms back to the nest. If a female was observed constantly for 30 minutes or more without going to a nest, I concluded she didn't have one. Nesting females usually return to the nest within 7 minutes (Armstrong et al. 2000). On first discovering nests, and when necessary thereafter, I checked the contents visually. Fledglings could be found by feeding adults and seeing where they took the mealworms. Young are often tucked away and hard to find for the first few days after fledging, but subsequently become more conspicuous allowing identity to be confirmed by checking leg bands.

Surveys of the population were made by searching all suitable habitat on the island and recording all birds seen. Tiritiri Matangi Island is easily surveyed, because the suitable habitat is patchy, covering only a fraction of the island's entire area, and is well divided by trails. I searched for birds by following regular routes through each bush patch. Where necessary a tape of a robin territorial call was played to attract any birds in the area not found by searching. All sightings of individuals were recorded so that the timing of subsequent disappearances could be determined.

THE TRANSLOCATION

During March 1999, 21 birds were captured on Tiritiri Matangi Island (Fig 2.1). This included 16 adults and 5 juveniles. Removing 20 to 30 birds was predicted to have no effect on the following year's breeding population based on a density dependent model of juvenile survival. Under this model juvenile survival was assumed to be 64% at low density, but to be truncated at higher densities due to the population being limited to a carrying capacity of 65 at the start of breeding. This was a plausible model, given that the population had levelled off at 65-67 birds for the previous 3 years, and the model gave a good fit to the data (Armstrong & Ewen, in press). The model further assumed that the juvenile survival probability was constant from the time they fledged until the start of the next breeding season.

Young birds were caught with a hand-net, whereas most adults were captured with baited claptraps. Two trap-shy adults were caught with a mist-net. Adults were targeted, to maximise the sample size of juveniles available for our test of density dependence. The 5 juveniles removed were previously unbanded, so could not be used in the analysis. Adults were taken from 5 different forest patches (Fig 2.1).

This was done to clear territories, although Armstrong's (1995) experimental translocation to Tiritiri Matangi suggested that familiarity in translocated robins does not affect subsequent survival, pairing, or reproductive success.

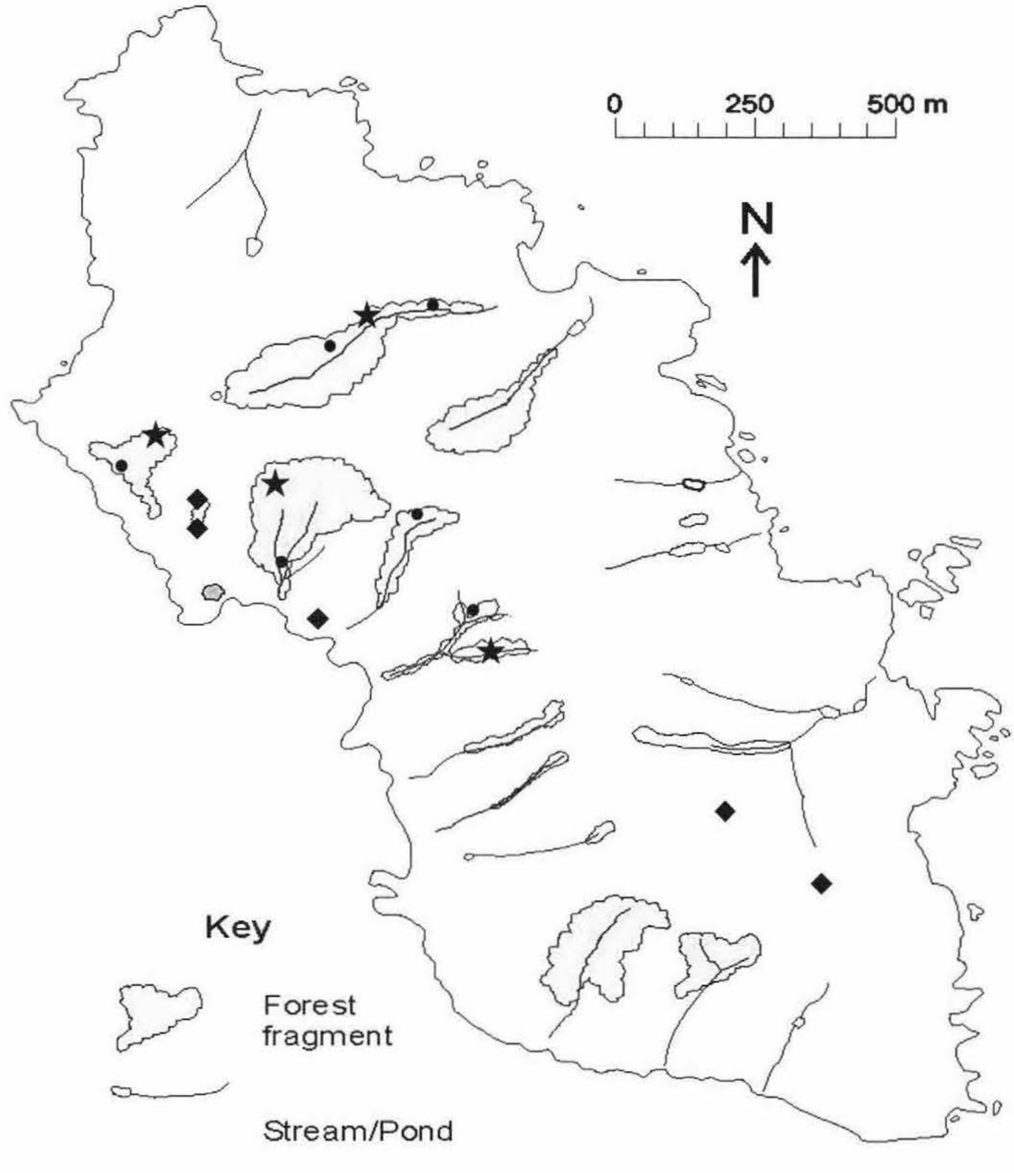

Fig 2.1. Locations of paired adult (●), unpaired adult (★) and juvenile (◆) North Island robins removed from Tiritiri Matangi Island for translocation to Wenderholm Regional Park. Shaded areas show forest patches where robins have held long-term territories, which correspond to the most mature patches. The remainder of the island is mostly regenerating planted vegetation or grassland.

ANALYSIS

Modelling Survival

Analysis was carried out using MARK version 1.9 (White & Burnham 1999) http://www.cnr.edu/~gwhite/mark/mark.htm. MARK is a program designed for use with capture-recapture survey results. The data were analysed using the Cormack-Jolly-Seber (CJS) model (live animal recaptures that are released alive) (Seber 1965; Clobert & Lebreton 1991; Lebreton et al. 1992; White & Burnham 1999). The analysis was performed using a 466 Mhz computer with 64 megabytes of RAM, running Windows 98.

The CJS model has several underlying assumptions: 1) Every marked animal present in the population at time i has the same probability of recapture, p_i; 2) every marked animal in the population immediately after time i has the same probability of surviving to time i+1; 3) marks are not lost or missed; 4) all samples are instantaneous, relative to the interval between occasions i and i+1; and 5) each release is made immediately after the sample (Clobert & Lebreton 1991; Cooch & White 1998). MARK allows the interval between the captures to be unequal. It also allows assumptions (1) and (2) to be relaxed by creating different groups of animals with different survival and resighting probabilities, fitting individual covariates, or adding age structure. The CJS model calculates separate survival (ϕ) and resighting (p) probabilities for each interval, but MARK allows the model to be simplified by adding constraints (see below).

Instead of recapturing marked animals, resightings may be used to make encounter histories. In this case animals are encountered when they are next seen alive as opposed to being captured. This has several advantages over recapturing in terms of the assumptions listed above. Some animals captured repeatedly may become trap-shy or attracted to traps; hence not all animals in the population would show the same probability of recapture.

Capturing animals may also affect their survival (e.g. through stress). In this study birds were resighted, rather than recaptured, each encounter occasion.

Capture-recapture models like CJS estimate survival (ϕ) and recapture (p) rates based on a series of encounter occasions. Animals are captured from the population, marked and released at time t_1. The marked animals are encountered when they are seen (or captured) alive again at times $t_2, t_3, t_4 \ldots t_n$. Each succeeding capture occasion after t_1 is one encounter occasion (White & Burnham 1999). Encounter histories are coded as 1s or 0s according to whether the animal is seen (captured) alive (1) or not (0) respectively at each encounter occasion. Survival rates (ϕ) are calculated between encounter occasions (e.g. t_1 to t_2) and recapture rates (p) are calculated at encounter occasions (e.g. at t_2) (Fig. 2.2).

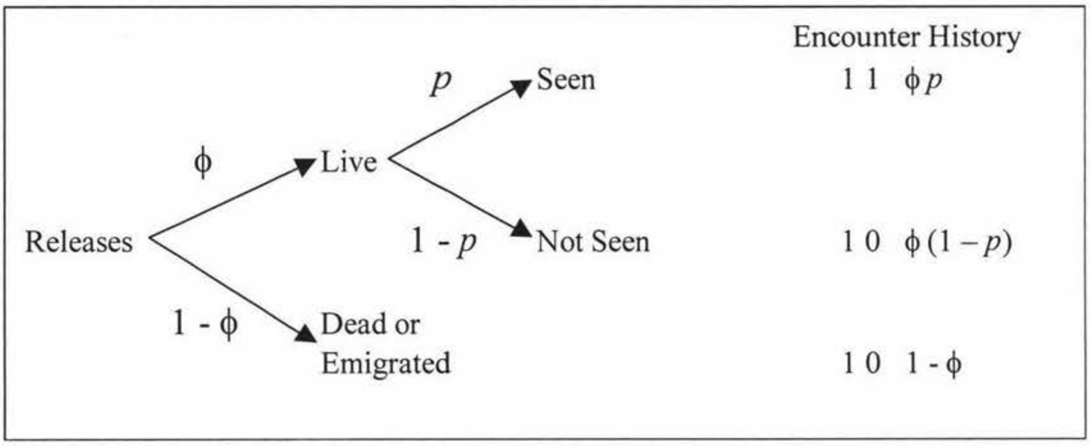

Figure 2.2. The Cormack-Jolly-Seber (CJS) model. Live recaptures are the basis of the CJS model. Marked animals are released into the population, usually by trapping them from the population. Marked animals are then encountered by catching them alive, and re-releasing them, or resighting them. If marked animals are released into the population on occasion 1, then each succeeding capture occasion is one encounter occasion. ϕ is the survival probability from one encounter to another, and p is the resighting probability at each encounter occasion. (From White & Burnham 1999).

Encounter histories were compiled from data covering the eight years 1992 – 2000. This includes the data from both before and after the translocation. Seventy-seven encounter occasions (including the two releases) were recorded over these eight years. However only 18 of these were used in the encounter history for this analysis. The encounter occasions used were taken from January and September each year (starting with September 1992) except for January 1998. An additional occasion was included in Mid-October 1993, which corresponded to three weeks after a poison drop (Brodifacoum cereal bait) to eradicate kiore (*Rattus exulans*). An extra encounter occasion in October 2000 was added at the end so survival could be calculated right up until September 2000. Birds translocated to Tiritiri Matangi Island entered the population in the September after the translocation (if still alive). Juveniles were considered to enter the population all at once at the end of the breeding season in January. Birds were considered adults once they survived to the September following their fledging. The encounter history contained 68 unique histories. No immigration of robins into this population occurred, and any emigration is equivalent to mortality.

Once the encounter histories are entered, MARK uses two types of matrices to add age structure or constrain the parameters. 1) The Parameter Index Matrices (PIM) allows the user to modify the underlying model including modifications based on time or cohorts. In this study the PIM were used to separate survival and resighting parameters for adults and juveniles. 2) The Design matrix is used to constrain the parameters resulting from the PIM. 'In the present context we are referring to a mathematical constraint – "forcing" MARK to estimate survival and recapture rates after imposing a specific set of *linear* constraints on the structure of the *underlying* model' (Cooch & White 1998). The design matrix in this study was coded to initially recognise four parameters that could affect survival (ϕ) and/or resighting (p): age (a), year (y), season (s), and poison (p). Age simply groups the birds into adults and juveniles. There were eight years stretching from September to September (except for 1997/1998 which ran from October to October). There were two seasons, the breeding season from September to January, and the non-breeding season from January to September. Armstrong & Ewen (2000) found that there was strong evidence that the survival probability was lower immediately after the poison drop in September 1993. The poison effect was therefore added to account for the unusually low survival at this time.

The design matrix is used to try and reduce the number of parameters in the model while retaining a reasonable fit to the data. This process is part of model selection.

Models are written in the form {ϕ (••••), *p* (•••)}. Here the dots (•) represent the parameters used to model survival (ϕ) and resighting (*p*). An explanation of notation can be found in (Lebreton et al. 1992).

Model Selection

Lebreton et al. (1992) recommend that the model selection process start from a global model compatible with the biology of the species studied and with the design of the study. The global model must include all the factors included in any of the simpler models considered. Once the global model is confirmed to have a good fit to the data, a more parsimonious model is selected based on Akaike's Information Criterion (AIC).

Goodness of Fit (GOF)

The global model used for this study was {ϕ (a*y + s*y + p), *p* (a*y + s*y + p)}. The * indicates an interaction term. I considered interactions between age and year and season and year (time) to be potentially important, hence they were included in the global model. Including these interactions allowed for the possibility that patterns if annual variation in survival differed between age classes or seasons. This model has 24 survival and 24 resighting parameters. Comparing the relative fit of a general model with a simpler (reduced parameters) model provides good inference only if the more general model adequately fits the data (Cooch & White 1998). The Goodness of Fit (GOF) test in program MARK uses a parametric bootstrapping approach in which the parameter estimates for the model in question are used to simulate data. The bootstrapped values are used to see where the deviance of the observed model falls in comparison to the distribution of all the deviances from the simulated data. I simulated 500 bootstrap data sets.

Akaike's Information Criterion (AIC)

After testing the global model, subsequent model selection was based on AIC. Aikaike's Information Criterion (AIC, or AIC_c as implemented in MARK) is a means of showing support for different models. AIC_c is not a test statistic but a measure of the information value of a model. It is calculated as

$$\mathbf{-2\log Likelihood + 2K + 2K(K + 1)/(\mathit{n\text{-}ess} - K - 1)}$$

where K is the number of parameters estimated and *n-ess* is the effective sample size (Akaike 1985; Cooch & White 1998). AIC_c is recommended by Burnham and Anderson (1992), Lebreton et al. (1992) and Burnham et al. (1995) and corrects for the bias that AIC has when sample size is low. The best (most parsimonious) model is that with the lowest AIC_c value. Likelihood Ratio Tests (LRTs) may also be used to statistically test for significant differences between models. However, this approach has several drawbacks including the fact that tests cannot be performed between non-nested models. Debate is continuing as to which method is the best or whether to use both (Cooch & White 1998). This chapter uses AIC_c.

Overdispersion may occur in the data, this is when the sampling variance exceeds the theoretical (model based) variance. To counter this a variance inflation factor *c* can be estimated from the global model. The estimate of *c*, ĉ, is then incorporated into AIC_c to produce $QAIC_c$. This is the quasi-likelihood AIC_c and is calculated by modifying the formula for AIC_c:

$$\mathbf{-2\log Likelihood/\hat{c} + 2K + 2K(K + 1)/(n\text{-}ess - K - 1)}$$

When no overdispersion exists, $c=1$ and the formula for $QAIC_c$ reduces to AIC_c. (Lebreton et al. 1992) suggest ĉ should not exceed ≈ 3, with values like 10 almost certainly indicating that the model structure is grossly inadequate.

Burnham and Anderson (1992) recommend that models having $\Delta AIC_c < 1\text{-}2$ are nearly tied. In this case normalized Akaike weights can be used to provide an index of relative plausibility from the formula:

$$\mathbf{AIC_c\ Weight\ of\ Model\ M_i = \exp(-1/2 * \Delta AIC_c\ of\ Model\ M_i) / [\Sigma \exp(-1/2\ \Delta AIC_c)].}$$

The biology of the population under study drives the selection of an appropriate set of models to select among (Lebreton et al. 1992; Akaike 1985; Cooch & White 1998; Burnham et al. 1995). I therefore nominated a set of survival models plausible for juvenile robins on Tiritiri Matangi, following Armstrong and Ewen (in press).

Resighting Probability

Models include both survival (ϕ) and resighting (*p*). However, these can be resolved separately. As recommended by Lebreton et al. (1992), I simplified the resighting model first to save greater power for survival estimation (Table 2.2). Eleven resighting models were compared to the global model (ϕ(a*y + s*y + p) *p* (a*y + s*y + p)). The aim is to find biologically sensible models that describe the population, not to attempt to exhaustively explore every possible combination of model parameters. By removing the interaction s*y (season*year), time specific events were first removed. To examine if separating age into first year and adult birds was necessary the a*y (age*year) interaction was eliminated, followed by 'a' (age). Finally the model $p_.$ was tested as this was found to be the best resighting model in a previous analysis of this population (Armstrong & Ewen, in press).

Survival Probability

Analysis of survival had two aims. The first was to see if the data still followed different yearly survival for adults and juveniles. This started with the model {ϕ (a*y + s*y + p) *p* (a*y + p)}, which was compared to a set of candidate models for survival. Armstrong and Ewen (in press) found survival of males and females to be the same under the best model, thus gender differentiation was not tested. Four models were considered (Table 2.3) where: (1) changes in survival had different patterns for adults and juveniles (a*y); (2) changes in survival were parallel for the two age groups (a + y); (3) survival varied among years for juveniles only (a + y(J)); and (4) survival varied among years for adults only (a + y(A)).

Models with no difference between ages and/or years, and models that did and did not have a seasonal effect were also included.

The second aim was to describe the nature of the yearly variation in juvenile survival, assuming juvenile survival was not constant under the best model in Table 2.3. The type of variation in juvenile survival should indicate whether any density dependence in juvenile survival is evident. Five models were considered for this second part (Table 2.5): (1) juvenile survival probability is constant until the population reaches carrying capacity, then drops to a lower constant (thresh J); (2) juvenile survival probability is constant until the population reaches carrying capacity and then is truncated based on the predicted number of spaces available at the end of the breeding season (trunc J); (3) juvenile survival depends on the number of pairs at the start of the breeding season (pairs J); (4) juvenile survival depends on the total population at the start of the breeding season, including unpaired birds (N J); (5) juvenile survival depends on the total number of potential competitors (the population at the start of the breeding season plus the number of juveniles produced during the breeding season) (comp J).

Model (1) (thresh J) was analysed by grouping years in which the population was below the carrying capacity (K, estimated to be 65 birds) separately from those above it. With the translocation, 1999 was expected to be below K. Therefore 1993–1995 and 1999 (below K) were grouped together and 1996–2000, excluding 1999, (above K) were grouped together (note no data for 1998). Model (2) (trunc J) used a covariate to predict what the exact juvenile survival should be for each year in the years after carrying capacity was first reached (1996–2000). The value of the covariate for each year was calculated with the formula in Fig. 2.3 (See Appendix A). For models 3-5 a covariate was used to indicate the number of pairs, birds, or potential competitors each year. The logit link was used, so these models assumed a logit-linear relationship between survival probability and the covariate.

$P = 65 - A$

$S = P/F$ or 64%, whichever is less.

$\beta = \ln(S/1\text{-}S)$

$C = 0.575 - \beta$

Where: P = No of places available for juveniles.
A = No of adults still alive at the beginning of the next breeding season.
S = Juvenile Survival.
F = No of fledglings produced in the current breeding season minus any translocated in the subsequent year.
β = Estimated parameter value.
C = Covariate used in MARK to predict juvenile survival.

Figure 2.3. Formula used to calculate the value for the covariates used in the design matrix of the model $\{\phi\ (a + \text{trunc } J + p)\ p\ (a{*}y + p)\}$.

In addition to these density dependent models an attempt was made to investigate the suggestion that the translocation occurred too late in the year to affect juvenile survival. Juvenile survival may not be constant from fledging to the start of the next breeding season, as was assumed when predicting the effect of removing birds. If juvenile mortality is highest just after fledging, then the translocation in March may have been too late to have an effect on the juvenile survival. In this case we would predict that the juvenile survival in 1999 would be same as if there had been no translocation.

To examine this, new versions of models 1 and 2 were incorporated with the analysis described above (Table 2.5). For model (1), (thresh J), the first three years, 1993–1995 (below K) were simply separated from the last four years, 1996–2000 including 1999, (above K). Here, if there had been no translocation, we would expect to see survival in 1999 similar to that in years where the population number had not been reduced below K. This is the "without translocation" version (*-Trans*). The "with translocation" version (*+Trans*) is as described above.

Model 2 was based on the prediction that if the 16 adults had never been removed for translocation in 1999, 14 of these would have survived until September (annual adult survival rate 79%), giving 14 extra adults in 1999. Therefore model (2), (trunc J), described above is the "with translocation" version (+*Trans*). The "without translocation" version (-*Trans*) had a covariate for the year 1999 calculated as: P = 65 - (A+14) for 1999 (See Appendix A).

RESULTS

After the March 1999 translocation the total number of birds found in September was reduced from 67 the year before to 49 (Table 2.1). The number of juvenile settlers after the translocation did not increase in comparison to the two previous years as predicted under models 1 and 2 (thresh J) and (trunc J).

Table 2.1. Breeding North Island robin population (minimum number alive) on Tiritiri Matangi Island for the first 9 years after reintroduction. The question mark indicates the year where no monitoring occurred over the breeding season. Adapted from Armstrong and Ewen (in press).

	1992	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
Total Population in September	33	41	36	55	66	66	67	49	55
Surviving residents in September	-	27	29	27	45	51	50	34	38
Juvenile settlers in September	-	4	7	28	21	15	17	14	17
Translocated settlers in September	33	10	-	-	-	-	-	-	-
N° of Juvs produced in previous breeding season	-	4	14	42	45	54	?	57	60
N° of pairs during breeding season	7	15	14	22	25	25	29	24	26

GOODNESS OF FIT.

Based on 500 bootstrap data sets, the global model {ϕ (a*y + s*y + p), *p* (a*y + s*y + p} appears to adequately fit the data (P = 0.14). The overdispersion parameter $\hat{c}$ was 1.21. When I adjusted for overdispersion using $\hat{c}$ there was little difference between the $QAIC_c$ values and the AIC_c values. I therefore continued with the default $\hat{c} = 1$ - i.e. I used AIC_c to evaluate the information value of the models. To get a sense of the underlying model structure and check for unexpected occurrences, I graphed the estimates from the most parameterised (i.e. global) model (Fig. 2.4). The dip in adult survival at 13 months corresponds with the poison drop.

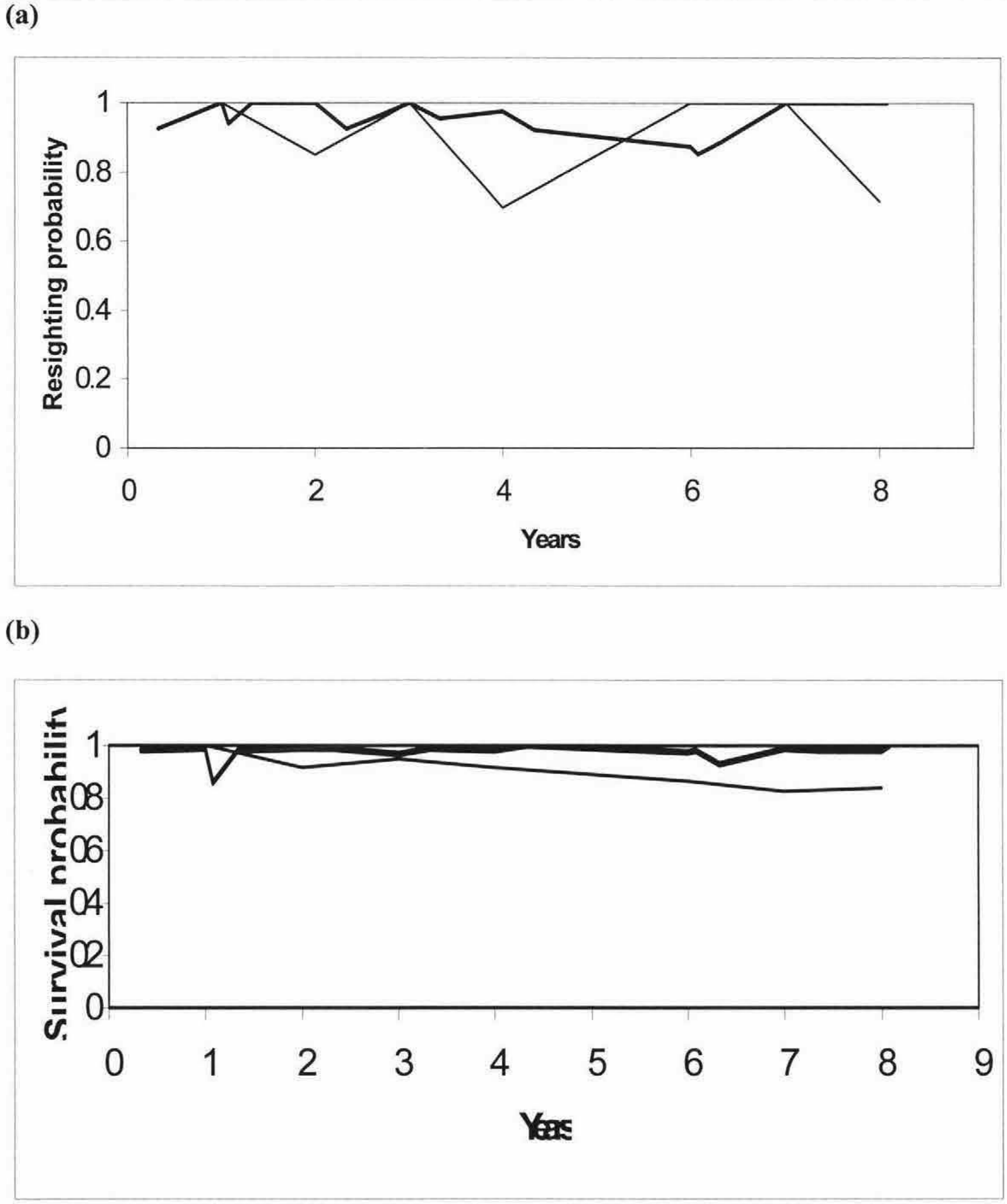

Figure 2.4. Survival probabilities **(a)** and resighting probabilities **(b)** for North Island robins on Tiritiri Matangi Island. Time (months) starts in September 1992, the time of the first breeding season after reintroduction. Adults are shown with a thick line (**——**) and juveniles with a thin line (——). Values were estimated using MARK 1.9 for the global model {ϕ (a*y + s*y + p), *p* (a*y + s*y + p}.

RESIGHTING PROBABILITY

The best resighting model (Table 2.2) was *p* (a * y + p). This model gives an estimated monthly resighting probability of 93.8% (SD=0.08). In this model, resighting probability varied between ages and years, but not with season. However, the model *p* (a * y + s), had an AIC_c within 2 of the best model. Akaike weights suggest the (best) model *p* (a * y + p) is nearly twice as plausible as the model *p* (a * y + s) (0.489/0.275 = 1.78). Removing the interaction between age and year (a*y) results in a large increase in the AIC_c indicating that the pattern of yearly differences in resighting probabilities were different for first year birds and adults.

Table 2.2. Models for resighting probability of North Island robins on Tiritiri Matangi Island. In all cases, survival was modelled as ϕ(a*y + s*y + p). The 'best' model is shown in bold. ΔAIC_c is the difference in the AIC_c of the current model and the model with the minimum AIC_c. W is the normalized Akaike weights. K is the number of parameters. Deviance is the difference in the –2log(likelihood) for the current model and the saturated model (model with a parameter for every unique encounter history). Models are shown in order of complexity (number of parameters). Model ϕ (a*y + s*y + p) *p* (a*y + s*y + p) is the global model. Age (a) is a separation between adults and juveniles. Year (y) is the year measured from September to September. There are two seasons (s), breeding and non-breeding. Poison (p) is the interval after the poison drop in 1993.

Model Resighting	**AIC_c**	**ΔAIC_c**	**W**	**K**	**Deviance**
p (a*y + s*y + p)	1133.124	3.85	0.071	48	269.716
p (a * y + s + p)	1131.464	2.19	0.164	42	281.259
***p* (a * y + p)**	**1129.276**	**0.00**	**0.489**	**41**	**281.259**
p (a * y + s)	1130.426	1.15	0.275	41	282.408
p (a + s + y + p)	1143.613	14.34	0	36	306.447
p (a + s + y)	1142.636	13.36	0.001	35	307.627
p (a + y)	1143.822	14.55	0	34	310.965
p (s + y)	1152.020	22.74	0	34	319.163
p (y)	1149.937	20.66	0	33	319.227
p (a)	1144.868	15.59	0	26	329.063
p (p)	1151.308	22.03	0	26	335.498
p .	1779.958	650.68	0	24	968.371

SURVIVAL PROBABILITY

The first survival models were designed to see if juveniles and adults showed different patterns of survival (Table 2.3). From the candidate models tested (see Methods, Survival Probability) the best model was {ϕ (a + y(J) + p) *p* (a*y + p)}. This model predicts constant monthly survival in adults (98%) except for the interval after the poison drop (85%). This corresponds to annual survival rates of 78.5% and 16.4% respectively. Juvenile survival varies over years under this model, with an average monthly survival of 90.2% (Table 2.4). Birds were considered juveniles for 8 months, from January to September. Therefore, the monthly survival probabilities were raised to the power of 8 to get probability of surviving until September. The best model had an AIC_c lower than all the other models and was weighted at over ten times more plausible than the next best model (Table 2.3).

Table 2.3. Models for survival probability of adult and juvenile North Island robins on Tiritiri Matangi Island. In all cases, resighting was modelled as *p* (a * y + p). The 'best' model is shown in bold. $\Delta\mathrm{AIC}_c$ is the difference in the AIC_c of the current model and the model with the minimum AIC_c. W is the normalized Akaike weights. K is the number of parameters. Deviance is the difference in the –2log(likelihood) for the current model and the saturated model (model with a parameter for every unique encounter history). Model ϕ (a*y + s*y + p) is the global model. Age (a) is a separation between adults and juveniles. Year (y) is the year measured from September to September. There are two seasons (s), breeding and non-breeding. Poison (p) is the interval after the poison drop in 1993.

Model Survival	**AIC_c**	**$\Delta\mathrm{AIC}_c$**	**W**	**K**	**Deviance**
ϕ (a*y + s*y + p)	1129.279	9.46	0.009	41	281.259
ϕ (a*y + s + p)	1132.714	12.90	0.002	35	297.705
ϕ (a*y + p)	1130.593	10.78	0.004	34	297.737
ϕ (a + y + p)	129.977	10.16	0.006	28	309.937
ϕ (a + y(A) + p)	1151.697	31.88	0	28	331.660
ϕ (a + y(J) + p)	**1119.816**	**0**	**0.977**	**26**	**304.008**

Table 2.4. Monthly juvenile survival and the probability of juveniles surviving until September for years 1993 – 2000. Results are from the model {ϕ (a + y(J) + p) p (a*y + p)}.

Year	**Monthly Juvenile Survival**	**Probability of a juvenile surviving until Sept.**
1993	1	1
1994	0.918	0.504
1995	0.946	0.641
1996	0.918	0.504
1997	0.867	0.319
1998	Unknown	Unknown
1999	0.824	0.213
2000	0.841	0.25
AVERAGE	0.902	0.49
STANDARD DEVIATION	0.062	0.273

The second set of survival models were used to investigate how juvenile survival varied over the years (Table 2.5). The best of these models was {ϕ(a + pairs J + p) p (a*y + p)}, suggesting that juvenile survival is dependent on the number of pairs in the breeding season that the juveniles were produced. This is better than the best model from Table 2.3, with the (pairs J) model being weighted five times more plausible. The model closest to the (pairs J) model was the (comp J) model. This had a $\Delta AIC_c > 2$ and the (pairs J) model is weighted 3.3 times better.

With respect to the "with" and "without translocation" models, in both cases the "without translocation" (-*Trans*) versions show lower AIC_c values than the "with translocation" (+*Trans*) models. This suggests that the translocation had little effect on the survival of the juveniles in the year of the translocation.

Table 2.5. Models for survival probability of North Island robins on Tiritiri Matangi Island, incorporating explanations for yearly variation in juvenile survival. In all cases, resighting was modelled as *p* (a * y + p). The 'best' model is shown in bold. ΔAIC_c is the difference in the AIC_c of the current model and the model with the minimum AIC_c. W is the normalized Akaike weights. K is the number of parameters. Deviance is the difference in the –2log(likelihood) for the current model and the saturated model (model with a parameter for every unique encounter history). Model ϕ (a + y(J) + p) *p* (a * y + p) is the best model from Table 2.3. Age (a) is a separation between adults and juveniles. Year (y) is the year measured from September to September. There are two seasons (s), breeding and non-breeding. Poison (p) is the interval after the poison drop in 1993.

Model Survival	**AIC_c**	**ΔAIC_c**	**W**	**K**	**Deviance**
ϕ (a + y(J) + p)	1119.813	3.30	0.124	26	304.008
ϕ (a + thresh J + p)+*Trans*	1140.196	23.68	0	21	334.903
ϕ (a + thresh J + p)-*Trans*	1123.293	6.78	0.022	21	318.000
ϕ (a + trunc J + p)+*Trans*	1138.853	22.34	0	21	333.559
ϕ (a + trunc J + p)-*Trans*	1125.422	8.91	0.008	21	320.129
ϕ (a + pairs J + p)	**1116.509**	**0.00**	**0.646**	**21**	**311.216**
ϕ (a + N J + p)+*Trans*	1126.523	10.01	0.004	21	333.491
ϕ (a + comp J + p)	1118.903	2.39	0.196	21	320.089

DISCUSSION

Where habitats are not disturbed, most bird species remain relatively stable in abundance over long periods. Breeding numbers may fluctuate from year to year, but between limits that are restricted compared with what their reproductive and mortality rates would allow (Lack 1954). Armstrong and Ewen (in press) found that the Tiritiri Matangi Island robin population increased until it reached a breeding population of about 65 birds and stayed at that level over three breeding seasons. General year-to-year stability in bird numbers is usually attributed to limiting factors acting in a density dependent 'regulating' manner (Newton 1998). In this study the aim was to look for a density dependent response in juvenile survival.

RESIGHTING PROBABILITY

When studying a population it rarely occurs that all individuals are followed all of the time from birth to death even if they are uniquely marked (Lebreton et al. 1992). Burnham et al. (1995) discovered that heterogeneity in capture probabilities had little effect on model selection using AIC. The use of the AIC-type approach here means heterogeneity should have little bearing on the resighting results. The fact that the best resighting model was *p* (a*y + p), and there was a large drop in AIC_c when the interaction a*y is removed, indicates that the resighting probability is affected by the age of the bird, and that the two age classes show different patterns of yearly variation. The age effect could occur due to a bias in surveying, to be less likely to spot new birds, especially in new locations, with variability mostly depending on the behaviour of the surveyor.

SURVIVAL PROBABILITY

In the initial survival analysis (Table 2.3) I was testing whether juvenile survival varied from year-to-year independently to adult survival. This was based on the conclusions from Armstrong and Ewen (in press) who suggest that a large number of juveniles are produced that do not survive due to the population being at carrying capacity.

Loery et al. (1987) suggest that there is a widespread belief in two generalizations about the age-specificity of avian survival rates: 1) survival probabilities of young birds for some period (e.g., 6 mo, 1 yr) following fledging are generally lower than survival probability for older birds, and 2) after reaching sexual maturity (or some other indicator of "adulthood") birds exhibit relatively constant survival probabilities. My analysis suggests that survival in the Tiritiri Matangi robins varies among years for juveniles, whereas adult survival is constant over time and higher than juvenile survival (Model ϕ (a + y(J) + p), Table 2.3). This supports Loery et al.'s (1987) generalizations, and is unchanged from the result reported by Armstrong and Ewen (in press) from the first 6 years of data.

I then investigated whether juvenile survival did in fact follow a density dependent pattern as suggested by Armstrong and Ewen (in press). Density dependent juvenile survival, with density independent adult survival has been found in a number of bird species (Silvereyes (*Zosterops lateralis chlorocephalus*), (McCallum et al. 2000); Song Sparrow (*Melospiza melodia*), (Arcese et al. 1992) and Blue Tit (*Parus caeruleus*), (Dhondt et al. 1990)). Newton and Marquiss (1986) found that density dependent loss in sparrowhawks (*Accipter nisus*) only occurred in birds that had left the nest but not yet entered the breeding population. With the density manipulation carried out, the threshold and truncation models of density dependence did not predict juvenile survival as well as expected. The best model, relating juvenile survival to the number of pairs present (pairs J) ϕ(a + pairs J + p), fitted the data well (Table 2.5) and was better than the model assuming that juvenile survival rates fluctuated stochastically over time ϕ (a + y(J) + p).

The (pairs J) model suggests that juvenile survival shows a density dependent response to the density of pairs in the breeding season that the juveniles are produced. It is reasonable to suggest that, in fact, juvenile survival is closely related to the total number of birds present in the population, not just paired adults. This was tested in the (N J) models (Table 2.5) and was found to have an AIC_c value >10 more than the best model. Therefore direct competition with the total number of birds (adults and juveniles) in this population seems unlikely. Arcese et al. (1992), Alatalo and Lundberg (1984) and Dhondt (1971) suggest that territorial behaviour of adults affects population size. This result was found in an island population of silvereyes where analysis suggested that density dependence in juvenile survival operated via territory-holding birds, rather than through the total population (McCallum et al. 2000). If territoriality affects juvenile survival, then for the observed relationship I would suggest that paired birds are more likely to show aggressive responses to juveniles. This would not be unexpected if we consider that unpaired birds holding territories are more likely to investigate new arrivals into their territory for breeding opportunities rather than showing an immediate aggressive response. Pairs may be more aggressive as they have chicks to defend/feed. Juveniles that have not left their natal territory may be affected by numbers of pairs via food requirements.

The comparison between "with translocation" and "without translocation" models (Table 2.5) suggests that the translocation was too late to have an effect on juvenile survival that year. To investigate density dependence in juvenile survival, any manipulation of bird numbers needs to occur before the bulk of the density dependent mortality occurs. In planning the translocation for this study it was assumed that juvenile survival was constant from the time they fledged until the next breeding season. Further analysis of my juvenile survival data (D. Armstrong, pers com) has shown that this assumption is incorrect. Juvenile survival was at its lowest in the first 2 months after fledging in both 1998-1999 and 1999-2000, and survival was close to the adult rate after that. Therefore, the majority of juvenile mortality in the 1998-1999 cohort occurred before the translocation.

This pattern has been found in other birds. In wood thrush (*Hylocichla mustelina*) survival was at its lowest during the first three weeks post-fledging (Anders et al. 1997). Dhondt (1979) found a survival probability of 0.252 for great tits (*Parus major*) during the first 10 weeks after fledging. Lack (1946) found that juvenile lapwings (*Vanellus vanellus*) showed lowest survival during their first month of life with a gradual increase in subsequent months. Flack (1976) indicated that an important factor in Kaikoura South Island robins, in some years, was high mortality of young in the stages before independence. The data here suggested that juvenile robins had an average monthly survival of 0.902 (Table 2.4). Nilsson (1987) found that density dependent local survival of nuthatch (*Sitta europaea*) fledglings is only found between fledging and autumn but the largest reduction in density of experienced birds occurs in winter.

Given that the translocation was too late to have an effect on juvenile survival it is important to note that the (pairs J) model is based on the number of pairs present at the start of the season that the juveniles are produced. In this model the survival of juveniles throughout 1999 is based on the number of pairs at the start of the 1998/1999 breeding season, well before the translocation occurred in March 1999. This being the case, the effect of the translocation would be expected to show in juveniles from the 1999/2000 breeding season.This is based on the premise that the removal of adults in March 1999 would affect the number of adults alive in the 1999/2000 breeding season. However, having fewer adults at the beginning of the breeding season would also result in fewer juveniles being produced and therefore fewer potential competitors. Therefore any increase in juvenile survival found could be a result of either a reduction in adults or other juvenile competitors, although this study suggests that competition from other birds (adults and juveniles) has little effect on juvenile survival (Table 2.5).

The slight increase in juvenile survival in 2000 is consistent with the density dependent mechanism of the (pairs J) model. However, the reduction in number of pairs in 1999/2000 was fairly minor, the 24 pairs present being similar to the 25 pairs in 1996/1997 (Table 2.1). A strong test of this model would require a greater reduction in the number of pairs down to the level observed in the first 3 years after reintroduction. The reduction experiment reported here did allow me to reject the model originally used to predict the effect of removal – i.e. that juvenile survival was truncated to a carrying capacity and was constant from fledging through to the next breeding season. That model predicted a strong and immediate response to my reduction in density. The best explanation based on observed patterns of juvenile survival is still a density dependent model (pairs J) but one that predicts a slower and weaker response to population reduction.

SUMMARY

- Juvenile survival is modelled well by the density dependent (pairs J) model.
- The translocation appears to have been too late to affect a strong density dependent response in juvenile survival in the year of the translocation.
- A larger reduction in the number of pairs would be a stronger test of the pairs model (pairs J).

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3

Population Viability Analysis

INTRODUCTION

Translocations can be used for conservation in two major ways. We might want to supplement a small population or we may wish to establish a species back in the wild (Caughley & Gunn 1996). Both of these options are accomplished by first selecting a population from which to remove individuals. With a translocation, for whatever reason, we must be aware that removal of animals from the wild would reduce already small populations (Caughley & Gunn 1996). Translocations could contribute to the decline of a population in a similar way to that of over-harvesting.

Population Viability Analysis (PVA) is often used in managing threatened or declining species and developing conservation strategies (Possingham et al. 1993, Bustamante 1996, Ballou 1997, Johnson & Braun 1999). PVA may also provide a framework for assessing the long-term costs and benefits of reintroduction and captive-breeding attempts (McCarthy 1994). Boyce (1992), McCarthy (1994) and Maguire et al. (1987) provide examples of PVA used in assessing the feasibility of translocations. Population viability analysis is a type of risk assessment, predicting the probability of extinction within a particular time interval for endangered species or population using either analytical or, more often, computer simulation techniques (Lacy 1993, Possingham et al. 1993, Ballou 1997, Johnson & Braun 1999, Harwood 2000).

Population models represent a rigorous synthesis of available knowledge and intuition regarding the dynamics of a species (McCarthy 1994). The PVA program VORTEX is perhaps the most widely used PVA simulation program (Lacy 1993). The VORTEX programme is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wildlife populations. VORTEX was originally written to model mammal and bird populations (Lacy et al. 1997).

The expected benefit from a translocation depends on the probability of establishing a new population in relation to the risk of endangering the source population. McCarthy (1994) studied this idea by looking at the risk of both populations becoming extinct. By doing this we can balance the costs to the source population with the conservation gains from the reintroduced population. McCarthy (1994) expressed the cost of reintroduction efforts as the increased risk of extinction faced by the source population due to the removal of individuals. The risk of both populations becoming extinct can be obtained by multiplying the risk facing the source population by the risk facing the reintroduced population. While translocated populations are often studied, the potential effects on source populations have been almost entirely ignored.

In early March 1999, 21 North Island robins (*Petroica australis longipes*) from Tiritiri Matangi Island were used as a source population for translocation to Wenderholm Regional Park. The Tiritiri Matangi robins have been studied since 1992, producing a large amount of data for estimating population parameters. This gave the opportunity to study the risk of extinction of the Tiritiri Matangi robin population with respect to its use as a source. Wenderholm Regional Park is a mainland site and has been used for research and management of New Zealand pigeons (*Hemiphaga novaeseelandiae*) since 1990 (Clout et al. 1995). The robins reintroduced there have been carefully monitored.

This chapter primarily examines the cost of this North Island robin translocation to the source population (Tiritiri Matangi). In addition I was interested in seeing what the overall cost of the translocation was in terms of both the source and reintroduced population. In this case cost is the increased risk of extinction faced by the source population due to the removal of individuals (McCarthy 1994). This is important because with the increasing use of translocations (or reintroductions) in managing threatened species, source populations are needed that can withstand possible repeat harvesting. To do this I carried out two PVAs to investigate probability of extinction (PE) of the source and translocated populations (Tiritiri Matangi and Wenderholm). These were carried out with two modelling programs – VORTEX, and a model built specifically for the Tiritiri Matangi population. I then investigated overall cost using McCarthy's (1994) multiplication rule.

METHODS

THE TRANSLOCATION

In 1998 a proposal was submitted to translocate North Island robins from Tiritiri Matangi Island to Wenderholm Regional Park north of Auckland (Fig 1.2). Approval was given to translocate up to 30 birds, 10 adult males, 10 adult females and 10 juveniles. Only 21 birds were taken including 15 adults and 6 juveniles. The majority of the birds translocated were adults, so that the maximum sample of juveniles was left to investigate the effects of the translocation on juvenile survival (Chapter 2). A translocation of 20-30 birds was predicted to have little impact on the Tiritiri Matangi population and to provide adequate numbers to establish a population at Wenderholm.

During the 1998/1999 breeding season robins on Tiritiri Matangi Island were monitored. All territory locations and nests were mapped and dates of fledging and dispersal were determined. This facilitated the translocation, as locations and ages of birds were known prior to commencing. Most North Island robins on Tiritiri Matangi Island are individually identified with a unique combination of a numbered, B-size, metal leg band and 1-3 coloured plastic leg bands.

Robins on Tiritiri Matangi Island had been regularly fed mealworms (*Tenebrio molitor*) as part of monitoring (Chapter 2, Methods). This training facilitated the capture of birds for translocation as well as aiding in subsequent monitoring at Wenderholm Regional Park. Robins were captured with the use of handnets, mistnets and claptraps. Claptraps were baited with mealworms, and lure tapes were played where necessary to attract birds. Faded combinations were replaced and unbanded birds were given a new combination. Tarsus measurements were taken to assist in sexing where sexes were unknown (Armstrong 2001). Birds captured for translocation were recorded according to their band combination. Once captured, robins were placed in individual cardboard cat carry boxes modified with a perch, additional mesh covered ventilation holes, and a small door at one end for placing the birds, food and water. Robins were fed a mixture of mealworms and waxmoth (*Galleria melia*) larvae. Leaf litter was placed on the floor to hold food and water. The birds remained in the boxes in a sheltered aviary on Tiritiri Matangi for a maximum of 2 days before being transported via boat and van to Wenderholm. Transport to Wenderholm from Tiritiri Matangi took just over two hours. Two trips were made releasing birds over two days in early March 1999.

The released birds were monitored at Wenderholm Regional Park using the same methods as those used on Tiritiri Matangi Island. In addition systematic searches along grid lines were made each spring with teams of up to 15 people. Banding was continued at Wenderholm using the same system as that used on Tiritiri Matangi Island
On the mainland, robins are vulnerable to predators like mustelids, cats and occasionally possums (squashing nests) (Brown 1997). As Wenderholm is on the mainland, protection from mammalian predators is of utmost importance. An extensive trapping programme is in place to control predator numbers. The geography of the Wenderholm peninsula facilitates this predator control and slows reinvasion by predators (Fig. 1.1).

POPULATION MODELLING.

The aim of this chapter is to look at the effect of the Tiritiri Matangi – Wenderholm robin translocation in terms of the probability of extinction. This required that we first look at the probability of extinction for both the source population (Tiritiri Matangi Island) and the "new" population (Wenderholm regional park). This was done with the use of PVAs as described below.

Simulation of the Tiritiri Matangi Population

R. S. Davidson designed the PVA model used in the analysis of the Tiritiri Matangi robin population. The original model, constructed using the computer programming language C++, was designed to model a North Island saddleback (*Philesturnus carunculatus rufusater*) population and is outlined in detail in Davidson (1999). It was modified to accommodate the data from the robin population and was rewritten in Microsoft Visual Basic 6 (appendix B). The model tracks the number of pairs each year and allows juvenile survival to change annually based on the number of birds present (i.e. incorporates density dependence in survival). This model was most appropriate, as the number of pairs present in the breeding season was the best predictor of juvenile survival in the Tiritiri Matangi robin population (Chapter 2). VORTEX cannot adjust survival probability according to the number of pairs present, so was inappropriate for the Tiritiri Matangi data. The model flows through a series of steps that are repeated each year:

1 *Reproduction*. Determines number of fledglings for each pair present at the start of the breeding season.
2 *Adult survival*. Determines how many adults survive the next 12 months, for both females and males.
3 *Juvenile survival*. Determines how many fledglings survive to the next breeding season.
4 *Juvenile sexing*. Determining sex of juveniles and increases the number of males and females accordingly.
5 *Number of pairs*. Determines number of pairs at start of next breeding season.
6 *Back to 1*. Time step = 1 year.

The demographic parameters for the simulation were estimated from the data collected on Tiritiri Matangi Island from 1992 until 2000 (Chapter 2). The main aim of the simulation is to find the probability of extinction within 20 years for the Tiritiri Matangi robin population. I considered 20 years a reasonable time frame for current management pratices.

Parameters

Survival and Density Dependence.

Survival was analysed by separating birds into two age groups, adults and juveniles. Survival is based on the (pairs J) model {ϕ (a + pairs J + p) p (a*y + p)} (Table 2.5). A juvenile becomes an adult at the start of its first breeding season. The (pairs J) model gave adult survival as constant over time (except in the event of a poison drop) with a yearly probability of survival of 0.78.

Juvenile survival is the probability that a bird survives from fledging until the beginning of the following breeding season. The (pairs J) model bases juvenile survival on the number of pairs present at the start of the current breeding season. This describes density dependence.

Parameters for adult and juvenile survival are specified in the model as β values, which were estimated by MARK usinging the logit link (Table 3.1). For adult survival, $\beta = 3.09$. For juvenile survival,

$$\beta = 4.07 - 0.087\mathrm{P}$$

where P is the number of pairs at the start of the breeding season. The β values are then inserted into the logit function:

$$\frac{e^{\beta}}{1+e^{\beta}}$$

to obtain the monthly survival probability for adults and juveniles with any number of pairs. The monthly adult survival probability was raised to the power of 12 to get annual survival. Monthly juvenile survival was raised to the power of 8 to obtain the probability of a juvenile surviving until the breeding season. Birds were juvenile for 8 months, as they were considered to enter the population in January and become adults in September in my survival analysis (Chapter 2).

No environmental variation was incorporated into survival because the best survival models did not include annual variation. Demographic stochasticity was produced in both adult and juvenile survival by a series of Bernoulli trials. In these trials, a random number generator selects a number from 0-1 for each bird from a uniform distribution. The bird is considered dead if the random number is less than the survival probability.

Reproduction.

From 1992 to 2000 the mean number of fledglings produced per female per year ($\bar{x}$) was 2.34 (var =2.53) (Table 3.1). Reproduction in the simulation model includes demographic stochasticity. This is calculated by picking values for p (probability of having offspring) and b (the number of fledglings produced by females that do have offspring) that would produce the same mean and variance as obtained from the data (Armstrong and Ewen, in press). The appropriate values are given by: $p = \bar{x}^2/(\text{var}+\bar{x}^2)$ and $b = \bar{x}/p$. Therefore, p = 0.68 and b = 3.42 for the estimated mean and variance. The exact b value was used to determine the total fledglings produced, and this total was then rounded to the nearest whole number. No environmental stochasticity was included in reproduction, as modelling of reproduction indicated that there was no significant variation among years.

Sex ratio.

Demographic stochasticity is incorporated in the sex ratio, each bird surviving to adult having a 50% chance of being either sex. Armstrong and Ewen (in press) found that assuming an expected sex ratio of 50:50 fitted the data well so this was retained.

Maximum age.

The oldest robins on Tiritiri Matangi Island are >9 years old. These are birds that were translocated to Tiritiri Matangi in 1992. Their ages at introduction were unknown. Heather and Robertson (1996) report the oldest robin recorded at Kowhai Bush was over 16. Lande (1988) suggested that maximum lifespan can be calculated as $(\alpha+4) / (1-s)$ where α is the age of first breeding and s is the average adult annual survival. This gives a maximum age of 33.3 years for robins. Including this in the model requires tracking the age of the birds and as most birds in the simulated population die long before they reach maximum age, this was removed from the model. This also meant the model ran a lot faster. Davidson (1999) found that including a maximum age for saddlebacks did not affect the population's size or growth rate.

Pairs.

The number of pairs is determined as the lesser of the number of males or females.

Simulations

Two different simulations were carried out. The first simulation was used to compare the model's predictions with the actual numbers recorded for the population. This model began with 36 birds (14 females and 22 males), the number at the beginning of the 1994/1995 breeding season. I did not start with the 1992/1993 or the 1993/1994 breeding seasons because (1) there was an additional translocation in June 1993, (2) there was a poison drop in September 1993 which caused some mortality, and (3) recently translocated females were present in both the 1992/1993 and 1993/1994 breeding seasons, and these had much lower fecundity than other females. The program would therefore have needed to be modified to incorporate these effects to model the first 2 years. I ran the model up to (and including) the 1998/1999 breeding season, the last breeding season before the 1999 harvest. This simulation was carried out 1000 times and the results averaged.

The second simulation started with 24 females and 25 males. These were the numbers in the population at the start of the 1999/2000 breeding season directly following the translocation. The model starts with these numbers to predict the probability of extinction in the years following the translocation. This model was then run 1000 times and the results averaged. This was used to determine the probability of the population going extinct within 20 years.

In addition, a sensitivity analysis was performed with the second simulation. Sensitivity analysis is an important component of modelling (McCarthy et al. 1995). Sensitivity analyses are useful when data on the population is scarce (Goldingay & Possingham 1995), to determine which parameters are most sensitive (McCallum 2000), and to help determine effective management strategies (McCarthy et al. 1995). I wanted to investigate the sensitivity of varying the main parameters on the predictions of future population size. These parameters were reproduction and the β values for adult and juvenile survival and density dependence (Table 3.1). The parameters were varied over their 95% confidence intervals. All parameters were varied together so that the worst possible and best possible scenarios were calculated.

Table 3.1. Parameter values for the Tiritiri Matangi Island robin population. Values are those estimated from the real data described above.

Parameter	**Worst values (Lower 95% confidence interval)**	**Predicted values**	**Best values (Upper 95% confidence interval)**
Intercept (β value) for adult survival	3.69	3.92	4.14
Intercept (β value) for Juvenile survival	-0.74	0.15	1.05
Density dependence (β value)	-1.23	-0.87	-0.51
Reproduction (Fledglings/female/year)	2.05	2.34	2.63

I ensured the model was working correctly by comparing it to other models. I removed the density dependence from my model then compared the results to the same parameters run through VORTEX. Assuming no density dependence the parameters indicated that the population growth rate was 0.54. Using this growth rate I ran a simple exponential growth model in EXCEL predicting population numbers over time. I then compared this to my model without density dependence. When all three models (my model, VORTEX and the exponential growth model) start with a population of 500 they predicted the same population sizes over time confirming that my model worked correctly.

Simulation of the Wenderholm population

The simulation of the Wenderholm robin population was carried out using VORTEX 8.41 (9 June 2000, http://pw1.netcom.com/~rlacy/vortex.html). VORTEX is a Monte Carlo simulation of demographic events. It models population dynamics as discrete, sequential events (e.g. births, deaths, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modelled as constants or as random variables that follow specified distributions (Lacy et al. 1997). VORTEX was used as opposed to the model used for the Tiritiri Matangi population analysis, because density dependence was not incorporated into juvenile survival for the Wenderholm population. The first six months of data were not used to estimate survival as it has been suggested that the period directly after translocation may be atypical (Armstrong & Ewen 2001). This left only one year of data from which to estimate the parameters. VORTEX input for this model can be found in Appendix C.

Parameters

Survival

Adult and juvenile survival were estimated from the data for the 12 months between the start of the first and second breeding seasons. Annual adult survival was estimated at 0.62, and juvenile survival at 0.17. Birds were not separated by sex, as no significant difference in adult survival between sexes has been found in the Tiritiri Matangi robin population. There is no reason to believe that this would be any different at Wenderholm so adult survival was considered the same for males and females.

Reproduction

The typical reproductive rate for the Wenderholm population was based on the first breeding season. The breeding system was set as monogamous, which means that the number of males present, if females are more abundant, will limit the number of females breeding. Breeding age set at age 1 for both males and females, which means that all birds attempt to breed in their first breeding season after fledgling, as is the case for robins. The maximum young per female per year was set at zero in VORTEX. This means the number of offspring for each female is selected from a normal distribution with mean and variance specified by the user. I entered the mean (3.29) and variance (2.4) in number of fledlings produced by the 6 females present in the first year. The percentage females breeding was set at 100%, and the mean number of fledglings per female was calculated for all birds (not just the ones breeding).

Maximum Age

Maximum age of breeding was set at 100. It is highly unlikely that a robin will live this long, so this means I am assuming senescence is not an issue. If the prediction of a maximum age of 33.3 years is assumed then the birds in this model will not be able to reach a maximum age anyway as the model only runs for 20 years. Additionally there is no evidence of senescence in robins.

The initial population was made of 7 males and 6 females, the number at the beginning of the 1999/2000 breeding season. The carrying capacity was set at 120 based on the size of the forest block (60 ha) and reported robin densities on islands and other mainland sites (Lovegrove & Greene 1998). No harvesting or supplementation was included in the model. Inbreeding depression was considered to have no effect. Genetic variation is most likely to show an effect if time periods of more than a few generations are considered (White & Bartmann 1998).

With only one year of data, no variation between years in annual survival could be estimated. The standard deviations in annual adult and juvenile survival were therefore left at zero. This is reasonable based on the Tiritiri Matangi data as annual variation in juvenile survival was best described by density dependence as opposed to random variation between years, and adult survival was constant between years. The population dynamics were simulated 1000 times over 20 years and the probability of extinction was determined.

Where data needed to estimate parameters are sparse or unavailable, Boyce (1992) suggests that one may use data from a similar species or area, or explore the behaviour of the system over a range of reasonable parameter values. I therefore varied reproductive rate and adult and juvenile mortality over a range of reasonable values to assess the influence these parameters have on the model (Table 3.3). These values were based on data from other robin populations (Table 3.2). This is a form of sensitivity analysis (McCallum 2000). Varying the parameters gives an idea of how sensitive predictions are to changes in the parameters. It also indicates the parameters that have the largest impact on the results of the model (McCarthy et al. 1995), and that need more data collected on them before a reliable analysis can be performed (Norton 1995).

Table 3.2. Estimates of adult survival, juvenile survival and reproduction rate in robin populations.

Bird	**Reference**	**Juvenile Survival (to next breeding season)**	**Adult Survival (yearly)**	**Reproduction (Fls/female/year)**	**Mainland/Island**
North Island robin	(Powlesland et al. 2000)	-	-	3.7 - With predator control 1.5 - Without predator control	M - Tahae
				3.8 - With predator control 0.4 - Without predator control	M – Waimanoa
North Island robin	This study (Chapter 2)	Density dependent (see formula above)	78%	2.34	I – Tiritiri Matangi Island
South Island robin	(Powlesland 1983)	16.9%	38.6%	-	M – Kowhai Bush
North Island robin	(Flack 1979)	10 – 90%	~70%	-	M – Kowhai Bush
South Island robin	(Flack 1976)		80 – 85%	0.1–4.1	I – (general estimate)
			70%	3	M – (general estimate)
South Island robin	(Raeburn 2001)	29%	59%	1.9	M - Paengaroa

Table 3.3. Values over which the three parameters (adult and juvenile survival and reproduction rate) were varied. Each parameter was varied independently of the others. Values in bold indicate the values estimated from the one year's data from Wenderholm.

Parameter	**HIGH**				**LOW**
Reproduction Rate (fl/fem/yr)	4	**3.83**	2.5	1	0.5
Adult survival (%)	90	80	**61.54**	45	30
Juvenile Survival (%)	84	70	40	**17.4**	10

COSTS OF REINTRODUCTION

McCarthy (1994) noted that if the source and reintroduced populations are independent of each other, then the risk that both populations will become extinct is:

$$R_T(x) = R_S(x) . R_R(x)$$

where R_T is the risk that both populations will become extinct, R_S is the risk faced by the source population, R_R is the risk faced by the reintroduced population, and x is the number of birds reintroduced.

I used the results from the PVAs of Tiritiri Matangi Island and Wenderholm Regional Park to insert into the McCarthy's (1994) formula above.

RESULTS

THE TIRITIRI MATANGI POPULATION

The simulation was first run to model the data collected from 1994 to 1998 to see how well the model corresponded with the real data. The model data followed slightly below the real data (Fig 3.1).

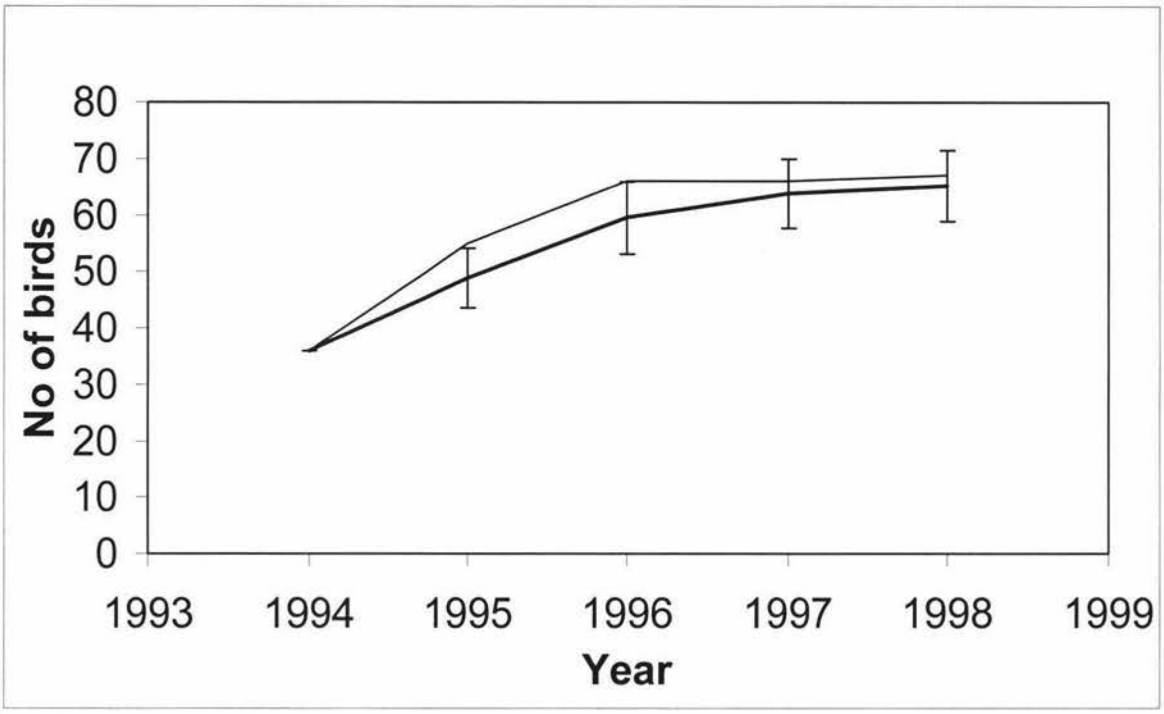

Figure 3.1. Trajectories of real (———) and simulated (**———**) robin populations on Tiritiri Matangi from 1994 to 1998 starting with 12 females and 23 males. Values for simulated populations are means +/- 1 standard deviations based on 1000 runs.

Predictions for the population after the removal of the 21 translocated birds bode well for the Tiritiri Matangi robin population. In over 1000 simulations for 20 years, the population never went extinct. This indicated a 0% probability of extinction in 20 years from the translocation. The population size increased over the first two or three years after the translocation (Fig. 3.2). The population size then levelled off around 65 birds for the next 15 years (Table 3.4). The best scenario (Fig. 3.2) showed a large increase in the number of birds initially, reaching around 160 birds (Table 3.4). It also showed a 0% probability of extinction. The worst scenario had a 1.3% probability of extinction with the population appearing to reach a low equilibrium (Fig. 3.2). After 20 years the worst case scenario indicated that only 20 birds were surviving (Table 3.4).

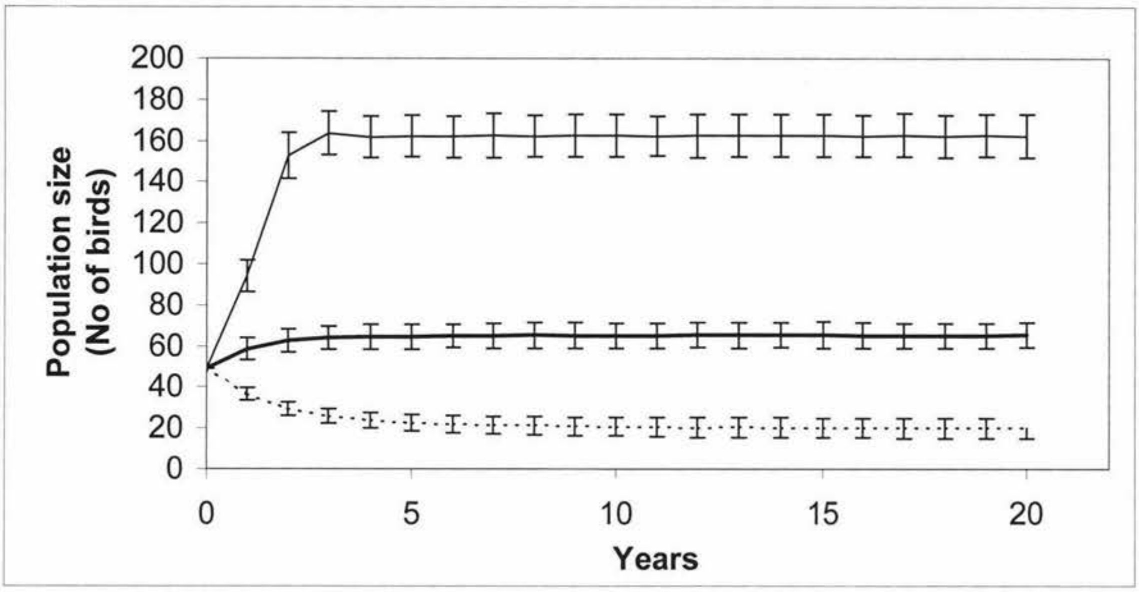

Figure 3.2. Simulated number of birds present in the Tiritiri Matangi robin population for 20 years after the translocation from the population. Trajectories show the predicted (**———**), best (———) and worst (--------) scenarios based on data in Table 3.1. The starting population was 24 females and 25 males. Values are means +/- 1 standard deviation based on 1000 runs.

Table 3.4. Expected population sizes +/- 1 standard deviation for the Tiritiri Matangi robin population 20 years after the translocation. The different scenarios correspond to the parameter estimates shown in Table 3.1. Results are based on 1000 runs.

Scenario	**Total population (number of birds)**	**Number of pairs**
Best scenario	162 +/- 11	76 +/- 5
Predicted	65 +/- 6	30 +/- 3
Worst scenario	20 +/- 5	8 +/- 3

THE WENDERHOLM POPULATION

From the model of the Wenderholm population based on the one year of Wenderholm data, the population was predicted to have 96% probability of extinction over 20 years.

Varying the reproduction rate (number of fledglings/female/year) from 0.5 to 4 had little effect with the probability of extinction ranging from 100% to 93%. Increasing adult survival had a much greater effect, so that at 80% survival (similar to Tiritiri Matangi) the population had a probability of extinction of 54% (Fig 3.5). When I varied juvenile survival a dramatic change was also seen in the probability of extinction (Fig 3.5b). Increasing juvenile survival from 17% to 40% caused the probability of extinction to decrease from 96% to 62%.

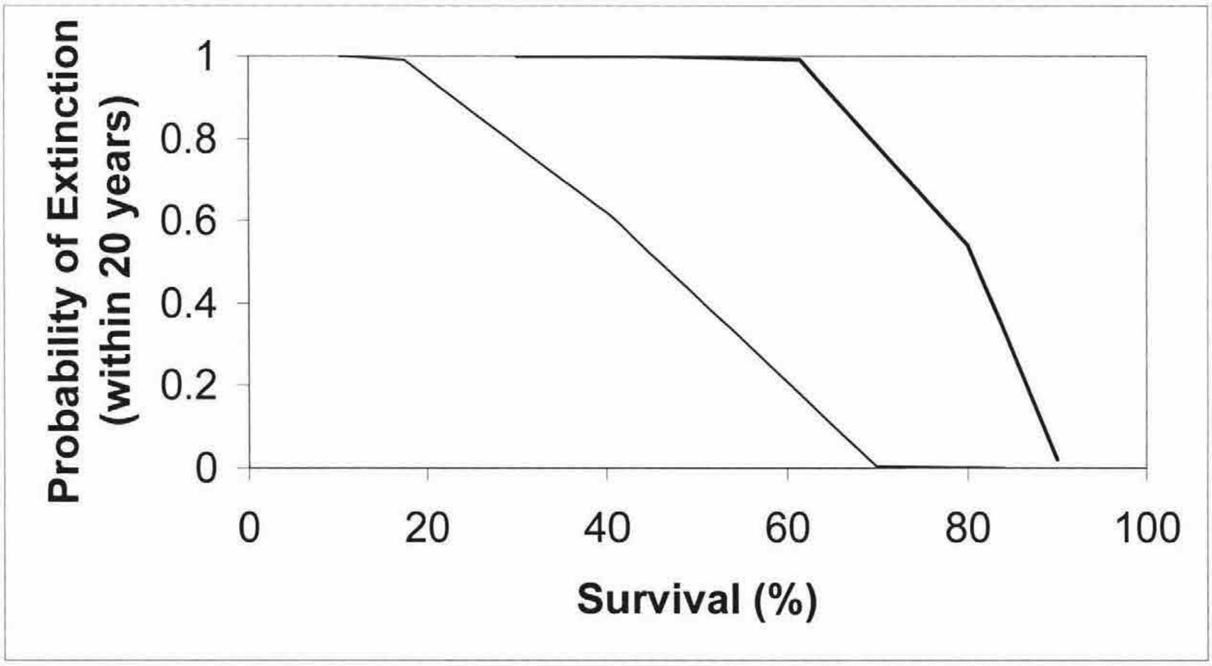

Fig. 3.3. Probability of the Wenderholm population going extinct within 20 years of reintroduction over a range of adult (▬▬) and juvenile (——) survival probabilities. Predictions are based on a population viability analysis carried out in VORTEX.

THE COST OF REINTRODUCTION

Using McCarthy's (1994) formula, the risk of both populations going extinct is 0. The Tiritiri Matangi Island robin population had a probability of extinction within 20 years of 0%. Therefore it is extremely unlikely that we could expect both populations to go extinct even though the Wenderholm population has a high probability of extinction in 20 years (96%).

DISCUSSION

THE TIRITIRI MATANGI POPULATION

The Tiritiri Matangi Island robin population presented an opportunity to study the effects of a translocation on the source population. A biologically important effect may be defined as a substantial change in the probability of decline in population size (Burgman 2000). McCarthy (1994) stated that there is considerable uncertainty associated with population forecasts and therefore, predictions of the size of future populations are best phrased in terms of probabilities. If a translocation were to have an effect on a source population one would expect to see this reflected in the probability that the population will go extinct in the future.

Parameters that were predicted to best describe the Tiritiri Matangi population indicated that the probability of going extinct within 20 years of the translocation was 0%. The population was predicted to reach a size of 65 birds after 20 years (Table 3.4) and appeared to reach this stage within 2 or 3 years after the translocation (Fig 3.2). It appears the viability of the population was placed under no threat by the removal of 21 birds.

To construct the best and worst scenarios, all parameters were set to their upper and lower 95% confidence limits. In these scenarios the parameters interacted with each other to give an overall extreme greater than the sum of the extremes put together (Fig. 3.2). These three scenarios (predicted, best and worst) indicated that the 95% confidence intervals for the parameters predicted a range of bird numbers from 20 to 160 birds (Fig. 3.2). Even if all the parameters are overestimated, the probability of extinction of the Tiritiri Matangi population within 20 years was still low (1.3% for the worst scenario). However, if the population were to reach as low an equilibrium as in the worst scenario, the population would be at risk of extinction from demographic stochasticity.

The simulation modelling the first few years of the Tiritiri Matangi population followed the actual data well, although the actual 1995 population size was about one standard deviation higher than the predicted value. This is due to the fact that reproduction and juvenile survival were both slightly higher than the expected values in 1994/1995, allowing the population to jump slightly faster than predicted to occur on average (Table 2.1).

The model used to predict the Tiritiri Matangi extinction probabilities is fairly simplistic while still incorporating the aspects of the population that were considered to be most important (e.g. density dependence). Boyce (1992) suggests that a strategic modeller will use the simplest possible model that retains the essential features of the system's ecology. A very complicated model may cover all knowledge of a system but is often unreliable due to the lack of information on required inputs (White 2000a).

THE WENDERHOLM POPULATION

The Wenderholm Regional Park robin population had only been present for just over a year when this analysis was performed. Such short-term data means that there are no measures of precision for the parameters entered. Using parameters based on the data available indicated that the Wenderholm robin population has a 96% probability of extinction within 20 years. This suggests that the release of 21 birds to Wenderholm Regional Park has bleak prospects for the establishment of a self-sustaining population.

Due to the lack of data, this model is very simple with no environmental variation and no consideration of immigration or emigration. This may lead to overestimates of persistence (White 2000b). However, as can be seen, even taking the risk of overestimating persistence the probability of extinction within 20 years for this population was very large.

Very preliminary models based on fragmentary data cannot indicate population trends with certainty. However, even with small data sets or fragmentary data, PVA can be useful to predict the effects of management actions (Hamilton & Moller 1995, Burgman 2000, South et al. 2000). With basic data producing simple models, sensitivity analysis can identify data needs that can be addressed to provide a more reliable analysis (McCarthy et al. 1995, Norton 1995, White 2000b).

The sensitivity analysis indicated that survival had the greatest influence on the probability of extinction (Fig. 3.3). In particular, juvenile survival had the greatest contribution to the extinction probability within 20 years at Wenderholm. Survival has been found to have a considerable effect in other sensitivity analyses. Hiraldo et al. (1996) found that a sensitivity analysis on lesser kestrels (*Falco naumanni*) indicated that adult followed by juvenile survival had the biggest effect on population growth. In the helmeted honeyeater (*Lichenostomus melanops cassidix*), McCarthy et al. (1995) found survival of breeding birds had an immediate impact on population growth. This indicates that future modelling of this population would benefit from careful monitoring of survival, especially that of juvenile birds. It also suggests that improvements in survival, especially juvenile survival, could significantly lower the risk of extinction faced by this population. Increasing juvenile survival above 20% would start to decrease the probability of extinction within the next 20 years (Fig. 3.3).

Identifying and managing sources of mortality to robins (in particular juveniles) could have a definite benefit to their likelihood of persistence. Mortality could be caused by several factors. Wenderholm Regional Park is situated on the mainland and, as such, is impacted by introduced mammalian predator. Wenderholm has an extensive trapping programme in place to control predator numbers. A month before robins were released at Wenderholm, permanent perimeter and central lines of mustelids kill traps were installed on the headland. From February 1999 to September 2000, 27 mustelids were caught. Numbers of rodents, cats and possums are low on the headland (Lovegrove et al. 2000). Another concern for the population is that of juveniles emigrating away from Wenderholm. Wenderholm has several adjoining bush areas that could act as reservoirs for surplus birds from Wenderholm itself (Lovegrove & Greene 1998). These areas are occasionally searched for robins. However, any emigration that was missed would be included in VORTEX as mortality.

Emigration could be a consequence of hunger, with food supply acting as a limiting factor. Newton (1998) points out that a shortage in food supply may not emerge in an obvious way, such as animals being observed to starve. Hungry birds may move elsewhere, where they may survive or die due to causes other than starvation (Newton 1998). Research carried out at Wenderholm suggests that the numbers of beetles, wetas and caterpillars have increased significantly since rodent control was initiated (Craddock 1997). Craddock (1997) concluded that Wenderholm has better overall abundance than a nearby forested farm patch. This suggests that food limitation may not be a problem at Wenderholm. It could be useful to compare abundances of insects at Wenderholm with abundances in other areas where robins are present to confirm this.

Mites may have a detrimental effect on survival of nestlings. Merino and Potti (1995) found that mite abundance negatively affected nestling mass and tarsus length in pied flycatchers (*Ficedula hypoleuca*). Merino and Potti (1995) also observed that adult birds were reluctant to enter infested nests. These effects could have repercussions on subsequent fledgling survival. In New Zealand, Powlesland (1977) found starling (*Sturnus vulgaris*) nests heavily infested with mites resulted in fledglings with significantly reduced growth rates and reduced weight at 15 days (shortly before fledging). Powlesland (1977) notes that the chief effect of undernourishment or stress on a nestling is not usually death in the nest, but reduced weight at fledgling. This could then result in lower survival after leaving the nest (Powlesland 1977). At Wenderholm, mites have been found in nests and are a serious problem in late nests (Lovegrove pers com). Dusting for mites is carried out but monitoring the occurrence of mites and chick weights could be useful to indicate whether they have an effect on juvenile survival.

Reproduction rate had little effect on the probability of extinction. This may be for two reasons: (1) uncertainty in the estimates of reproduction have little importance in the reliability of the models predictions, and (2) the parameters were varied independently of each other; that is, the decrease in extinction probability with higher survival would be less if reproduction wasn't so high.

Parameter estimates based on the first year's data may still have been influenced by the translocation. In Raeburn's (2001) study of the North Island robin population reintroduced to Paengaroa, removing the first year's data from the modelling procedure decreased the probability of going extinct from 83% within 10 years to 0% within 100 years. This is because reproduction and survival were lower in the first year than the second year after the translocation, suggesting the translocation may have depressed these parameters. Armstrong and Ewen (2001) found reproduction of robins reintroduced to Tiritiri Matangi was substantially lower for females in their first year after translocation. They discovered that their original population viability analysis based on the first year's data substantially underestimated the probability of survival of the population. Armstrong and Ewen (2001) also state that post-translocation survival is often lower than the subsequent survival rate and this must be taken into account when estimating survival rates for reintroduced populations. This means that monitoring of a recently translocated population should be carried out for more than just the first year.

The Wenderholm robin population has continuing monitoring, and with the data covering 2001, attempts can be made to test this theory. The extra data may mean that predictions of the viability of the Wenderholm North Island robin population could increase.

THE COST OF REINTRODUCTION

The risk of both populations going extinct is estimated to be zero. This is due to the fact that there is no risk of the Tiritiri Matangi population going extinct. McCarthy (1994) suggested that the potential costs must be assessed and weighed against the potential benefits of a translocation. Therefore based on this there was no "cost" to the source population.

McCarthy's (1994) formula suggests that if there is no risk of extinction in either the source or the reintroduced population, then there is no overall cost in performing the reintroduction. However it does not allow assessment of benefit. If both populations show a 0% probability of extinction then there has clearly been a benefit to the species in question. Not only has no harm come to the source population but a new population has been successfully established. In using McCarthy's (1994) formula, it is important to distinguish between cases where there is no risk of extinction in *either* the source or the reintroduced population and cases where there is no risk of extinction in *both* populations. The Tiritiri Matangi–Wenderholm translocation is an example of the former. In this case the PVAs suggest that although no cost was incurred by the Tiritiri Matangi population, the Wenderholm population did not provide a benefit to the species overall.

We must also consider what costs we are interested in assessing. Although no cost was found in terms of the risk of extinction of the source population, there was still a cost to the birds translocated in terms of their lives. It is highly likely that translocated birds experience stress during and after the translocation. The fact that survival directly after translocation has been shown to be lower than the normal adult rate (Armstrong & Ewen 2001) suggest that adults are disadvantaged by translocation. Can a translocation that will lose a lot of animals be justified, especially in the case of an endangered species? I think this depends on the probability of the new population establishing. Scott & Carpenter (1987) suggest that a low probability of survival of animals should deter translocations from occurring, especially when the costs of the translocation and the endangered status of many animals are considered. If predictions for the establishment of a new population are high, and little effect is to be had on the source population, then overall we would expect to see a benefit to the species regardless of the loss of a few individuals. This advocates the loss of a few individuals for the "greater good". Difficulties may arise in cases where there are insufficient data for prediction but delaying decisions carries risks (Ludwig 1999).

IUCN (1998) state "the principal aim of any re-introduction should be to establish a viable, free-ranging population in the wild, of a species, subspecies or race, which has become globally or locally extinct, or extirpated, in the wild". I believe that this should include the provision that "established populations should suffer no detrimental impacts".

This analysis suggests several factors that need to be considered in the future. The Wenderholm population could benefit from management that identifies primary causes of mortality. Modelling of the Wenderholm population should continue into the second year before consideration of supplementation. It ought to be noted in cases where both source and reintroduced populations are considered to have no risk of extinction after translocation, an overall benefit has occurred.

Having pointed out restrictions and cautions needed when performing a PVA, Burgman (2000) states that PVAs are still the only tool we have that avoids at least some of the pitfalls of subjective judgement. However, White (2000a) points out that models test hypotheses about models, not about actual populations. Ludwig (1999) cautions that PVA should include estimates of likely ranges for both parameter estimates and measures of extinction risk. PVA predictions about the future can be questionable (Boyce 1992, Burgman 2000, White 2000a). As Boyce (1992) notes, there is too much to gain from developing a stronger understanding of a population through modelling to avoid it for fear of misinterpretation.

SUMMARY

- The translocation from the Tiritiri Matangi Island robin population appears to have had no detrimental effects.
- The Wenderholm population appears to have a high probability of extinction within 20 years (96%) based on the first years data but management of juvenile survival may reduce this.
- Modelling the Wenderholm population with additional data may indicate a lower extinction probability.
- There was no overall cost involved in the translocation due to the 0% probability of extinction in the Tiritiri Matangi population.

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4

Harvesting

INTRODUCTION

Lande et al. (1997) noted that "environmental and demographic stochasticity together guarantee that extinction is the eventual fate of all species (regardless of whether or not they are harvested)". However, harvesting has the potential to speed up this decline to extinction. Efforts to minimize extinction risk whilst continuing harvesting are commonly referred to as sustainable harvesting. Sustainable harvesting "generally refers to activities that involve the extraction of a natural resource in such a manner that it is not depleted and can renew itself so that similar levels of exploitation can occur indefinitely" (Struthsaker 1998). The concept of sustainable harvesting assumes density dependent population regulation (Rosenburg et al. 1993).

The scientific basis for sustainable use of renewable resources evolved during the first half of the 20th century to counter the prevailing view that oceanic resources were inexhaustible (Rosenburg et al. 1993). Fish populations have been the subject of a great deal of research because their economic value makes it important for us to predict their future population sizes, particularly in the presence of fishing mortality (Burgman et al. 1993).

Sustainable harvest modelling is carried out to explore the boundaries of a sustainable harvest (Burgman et al. 1993, Taylor et al. 1987). Similar life history parameters are used here as in other population modelling – i.e. survival rates, reproduction rates, etc. Optimal harvesting models were first used in fisheries population management, and employing them in harvest regimes has been subject to debate (Beissinger & Bucher 1992). Lebreton and Clobert (1991) note that they appear difficult to use with realism and precision for bird populations as they assume knowledge of density dependent mechanisms. Overharvesting is the greatest problem in sustained-yield harvest programs because these programs overestimate the capacity of populations to increase their reproduction or survival rates as density is reduced (Beissinger & Bucher 1992). Thresholds are frequently set far too low to sustain the resources, with harvesting stopped only after severe depletion (Lande et al. 1997).

Harvesting of game birds has been in practise for more than 3400 years (Robertson & Rosenburg 1988). Harvesting of wildlife populations for recreation and profit is widely represented in the literature because it affects a wide range of people and threatened animals (e.g. Beissinger & Bucher 1992, Robertson & Rosenburg 1988). Harvesting models for game populations are usually centred around obtaining the maximum long-term yield (Robertson & Rosenburg 1988). Harvesting populations for translocations are less likely to have this emphasis because establishing a new population does not necessarily require large numbers of animals. Even if large numbers of animals are wanted for translocation the number may still be harvested at a rate that falls short of the maximum long-term yield. Griffith et al. (1989) note that releasing animals in small numbers over several years is a more successful strategy than all at once.

Determining levels of sustainable harvest is relevant to the planning of translocations because animals must be harvested from an existing population (either wild or captive). If the population does not readily sustain this harvesting we risk damaging a valuable resource. This is particularly important for species that have only one self-sustaining population that is used repetitively as a source population for translocations.

In Chapter 3 I investigated the probability of extinction (PE) of the Tiritiri Matangi Island robins after a translocation removed 21 birds from the population. The model used to predict extinction can be used to look at the effects of harvesting. In this chapter I investigate the effect that different harvesting regimes might have on the probability of extinction. I assess the effect of changing the number removed and the frequency of harvest in terms of PE. I also asses the minimum population size to which harvesting could safely lower the population.

METHODS

The simulation model described in Chapter 3 was modified to include a harvesting subroutine that allows harvesting of different numbers of birds on different time frames (Appendix C). Harvesting occurs after reproduction and mortality but before juvenile sexing:

1 *Reproduction*. Determines number of fledglings for each pair present at the start of the breeding season.

2a *Adult survival*. Determines how many adults survive the next 12 months, for both females and males.

2b *HARVEST*

3 *Juvenile survival*. Determines how many fledglings survive to the next breeding season.

4 *Juvenile sexing*. Determining sex of juveniles and increases the number of males and females accordingly.

5 *Number of pairs*. Determines number of pairs at start of next breeding season.

6 *Back to 1*. Time step = 1 year.

The model allows specification of how many birds of each sex are removed. The harvest occurs before juvenile sexing, so only adults are available for harvest. Further analysis of juvenile survival data has shown that juvenile survival was lowest in the first 2 months after fledging in both 1998-1999 and 1999-2000 (Armstrong pers com). After this juvenile survival was close to the adult rate. Therefore the use of a model only harvesting adults was considered appropriate.

The model was initially run with a starting population of 36 birds (22 males and 14 females). A harvest of 21 adult birds (11 males and 10 females) was carried out six years later. The purpose of this was to simulate the real data, as was done in Chapter 3, but this time including the translocation. This allowed me assess how well the model followed the translocation. There were 36 birds present in the population in 1994, and the translocation removed 21 birds (16 adults and 5 juveniles) in 1999.

Three simulations were run to address three questions:

First, if we were to do just one harvest of the Tiritiri Matangi robin population what would be the largest number of adults we could take?

Secondly, source populations may be harvested repeatedly to supply birds for supplementation to recently established populations or to establish new populations. This part of the analysis assesses the effects of annual, biennial and triennial harvesting of different numbers of birds on the Tiritiri Matangi robin population. If the population were to be harvested continuously, what would be the best interval to leave between harvests?

Thirdly, harvesting should occur only from populations with enough animals to support it. What would be the lowest size that it would be safe to lower the Tiritiri Matangi robin population to?

The first and second simulations began with 55 birds (29 males and 26 females), the number present in September 2000 (Table 2.1). Harvesting began at year 5. Only adult birds were taken, with equal numbers of males and females. Harvesting occurred after reproduction. Therefore, harvesting the population to extinction is just about impossible as there are juveniles available after harvest to repopulate the island.

The second simulation harvested birds in three regimes, annual, biennial and triennial. Harvesting was carried out for 6 years. The probability of extinction within 20 years and the maximum number of birds taken was assessed. I arbitrarily chose a probability of extinction of 5% in the next 20 years as the lowest extinction probability that I would want to reduce the population to. The model allowed a set harvest to be entered for males and females. However, the set harvest is not always equal to the number actually removed from the population. If there are insufficient numbers of birds for the model to carry out the set harvest it takes as many as are available. I therefore also recorded the actual total birds taken over the 6 years harvesting.

The third simulation was accomplished by running the model from Chapter 2 to simulate the Tiritiri Matangi robin population over a range of starting sizes. The probability of extinction was then recorded for the different starting populations. This was done to indicate the smallest size to which the population could be reduced to by harvesting and still have a 0% extinction probability.

RESULTS

The mean trend of the simulated population for 1994-2000, including the translocation, followed the observed trend quite well (Fig. 4.1). The only year where the observed population value fell outside one standard deviation of the mean simulated population is 1995, as in Chapter 3.

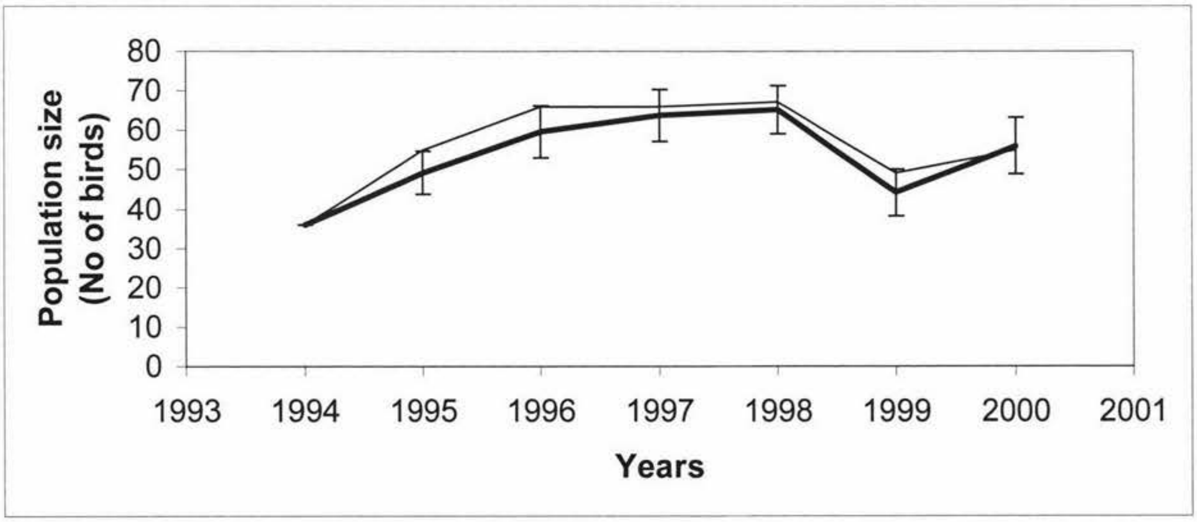

Figure 4.1. Trajectories of the real (——) and the simulated (**——**) robin populations on Tiritiri Matangi from 1994 to 2000, starting with 12 females and 23 males. Values for simulated populations are means +/- 1 standard deviation based on 1000 runs.

A one off harvest five years after the simulation began could harvest a maximum of 42 adults (SD = 4.6). This is was the most the model was capable of removing, and resulted in a probability of extinction of 0%. On average, the population took, about 6 years to recover (Fig. 4.2).

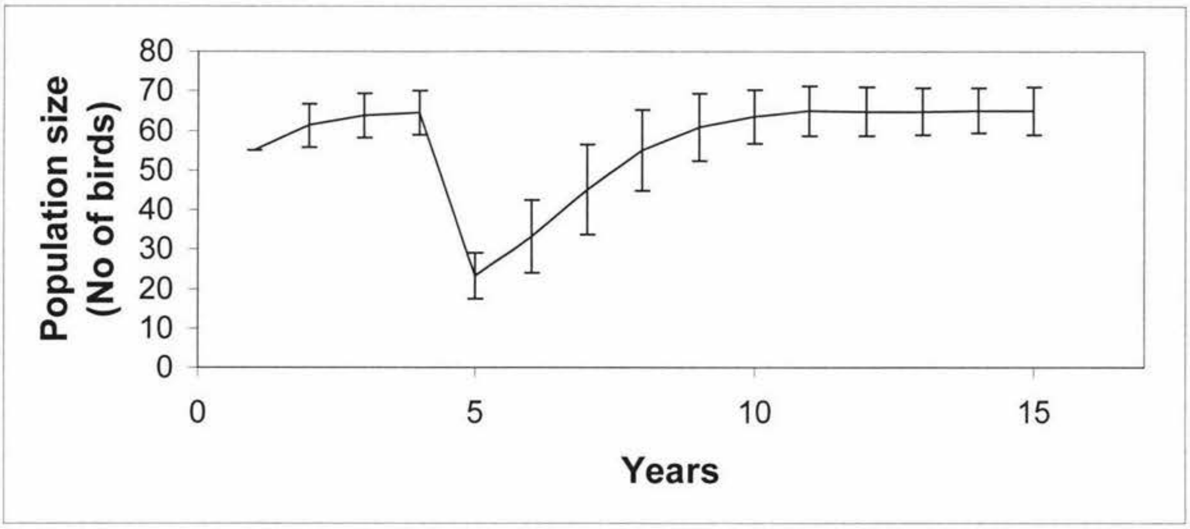

Figure 4.2. Simulated number of robins present on Tiritiri Matangi before and after a harvest of 42 adults. The starting population was 29 males and 26 females. Values are means +/- one standard deviation based on 1000 runs.

With an extinction probability of 5, the annual harvesting regime allowed the greatest number of birds to be removed over the 6 years. This removed just over 100 birds (Fig. 4.3 a) whereas biennial and triennial harvesting allowed about 90 and 75 birds respectively (Fig. 4.3 a & b). In all three cases a 5% probability of extinction is reached when the set harvest averages around 20 birds/year (Fig. 4.3). In all cases the total number of birds taken levelled off at high set harvests, and for biennial and triennial regimes began to drop off again. For set harvests, the regime that increased the probability of extinction the slowest was triennial harvesting, with annual harvesting the most rapid.

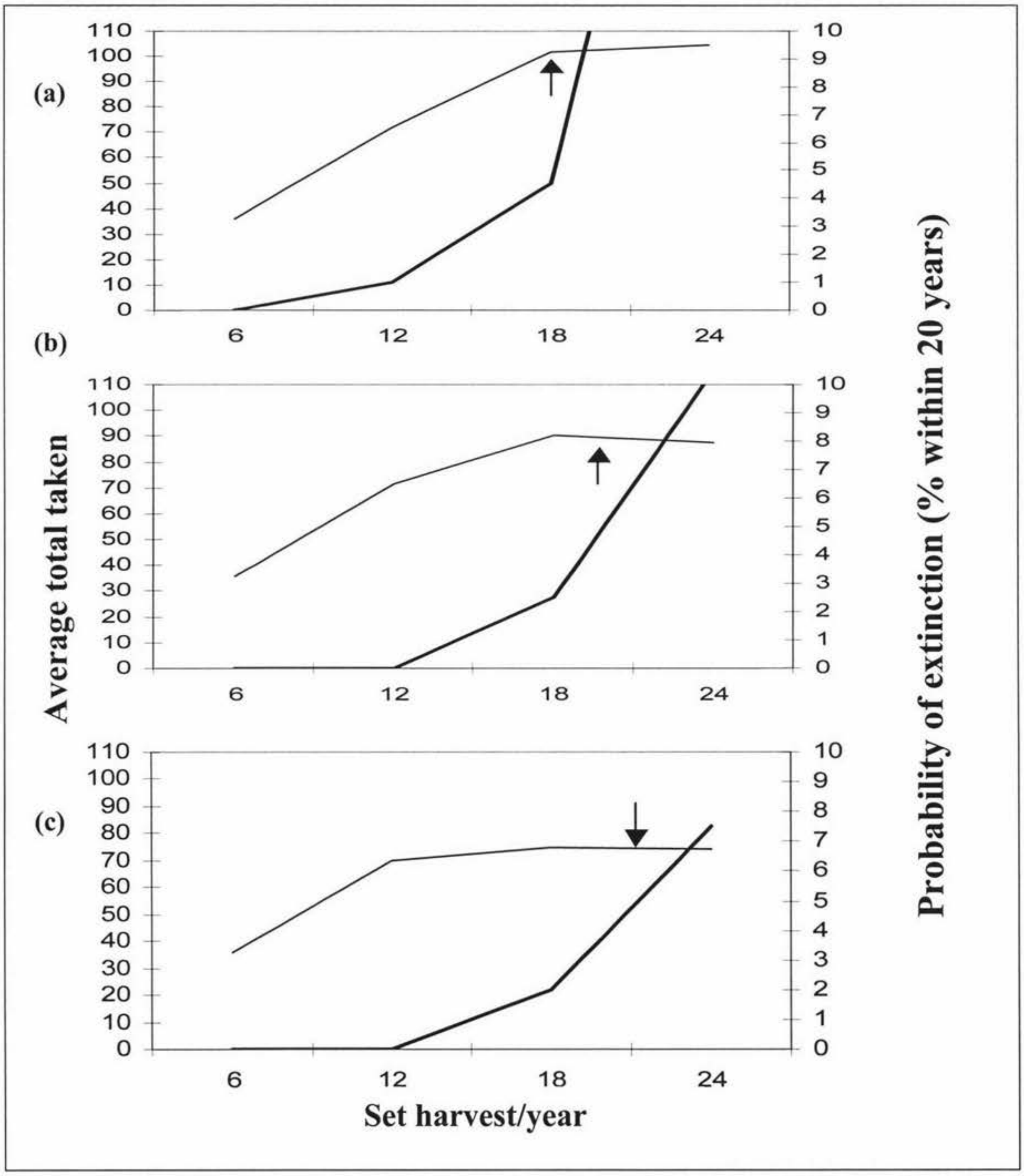

Figure 4.3. Simulations of the Tiritiri Matangi robin population over three harvesting regimes **(a)** annual **(b)** biennial **(c)** triennial. The dark line (**——**) shows the probability of extinction over 20 years, and the light line (——) shows the total number of birds

removed over the 6 years harvesting for each set harvest level. The arrow indicates where the probability of extinction reaches 5%. The starting population was 29 males and 26 females. Values are means based on 200 runs.

The third simulation indicated that if the starting population consisted of 4 or more pairs, the population would have a 0% probability of extinction within 100 years (Fig. 4.4). This simulation further indicated that the population would recover within about 10 years after being reduced to 4 pairs (Fig. 4.5).

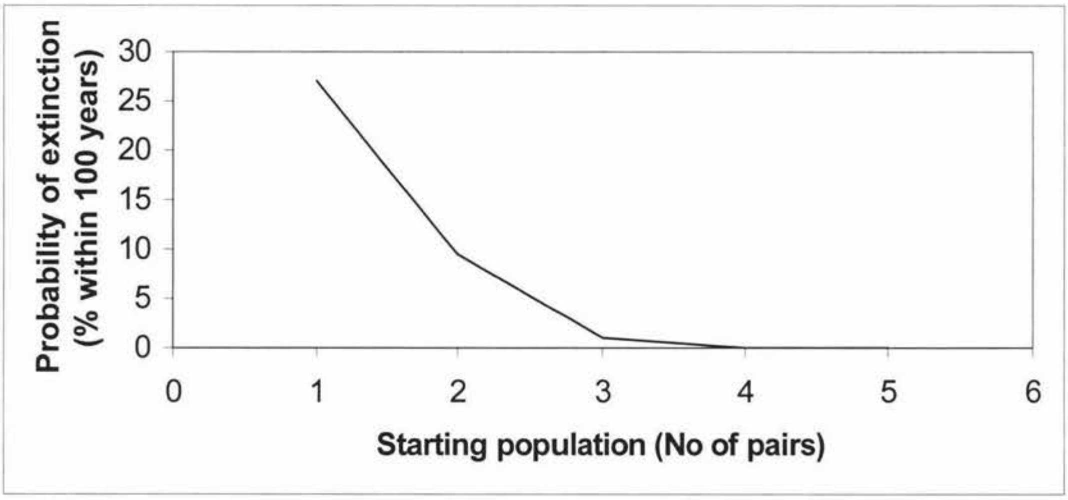

Figure 4.4. Reduction in extinction probabilities predicted by the Tiritiri Matangi model when the starting population, in numbers of pairs, is increased.

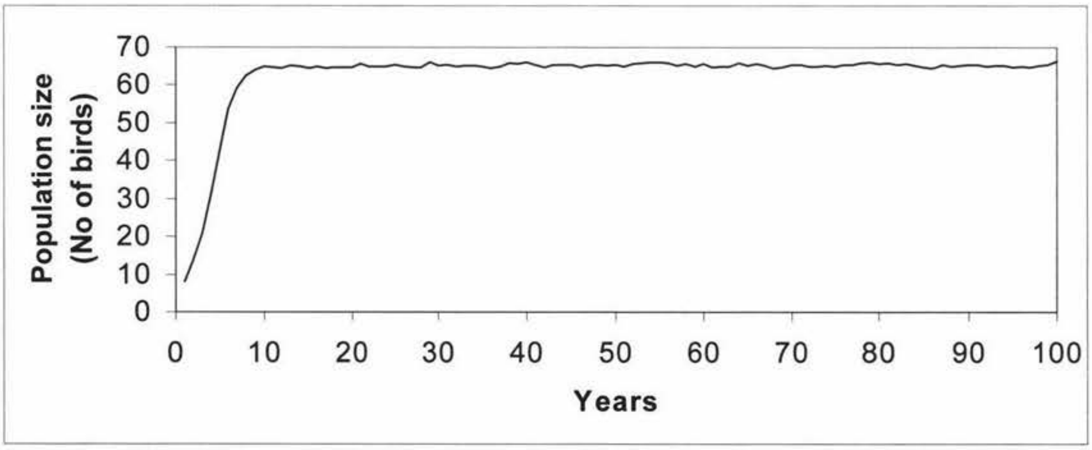

Figure 4.5. Simulated growth of the Tiritiri Matangi Population when the population starts at 8 birds (4 males and 4 females). Values are means of 200 runs.

DISCUSSION

Modelling of the Tiritiri Matangi juvenile survival rates, subsequent to the Chapter 2 results, indicated that most juvenile mortality occurs 1-2 months after fledging (Armstrong pers com). In light of this, the best sustainable harvesting would be to obtain juveniles as they become independent. However, this is impractical. By the time the translocation of Tiritiri Matangi robins occurred most juveniles were older than 2 months, and therefore probably had a survival rate not much lower than adults. For this reason using a model that harvests only adults was considered justifiable, and harvesting 21 birds with this was logical.

HIGHEST ONE-OFF HARVEST

The model suggested that the largest number of birds available for harvest from the Tiritiri Matangi robin population in one year was 42 adults. It is difficult to harvest the population to extinction with one harvest, since birds in their first year are not available for harvest. Therefore this number of birds left the population with an extinction probability of 0%.

The model suggested that after a harvest of such magnitude, the population will take about 6 years to recover back to the population size prior to harvesting. Is a harvest of 40 robins likely? The original translocation of robins to Tiritiri Matangi Island consisted of 44 birds, and 40 appears to be the accepted number for bird translocations in New Zealand (Armstrong & McLean 1995). Wolf et al.'s (1996) formula for determining translocation success suggests that a translocation of 40 robins into good habitat has a 63% probability of success if no other information is taken into account. Lovegrove &

Veitch (1994) suggests that for most New Zealand forest birds it is probably not necessary to release large numbers. Fewer birds may be required if their sexes are known because this eliminates the problem of having low numbers of one sex by chance. For example the first translocation of robins to Tiritiri Matangi Island consisted of 44 robins. These were birds of unknown sex and the translocation resulted in only 7 females in the first breeding season. In contrast the Wenderholm translocation of 21 robins (16 of known sex) resulted in 6 females in the first breeding season.

Even if a translocation of around 40 robins were planned using the Tiritiri Matangi population, all 40 birds would not necessarily be adults. Juvenile robins are often tamer and easier to catch. Juveniles may prove to be more adaptable to new conditions but are also less experienced (Armstrong & McLean 1995). However, as discussed above these juveniles would probably be caught at a stage where their survival rate is close to that of adults.

It has been suggested that all organisms produce more offspring than will survive and hence provide a surplus for utilisation (Beissinger & Bucher 1992, Kemp 2000). Beddington and Taylor (1973) showed that when age groups are selected for harvesting the best strategy is to harvest all of the older age groups with partial harvest of the younger age classes. These suggestions apply if the juveniles are harvested while they are still experiencing density dependent survival. In the Tiritiri Matangi robins this requires catching juveniles when they first become independent. There is only a brief time when they are still in the natal territories, and then they become difficult to find.

HARVESTING REGIMES

The important thing to note with this model is that the number of birds you set out to harvest per year is not necessarily the number that is actually taken. If there are not as many birds available as set to harvest, the largest number possible is taken. Therefore as the set number to harvest increases, the population is depleted more quickly. Higher set harvests can actually take fewer birds in total than lower set harvests (Fig. 4.3 c).

Modelling of the Tiritiri Matangi population indicates that for equivalent set harvests/year, triennial harvesting showed lower probabilities of extinction than annual or biennial harvesting. However, triennial harvesting resulted in lower total numbers actually taken from the population over the 6 years. Therefore the optimal harvesting regime depends upon whether the harvesting aims to (1) take the most birds for a set probability of extinction or, (2) minimise the extinction probability for a set number of birds taken. Annual harvesting would be best in the former case and biennial harvesting would be best in the latter case. This is better than triennial even though triennial harvesting has lower probabilities of extinction for equivalent set harvests per year, because the numbers actually taken from the population are higher (Fig. 4.3).

The harvesting model employed here, as explained above, only takes adult birds. Although it was difficult to cause the population to go to extinction from a one off harvest of adults, this was not the case for repeat harvests. If harvesting of adults is repeated, the population is driven to extinction because the combined loss of individuals through harvesting and mortality is greater than recruitment.

LOWEST POPULATION TO HARVEST FROM

The model suggested that the Tiritiri Matangi robin population could recover from as few as 4 pairs of robins (Fig. 4.5). This suggests that any harvest should not reduce the number of birds left to fewer than 4 pairs. For example, if 20 birds were required for a translocation then at least 28 birds need to be on the island with the 8 left behind being consisting of 4 females and 4 males. It may be that there needs to be more than 28 birds on the island depending on the sex ratio of birds present and the sex ratio required for translocation.

Is it reasonable to expect the Tiritiri Matangi population to recover with as few as 4 pairs? To begin with, it is important to note the simplicity of the model used to make these predictions. Environmental variation, catastrophes and genetics are assumed to have little to no effect. This may not be true, and with such a small population a catastrophe could easily wipe it out or inbreeding depression may take its toll. However, two populations of South Island robins have been established from 5 birds on Motuara and Allports Islands (Armstrong 2000).

SUMMARY

- Modelling harvests with adults only is justifiable when the change in juvenile survival after 2 months is considered.
- The largest number of adults available for removal by harvesting is 42.
- The best harvesting regime for the Tiritiri Matangi robin population depends on the aim of harvesting: (1) take the most birds for a set probability of extinction or, (2) minimise the extinction probability for a set number of birds taken.
- The lowest population size to harvest from is the size of the harvest plus 4 pairs.

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5

Summary and Conclusions

It is widely agreed that monitoring of translocated populations is important (Scott & Carpenter 1987, Griffith et al. 1989, IUCN 1998). Monitoring a population following a translocation can provide useful information on the outcome of the translocation and suggest improved techniques for subsequent translocations. However, a translocation requires not only the release of animals but also the capturing of these animals from a source population.

The IUCN (1998) state, "removal of individuals for reintroduction must not endanger the captive stock population or the wild source population". I have only managed to find a couple of papers that report the effects of the translocation on the source population (Stevens & Goodson 1993, Mumme & Below 1999). My thesis is based on the question what happens to a source population when animals are removed (harvested) from it?

To study this I used the Tiritiri Matangi North Island robin (*Petroica australis longipes*) population as a case study. Armstrong and Ewen (in press) studied this population and suggested "if survival and/or reproduction is suppressed at high density, the population can be sustainably harvested for translocation or other purpose with no cost to the source population". To test this prediction I followed three steps. First I used the translocation as an experiment to test for density dependence in juvenile survival. I then used population viability analysis (PVA) to assess whether there was any effect of the translocation on the source population. Finally, I used a population model to predict the effects of harvesting on the source population.

DENSITY DEPENDENCE

Density dependence appears to be present in the Tiritiri Matangi population. Survival of juvenile robins is correlated with the number of pairs present in the population during the breeding season they are produced.

An important discovery has been that juveniles do not have constant survival from the time they fledge until the next breeding season (Armstrong pers com). Juveniles have lower survival in the first 2 months after fledging. Classification of birds as juveniles may only be appropriate for this time period. This means, as the translocation occurred more than 2 months following the majority of juvenile fledging, most of the juvenile mortality was missed for this year. For the manipulation to have indicated density dependence in juvenile survival, it had to have occurred before this mortality.

Removing adults from the population just before the breeding season would have better revealed density dependence in the Tiritiri Matangi population. This way the manipulation could be in time to affect the two months when juvenile survival is at its lowest. Trying to remove adults within the two month period after fledging isn't practical, because adults would need to be removed directly after their juveniles become independent. This would not work because (1) fledging is not synchronous, (2) if adults were removed after the first young were fledged, they would be unable to produced subsequent clutches (they normally produce 2-3 clutches over 5 months), (3) if adults were removed after the last young fledged, this would affect only a small portion of juveniles and would affect only a small portion of juveniles and would mean that adults were translocated while moulting.

The removal of birds in my study probably had some effect on the juveniles in the following breeding season (1999/2000). As was noted, juvenile survival increased slightly in 2000. A stronger test of the density dependent response in the Tiritiri robins would be to reduce the numbers of adults in the population to a similar level as that in the first few years.

TIRITIRI MATANGI

Given that there appeared to be density dependent survival in the population, the next step was to test the effect of the translocation on the population. The prediction was that as there is density dependent survival, a reduction in adult density should increase juvenile survival to compensate. I examined this effect in terms of the probability of the population going extinct within the next 20 years. The Tiritiri population was predicted to have a 0% probability of extinction within 20 years, hence was predicted to recover from the manipulation. This result was fairly robust to changes in parameter values, with the worst-case scenario predicting an extinction probability of only 1.3% in the next 20 years.

This supports the hypothesis that the translocation would have no detrimental effect on the Tiritiri Matangi population.

WENDERHOLM

The Wenderholm population was predicted to have a large (96%) probability of extinction within the next 20 years based on the first year of data after translocation. Such short-term data means that the model was fairly crude. However, short-term data may be useful to assess alternative management actions using sensitivity analysis (Possingham et al. 1993, Johnson & Braun 1999, White 2000). My sensitivity analysis suggested that the population's extinction probability was very sensitive to increasing juvenile survival, suggesting that the Wenderholm population could benefit from attempts to identify sources of mortality acting on juveniles.

Raeburn (2001) studied the reintroduction of North Island robins to Paengaroa, and found that reproduction and survival were lower in the first year following reintroduction.

Reproduction was also atypically low in the Tiritiri Matangi robins in the first year after reintroduction; resulting in the first year's data substantially underestimating the population's probability of survival (Armstrong & Ewen 2001). The Wenderholm population needs to be remodeled with additional data from subsequent years. This can then indicate whether the population needs supplementation, and would benefit from it. It is important for a newly translocated population that monitoring continue for more than the first year. Decisions on supplementary translocations based on reproduction and survival from the first year may be misleading.

If the depression of reproduction and survival by translocation in the first year can be confirmed in other populations and species, then future modeling should incorporate a way to model a population where parameters differ between the first year and subsequent years. This would be useful if a relationship could be found between the first and second year parameters. It would mean prediction of future populations could be made, based only on the first year's data, with better precision than what is currently available.

HARVESTING

Assuming that juvenile survival is density dependent, the Tiritiri Matangi population will recover from the translocation removing 21 birds. In the light of these discoveries can the Tiritiri Matangi robin population be harvested repeatedly?

I modeled the harvesting by removing adults from the population, and assessing the effect by determining the probability of extinction within 20 years. The model suggests that removing all adults from the population between breeding seasons in a one-off harvest will result in a 0% probability of extinction. This harvest would consist of about 42 birds, and the population is predicted to take 6 years to recover back the population size prior to the harvest.

I modelled repeated harvesting to investigate the impact that three different harvesting regimes (annual, biennial and triennial) would have on the population. The model allows a number for harvest to be set, then outputs how many birds were actually taken in total. This is because even though the model attempts to take a set number each year, if there are not enough adults in the population the model harvests as many as are available.

The best regime depends on what the harvest is trying to achieve. The aim could be to take the most birds possible at a particular probability of extinction (for example 5%), or to get a particular number of birds for the lowest possible extinction probability. The model suggests that annual and biennial harvesting are, respectively, the best regimes for each of these two aims.

The Tiritiri Matangi population could potentially recover from as few as 4 pairs of robins. At this level the population still has a 0% probability of extinction within 100 years and would take about 10 years to recover back to its equilibrium level (Fig 4.5). This suggests that any harvest carried out should not harvest the population any lower than 4 pairs, and that the population would not be available for harvest again for a number of years. Although the population would be vulnerable to extinction from catastrophes and environmental stochasticity, other populations have been established from as few as 5 birds (Armstrong 2000).

Species for which there are only one or two stable populations are likely to experience repeated harvesting from these populations for translocation. I think it is important in these cases to carefully consider exactly what the translocation is trying to achieve before carrying it out. Modelling, as I have done for the Tiritiri Matangi population, can suggest alternative ways of repeat harvesting that minimize the impact on the source population while still achieving the harvesting goals. Even with limited information on population parameters, modelling could still be useful in assessing the merits of alternative strategies (Possingham et al. 1993, Burgman 2000, White 2000)

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Appendices

A. Covariates for the model (trunc J)

Year	**P = (65 – A)/F or 0.64, whichever is less.**	**$\beta = \ln(S/1-S)$**	**$C = 0.575 - \beta$**
SEPT 1996	(65 – 45)/45 = 0.44	$\ln\left(\frac{0.44}{1-0.44}\right) =$ -0.241	0.575 – (-0.241) = 0.816
0CT 1997	(65 – 51)/54 = 0.26	$\ln\left(\frac{0.259}{1-0.259}\right) =$ -0.1.051	0.575 – (-1.051) = 1.626
SEPT 1999 – With Translocation	(65 – 34)/(57-5) = 31/52 = 0.60	$\ln\left(\frac{0.596}{1-0.596}\right) =$ 0.389	0.575 – 0.389 = 0.186
SEPT 1999 – Without Translocation	[65 – (34 + 14)]/57 = 0.30	$\ln\left(\frac{0.298}{1-0.298}\right) =$ -0.857	0.575 – (-0.857) = 1.432
SEPT 2000	65 – 38/60 = 0.45	$\ln\left(\frac{0.45}{1-0.45}\right) =$ -0.201	0.575 – (-0.201) = 0.776

Table A.1. Calculated values for the covariates used in MARK for the truncation model (Fig. 2.3). Two sets of covariates were used. In the first the 1999 value used was "With Translocation" in the second "Without Translocation" was used. In the formulae above, A is the number of adults still alive at the beginning of the next breeding season. F is the number of fledglings produced in the current breeding season minus any translocated. S is the Juvenile Survival. β is the estimated parameter value and C is the covariate used in MARK to predict juvenile survival. 65 is the predicted carrying capacity. Juvenile survival was not expected to exceed 64% with the β (0.575) corresponding to this.

B. Tiritiri Matangi Program

```
Sub robinmain()

' robin Macro
' Macro recorded 17/07/2001 by Scott Davidson
' based on Wendy Dimond's robin data from Tiri
'

Randomize
    Worksheets("robin model").Activate
    var3 = Cells(13, 3).Value
    'here is main body of program
   Worksheets("num pairs").Range("a1:az1000").Clear
   Worksheets("num males").Range("a1:az1000").Clear
   Worksheets("num females").Range("a1:az1000").Clear
   Worksheets("pop size").Range("a1:az1000").Clear
   Cells(21, 3).Value = 0
   For replicate = 1 To Cells(14, 3).Value
    Cells(29, 1).Value = 0
    robininitpopsize
    ' counter to show that model is turning over
    Cells(22, 2).Value = replicate
    For var2 = 1 To var3
     ' second part of counter to show that the model is turning over
     Cells(22, 3).Value = var2
     ev = ((Sqr(-2 * Log(Rnd()))) * (Cos(2 * 3.14159 * Rnd())))
     robinreproduction
     If var2 = 1 Then
        robinsurfirstyear (ev)
        Else
        robinmortalityadult (ev)
        robinmortalityjuve
        End If
     robinjuvesexing
     nm = Cells(29, 4).Value
     nf = Cells(29, 5).Value
     If nm > nf Then np = nf Else np = nm
     Cells(29, 1).Value = np
     Worksheets("Num pairs").Cells(replicate + 1, 1).Value = replicate
     Worksheets("Num pairs").Cells(1, var2 + 1).Value = var2
     Worksheets("Num pairs").Cells(replicate + 1, var2 + 1).Value = np

        Worksheets("num males").Cells(replicate + 1, 1).Value = replicate
        Worksheets("num males").Cells(1, var2 + 1).Value = var2
        Worksheets("num males").Cells(replicate + 1, var2 + 1).Value = nm


        Worksheets("num females").Cells(replicate + 1, 1).Value = replicate
```

```
        Worksheets("num females").Cells(1, var2 + 1).Value = var2
        Worksheets("num females").Cells(replicate + 1, var2 + 1).Value = nf


        Worksheets("pop size").Cells(replicate + 1, 1).Value = replicate
        Worksheets("pop size").Cells(1, var2 + 1).Value = var2
        Worksheets("pop size").Cells(replicate + 1, var2 + 1).Value = nf + nm

      Worksheets("robin model").Activate
      If np = 0 Or nm = 0 Or nf = 0 Then
           Cells(21, 3).Value = Cells(21, 3).Value + 1
           var2 = var3 + 1
           End If
      Next var2

  Next replicate
  statspairs2
  If Cells(25, 5) = "yes" Then statsmales2
  If Cells(26, 5) = "yes" Then statsfemales2
  statstotal2
End Sub
----------------------------------------------------------------------------------------------------

Sub robininitpopsize()
   '  assign ages to intial individuals.
   'initial males
   nm = Cells(15, 3).Value
   nf = Cells(16, 3).Value

   Cells(29, 4).Value = nm
   Cells(29, 5).Value = nf
   Cells(29, 1).Value = 0
End Sub
----------------------------------------------------------------------------------------------------

Sub robinsurfirstyear(ev)
   ' mortality of adults
   ' routine goes through all individuals,
   ' paired adults, and un paired adults
   lengthm = (Cells(17, 3).Value)
   evdeath = ((Sqr(Cells(4, 2).Value) * ev))
   mort = Cells(3, 2).Value
   reapersprob = ((Exp(mort)) / (1 + Exp(mort))) ^ lengthm + evdeath
   ' males
   deathscount = 0
   For charon = 1 To Cells(29, 4).Value
      If Rnd() > reapersprob Then deathscount = deathscount + 1
   Next charon
   Cells(29, 4).Value = Cells(29, 4).Value - deathscount
   ' females
```

```
   deathscount = 0
   For charon = 1 To Cells(29, 5).Value
     If Rnd() > reapersprob Then deathscount = deathscount + 1
      Next charon
    Cells(29, 5).Value = Cells(29, 5).Value - deathscount
End Sub

----------------------------------------------------------------------------------------------------------

Sub robinjuvesexing()
   ' assigning sex to juvenile robin
   sexratio = Cells(11, 2).Value
   males = Cells(29, 4).Value
   females = Cells(29, 5).Value
   juves = Cells(29, 6).Value
   newmales = 0
   newfemales = 0
   For q = 1 To juves
      If Rnd() > sexratio Then
         newmales = newmales + 1
         Else
         newfemales = newfemales + 1
         End If
   Next q
   Cells(29, 4).Value = males + newmales
   Cells(29, 5).Value = females + newfemales
   Cells(29, 6).Value = 0
   End Sub
----------------------------------------------------------------------------------------------------------

Sub robinmortalityjuve()
   ' mortality routine for juveniles
   ' no ev in juve mortality
   pairs = Cells(29, 1).Value
   dd = Cells(6, 2).Value
   mort2 = Cells(3, 2).Value + Cells(5, 2).Value
   juvelength = Cells(19, 3).Value
   ddjuve = dd * (pairs / 10)
   reapersprob2 = (Exp(mort2 + ddjuve)) / (1 + Exp(mort2 + ddjuve))
   reapersprob = reapersprob2 ^ juvelength
   numjuves = Cells(29, 6).Value
   deadjuves = 0
   ' count of dead juves
   ' remmember only number of juves is stored, no individual details
   For charon = 1 To numjuves
      If Rnd() > reapersprob Then deadjuves = deadjuves + 1
   Next charon
   Cells(29, 6).Value = numjuves - deadjuves
 End Sub

------------------------------------------------------------------------------------------------------------
```

```
 Sub robinmortalityadult(ev)
   ' mortality of adults
   ' routine goes through all individuals,
   ' paired adults, and un paired adults
   evdeath = Sqr(Cells(4, 2).Value) * ev
   If evdeath > 1 Then evdeath = 1
   mort = Cells(3, 2).Value
   reapersprob = ((Exp(mort)) / (1 + Exp(mort))) ^ 12 + evdeath
   males = Cells(29, 4).Value
   females = Cells(29, 5).Value
   ' and no I don't really believe the senscence hocus pocus!
   ' males
    deathscount = 0
   For charon = 1 To males
       If Rnd() > reapersprob Then deathscount = deathscount + 1
   Next charon
   Cells(29, 4).Value = males - deathscount
   ' females
   deathscount = 0
   For charon = 1 To females
      If Rnd() > reapersprob Then deathscount = deathscount + 1
      Next charon
    Cells(29, 5).Value = females - deathscount
   Cells(34, 3).Value = deathscount
 End Sub
---------------------------------------------------------------------------------------------------

Sub robinreproduction()
   ' reproduction for robins
   ' using Doug's formulae

'   use individuals from pairs to calculate number of new offspring
       bmean = Cells(9, 2).Value
       newjuves = 0
       Cells(29, 6).Value = 0
       birthvar = Cells(10, 2).Value
       p = (bmean ^ 2) / (birthvar + bmean ^ 2)
       n = bmean / p
   pairs = Cells(29, 1).Value
   If Cells(29, 4).Value = 0 Then pairs = 0
   For astartes = 1 To pairs
       If Rnd() < p Then newjuves = newjuves + n
       Next astartes
       Cells(29, 6).Value = Int(newjuves)
End Sub
---------------------------------------------------------------------------------------------------

Public Sub statsmales2()
  Dim nyears As Integer, q As Integer
  Dim nrep As Integer, nvalid As Integer
```

```
  Dim ra As String, letter As String
  Dim temp As Integer

  nyears = Cells(13, 3).Value
   nrep = Cells(14, 3).Value
   Worksheets("num males").Activate
   'stats for number of pairs
   Dim avyp1(100) As Double, sdyp1(100) As Double, ciyp(100) As Double
   For q = 1 To nyears
    letter = ""
    temp = q Mod 26
    If Int(q / 26) > 0 Then letter = Chr(Int(q / 26) + 64)
    letter = letter & Chr(temp + 65)

    ra = letter & CStr(2) & ":" & letter & CStr(nrep + 1)
    nvalid = Application.WorksheetFunction.CountIf(Range(ra), ">0")
    avyp1(q) = Application.WorksheetFunction.Average(Range(ra))
    sdyp1(q) = Application.WorksheetFunction.StDev(Range(ra))
    If sdyp1(q) = 0 Then
      ciyp(q) = 0
    Else
      ciyp(q) = Application.WorksheetFunction.Confidence(0.05, sdyp1(q), nvalid)
    End If
    Worksheets("Robin model").Cells(q + 3, 9).Value = avyp1(q)
    Worksheets("Robin model").Cells(q + 3, 10).Value = sdyp1(q) '/ Sqr(nrep)
    Worksheets("Robin model").Cells(q + 3, 11).Value = ciyp(q)
   Next q
  Worksheets("Robin model").Activate
End Sub
------------------------------------------------------------------------------------------

Public Sub statsfemales2()
  Dim nyears As Integer, q As Integer
  Dim nrep As Integer, nvalid As Integer
  Dim ra As String, letter As String
  Dim temp As Integer

  nyears = Cells(13, 3).Value
   nrep = Cells(14, 3).Value
   Worksheets("num females").Activate
   'stats for number of pairs
   Dim avyp1(100) As Double, sdyp1(100) As Double, ciyp(100) As Double
   For q = 1 To nyears
    letter = ""
    temp = q Mod 26
    If Int(q / 26) > 0 Then letter = Chr(Int(q / 26) + 64)
    letter = letter & Chr(temp + 65)

    ra = letter & CStr(2) & ":" & letter & CStr(nrep + 1)
    nvalid = Application.WorksheetFunction.CountIf(Range(ra), ">0")
```

```
    avyp1(q) = Application.WorksheetFunction.Average(Range(ra))
    sdyp1(q) = Application.WorksheetFunction.StDev(Range(ra))
    If sdyp1(q) = 0 Then
      ciyp(q) = 0
    Else
      ciyp(q) = Application.WorksheetFunction.Confidence(0.05, sdyp1(q), nvalid)
    End If
    Worksheets("Robin model").Cells(q + 3, 12).Value = avyp1(q)
    Worksheets("Robin model").Cells(q + 3, 13).Value = sdyp1(q) '/ Sqr(nrep)
    Worksheets("Robin model").Cells(q + 3, 14).Value = ciyp(q)
  Next q
  Worksheets("Robin model").Activate
End Sub
------------------------------------------------------------------------------------------

Public Sub statspairs2()
  Dim nyears As Integer, q As Integer
  Dim nrep As Integer, nvalid As Integer
  Dim ra As String, letter As String
  Dim temp As Integer

  nyears = Cells(13, 3).Value
   nrep = Cells(14, 3).Value
   Worksheets("num pairs").Activate
   'stats for number of pairs
   Dim avyp1(100) As Double, sdyp1(100) As Double, ciyp(100) As Double
   For q = 1 To nyears
    letter = ""
    temp = q Mod 26
    If Int(q / 26) > 0 Then letter = Chr(Int(q / 26) + 64)
    letter = letter & Chr(temp + 65)

    ra = letter & CStr(2) & ":" & letter & CStr(nrep + 1)
    nvalid = Application.WorksheetFunction.CountIf(Range(ra), ">0")
    avyp1(q) = Application.WorksheetFunction.Average(Range(ra))
    sdyp1(q) = Application.WorksheetFunction.StDev(Range(ra))
    If sdyp1(q) = 0 Then
      ciyp(q) = 0
    Else
      ciyp(q) = Application.WorksheetFunction.Confidence(0.05, sdyp1(q), nvalid)
    End If
    Worksheets("Robin model").Cells(q + 3, 6).Value = avyp1(q)
    Worksheets("Robin model").Cells(q + 3, 7).Value = sdyp1(q) '/ Sqr(nrep)
    Worksheets("Robin model").Cells(q + 3, 8).Value = ciyp(q)
   Next q
  Worksheets("Robin model").Activate
End Sub
------------------------------------------------------------------------------------------

Public Sub statstotal2()
```

```
  Dim nyears As Integer, q As Integer
  Dim nrep As Integer, nvalid As Integer
  Dim ra As String, letter As String
  Dim temp As Integer

  nyears = Cells(13, 3).Value
   nrep = Cells(14, 3).Value
   Worksheets("pop size").Activate
   'stats for number of pairs
   Dim avyp1(100) As Double, sdyp1(100) As Double, ciyp(100) As Double
   For q = 1 To nyears
     letter = ""
     temp = q Mod 26
     If Int(q / 26) > 0 Then letter = Chr(Int(q / 26) + 64)
     letter = letter & Chr(temp + 65)

     ra = letter & CStr(2) & ":" & letter & CStr(nrep + 1)
     nvalid = Application.WorksheetFunction.CountIf(Range(ra), ">0")
     avyp1(q) = Application.WorksheetFunction.Average(Range(ra))
     sdyp1(q) = Application.WorksheetFunction.StDev(Range(ra))
     If sdyp1(q) = 0 Then
       ciyp(q) = 0
     Else
       ciyp(q) = Application.WorksheetFunction.Confidence(0.05, sdyp1(q), nvalid)
     End If
     Worksheets("Robin model").Cells(q + 3, 15).Value = avyp1(q)
     Worksheets("Robin model").Cells(q + 3, 16).Value = sdyp1(q) '/ Sqr(nrep)
     Worksheets("Robin model").Cells(q + 3, 17).Value = ciyp(q)
   Next q
  Worksheets("Robin model").Activate
End Sub
```

C. VORTEX 8.41 input values for Wenderholm

Simulations: 1000
Years: 100
Reporting interval: 10
Definition of extinction (0 = 1 sex): 0
Populations: 1
Inbreeding depression? N
EV(repro) concordant with EV(surv)? N
Catastrophes: 0
Monogamous
Female breeding age: 1
Male breeding age: 1
Max. age for breeding: 100
Sex ratio (% males): 50
Max No of young/yr: 0 *(Putting 0 means number of offspring for each female sampled from a normal distribution with mean and variance specified).*
Density dependent reproduction: N

% females breeding: 100
SD in % breeding annually: 0
Mean No of progeny/yr: 3.29
SD in annual production: 2.4

MORTALITY

Adults: 38.5 %	SD: 0
Juveniles: 82.6 %	SD: 0

All adult males in the breeding population.
Stable age distribution: N
Initial pop size: 13
F age 1: 6
M age 1: 7

Carrying capacity: 120
SD in K due to EV: N
Trend projected in K: N

Harvesting? N

Supplementing? N

D. Harvesting subroutine

```
Sub harvesting(replicate)
  nummales = Cells(2, 7).Value
  numfemales = Cells(3, 7).Value
  males = Cells(29, 4).Value
  females = Cells(29, 5).Value
  If nummales < males Then
    Cells(29, 4).Value = Cells(29, 4).Value - nummales
    removedmales = nummales
    Else
    Cells(29, 4) = 0
    removedmales = males
    End If
  If numfemales < females Then
    Cells(29, 5).Value = Cells(29, 5).Value - numfemales
    removedfemales = numfemales
    Else
    Cells(29, 5) = 0
    removedfemales = females
    End If
  Worksheets("harvested").Cells(replicate + 1, 1) =
Worksheets("harvested").Cells(replicate + 1, 1) + removedmales
  Worksheets("harvested").Cells(replicate + 1, 2) =
Worksheets("harvested").Cells(replicate + 1, 2) + removedfemales
End Sub
```