



Population dynamics of reintroduced forest birds on New Zealand islands

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Abstract

Aim We studied dynamics of four populations of New Zealand forest birds for 5–9 years after reintroduction to islands. We primarily aimed to predict whether these populations were viable, and what, if any, management was needed to maintain them. However, the small scale of these islands also provided an opportunity to study density-dependent population growth over a short time frame.

Location We studied New Zealand robin (toutouwai, *Petroica australis*) and stitchbird (hihi, *Notiomystis cincta*) populations reintroduced to Tiritiri Matangi, a 220-ha offshore island near Auckland, and saddleback (tieke, *Philesturnus carunculatus*) and stitchbird populations reintroduced to Mokoia, a 135-ha island in Lake Rotorua. These islands are free of mammalian predators, but have highly modified habitat following clearing and regeneration.

Methods We closely monitored each population, individually marking all or most of the birds and in some cases experimentally manipulated population density or food supply. We used model selection procedures to understand factors affecting survival, fecundity and dispersal, and developed stochastic simulation models.

Results The Tiritiri Matangi robin and Mokoia saddleback populations grew without management and appear to be viable. Both showed strong evidence of density-dependent growth, with fecundity (saddlebacks) and juvenile survival (both populations) declining with increasing density. Neither stitchbird population appears viable without management and supplementation experiments showed reproduction and/or survival to be limited by food supply. The Tiritiri Matangi population appears viable as long as supplementary feeding continues. However, the Mokoia population has a high mortality rate regardless of supplementary feeding, resulting in tenuous viability even with intensive management. Mokoia stitchbirds suffer from infection by *Aspergillus fumigatus*, a pathogenic fungus that is prevalent in highly modified habitats and more abundant on Mokoia than Tiritiri Matangi.

Main conclusions Some forest birds can thrive in regenerating forest on islands and strong evidence of density dependence can be detected in such populations in as little as 5 years. This allows density-dependent models to be developed, providing guidance when island populations are harvested for further translocations. Other species are limited by food supply in regenerating environments, a problem potentially overcome by management. However, prevalence of *A. fumigatus* may render highly modified environments uninhabitable by some species regardless of management.

Keywords

Reintroduction, islands, population dynamics, population modelling, density dependence.

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INTRODUCTION

As other contributors to this volume have noted, island studies have played a key role in research on evolution, biogeography and community ecology. The field of population ecology is less immediately associated with islands, but there have been some seminal studies such as Mech's (1966) research on the wolf-moose system on Isle Royale. More importantly, basic concepts and theories in population ecology seem to have been initially developed with insular systems in mind. The term 'population' itself implies a discrete group of organisms bounded in space and it is often difficult, if not meaningless, to define populations in open mainland systems. The classic logistic model of density-dependent population growth (Pearl & Reed, 1920) is most easily applied to island systems, and attempts to apply similar models to open systems have sometimes led to disastrous consequences (Holt & Talbot, 1978; Lande *et al.*, 1997). The classic lab experiments in population ecology involved introducing organisms such as *Paramecium* (Gause, 1934) and *Daphnia* (Frank *et al.*, 1957) to micro-islands in the form of test tubes or beakers.

Reintroductions of New Zealand birds to islands share many characteristics with the microcosm experiments of Gause (1934) and Frank *et al.* (1957). First, because many of the species are extremely sedentary, the reintroduced populations are confined to closed systems. Secondly, the size of the islands (usually 100–300 ha) allows researchers to survey and monitor the whole system. Thirdly, because a relatively small 'propagule' of birds is usually reintroduced, we have the opportunity to monitor the growth of the population from low density. Fourthly, if conditions are favourable, the population may grow toward carrying capacity within a few years, providing an opportunity to test for density-dependent changes in population parameters. Fifth, conditions for reintroduced species may be unfavourable because of other species present on the islands. Just as Gause (1934) showed that *Paramecium caudatum* cannot survive if grown with *P. aurelia*, a series of island reintroduction attempts with saddlebacks [tieke, *Philesturnus carunculatus* (Gmelin)] showed that they cannot survive if ship rats [*Rattus rattus* (Linnaeus)] or stoats [*Mustela erminea* (Linnaeus)] are present (Lovegrove, 1996). Islands are larger than beakers and birds breed more slowly than *Daphnia*, hence we are much more limited in terms of replicates and generations. On the other hand, birds can be individually marked and observed, allowing us to obtain data on reproduction, survival and movements at the individual level.

Reintroductions to islands have been a major component of conservation management in New Zealand. Most New Zealand species declined substantially in range and abundance following European colonization in the mid-1800s (Atkinson & Cameron, 1993). Several species were completely extirpated from the mainland (i.e. North Island, South Island and Stewart Island, the three major islands of the New Zealand archipelago) and became restricted to one or more offshore islands (Daugherty *et al.*, 1990). These

declines can largely be attributed to introduction of mammalian predators and browsers and to loss or modification of habitat. Offshore islands have also been heavily modified. Maori and/or European colonists cleared and burnt vegetation on most islands and introduced a range of exotic species. However, many islands escaped invasion by the most damaging exotics such as ship rats and mustelids, providing refuges for native species unable to survive in the presence of these exotics. Most islands have now been unoccupied by humans for several decades, resulting in some natural regeneration of vegetation and since the 1980s there has been a major drive to restore island ecosystems by eradicating exotics (Veitch & Bell, 1990), replanting vegetation (e.g. Mitchell, 1985) and reintroducing native species (Saunders, 1994; Armstrong & McLean, 1995). In addition to reintroductions (species thought to have occurred on the site previously), there has been a smaller number of 'conservation introductions' (species that would not have occurred on the site historically, but which have minimal chance of survival in their original range; IUCN, 1998). As of March 2002, there had been 224 documented reintroductions or introductions of native species to New Zealand islands, 188 involving animals (Atkinson, 1990; Armstrong, 1999–2002) and thirty-six involving plants (Coumbe & Dopson, in press).

Until recently, most reintroductions (New Zealand and world-wide) have been one-off management exercises with little or no accompanying monitoring and no research objectives. Therefore, despite the opportunity that island reintroductions provide for studying population ecology, few data were collected. However, over the last 15 years there have been frequent calls for increased monitoring of reintroductions (Griffith *et al.*, 1989; Maunder, 1992; Kleiman *et al.*, 1994; Hein, 1997; IUCN, 1998; Seddon, 1999; Fischer & Linderemayer, 2000), and calls for reintroduction programmes to be designed to incorporate hypothesis testing and experimentation (Armstrong *et al.*, 1994a; Armstrong & McLean, 1995; Sarrazin & Barbault, 1996). The main reason for these calls has been the high failure rate of reintroduction attempts. New Zealand has not shared this trend, the majority of reintroductions having successfully established populations (Saunders, 1994). Nevertheless, the amount of research and monitoring associated with New Zealand reintroductions has increased substantially because of: (1) an increase in monitoring for all types of conservation management; (2) the need to improve reintroduction success for some species; and (3) the need for analysing case studies to provide guidance for more difficult situations, especially reintroductions to the mainland.

This paper reviews four case studies, all involving forest birds, in which intensive monitoring has been conducted for at least 5 years after reintroductions to New Zealand islands. These include New Zealand robins [toutouwai, *Petroica australis* (Sparrman)] reintroduced to Tiritiri Matangi Island, saddlebacks reintroduced to Mokoia Island, and stitchbirds [hihi, *Notiomystis cincta* (Du Bus)] reintroduced to both islands. In all cases, data were used to develop models of population dynamics, and these models used to

predict population viability under different management scenarios. We first outline our overall approach for studying reintroduced populations, then review the key questions and results for each case study and discuss the implications.

APPROACH

Identifying key questions

It is now widely recognized that reintroductions should be monitored. However, monitoring can be done in many different ways and at vastly different levels of intensity. In addition, there are so many reintroductions in New Zealand (Armstrong, 1999–2002) in comparison with the funding and personnel available that we must choose which ones warrant intensive monitoring. The first step in determining appropriate monitoring programmes is to decide what the questions are. The obvious questions concern factors that may affect the reintroduced population's survival. Factors affecting a population's survival can be divided into two categories: those affecting its survival over the initial establishment phase and those affecting its viability over the long-term. The first category includes characteristics of the release strategy, such as number released, composition, transport, timing, pre- and/or post-release training, and hard vs. soft release techniques. The second category may include genetic characteristics of the founder group, but mainly includes characteristics of the release site, namely the amount and distribution of habitat and the quality of that habitat (including predators, competitors and parasites). Comparisons of different release strategies require little post-release monitoring and therefore dominate the reintroduction biology literature (e.g., Kleiman *et al.*, 1991; Armstrong *et al.*, 1994b; Bright & Morris, 1994; Castro *et al.*, 1994; Fancy *et al.*, 1997; Combreau & Smith, 1998; Biggins *et al.*, 1999). However, we suspect that most failures result from poor habitat rather than from poor release strategies. The research programmes outlined here aimed to get the long-term data necessary to understand dynamics of reintroduced populations in relation to their habitat.

Monitoring

Understanding population dynamics requires measuring reproduction, survival, immigration and emigration. We were able to colour band most of the individuals in each population, allowing good data on these parameters. We monitored individual females throughout the breeding season and measured reproduction in terms of number of fledglings produced per female per year. We either monitored all females, or selected a sample stratified with respect to age and habitat. Stitchbirds nested almost entirely in nest boxes in the populations studied, hence monitoring mainly involved checking these boxes. For robins and saddlebacks, it is relatively easy to locate monitored individuals to determine their nesting status. In all cases we located active nests, estimated likely fledging dates, and checked for nestlings or fledglings around those dates to determine the

number fledged. If unable to find nests before fledging, a correction factor was added to the number of fledglings found to adjust for post-fledge mortality (Davidson, 1999).

We did at least two surveys a year, at the beginning and end of the breeding season, and used these to estimate survival. Surveys involved walking through all parts of the island where the species is likely to occur, and recording all individuals seen. Sightings were treated as 'recaptures' and survival and resighting probabilities estimated using the Cormack-Jolly Seber model (Lebreton *et al.*, 1992). Population size, N , at each survey was estimated as n/\hat{p} , where n is the number of individuals seen (both banded and unbanded) and \hat{p} is the estimated resighting probability for that survey. An approximate 95% confidence interval is given by $\hat{N} \pm 2SE$, where $SE(\hat{N}) = n[SE(\hat{P})]/\hat{p}^2$ (Wood *et al.*, 1998). This is a reliable method as long as the majority of the population is banded, ensuring that unbanded individuals are unlikely to be counted more than once.

Immigration and emigration are zero, as there are no source populations nearby and none of the three species have been documented to fly over the distance of water necessary to reach the mainland (3.5 km from Tiritiri Matangi and 2.1 km from Mokoia). The only information on dispersal we have used concerns dispersal of robins among the forest patches of Tiritiri Matangi (Armstrong & Ewen, 2002).

In addition to obtaining data on population parameters, we have monitored weights of stitchbirds to assess their condition with respect to food supply, abundance of fruits and flowers and soil and air levels of *Aspergillus fumigatus* (Fr.), a pathogenic fungus that is a major source of mortality in stitchbirds.

Experiments

Where possible, manipulative experiments provide a more powerful method of answering questions than simply monitoring (Armstrong *et al.*, 1994a). We initially did experiments manipulating levels of familiarity in founder groups for reintroductions of robins and saddlebacks (Armstrong *et al.*, 1994b) and manipulating transport and release methods for reintroductions of stitchbirds (Castro *et al.*, 1994). While possibly relevant to future reintroductions, there was no prior indication that these were likely to be key issues for the viability of the reintroduced populations involved. Our more recent experiments have attempted to test more critical hypotheses. We used supplementation experiments to test whether reintroduced stitchbirds were limited by food supply (Armstrong & Perrott, 2000; Armstrong & Ewen, 2001a) and translocated robins from Tiritiri Matangi as a test of density dependence in that population (Dimond, 2001).

Model selection and parameter estimation

Just as it is well recognized that reintroduced populations should be monitored, it is well recognized that the data collected should be used to estimate parameters such as survival and reproduction. However, for a parameter

estimate to be meaningful, it is critical to first have a reasonable model of the factors affecting it. For example, a combined survival rate for males and females is misleading if one sex has a substantially lower survival rate than the other. Obtaining a reasonable model requires first considering factors likely to affect the parameter of interest, then using the data to determine which factors are important. If only one or two factors are likely to be important, these can be tested by traditional statistical hypothesis testing. However, if there are several potentially important factors, traditional statistical analyses lead to a huge number of possible models being considered. This inevitably leads to overfitting, i.e. selection of overly complex models that include unimportant factors and have poor predictive power. In such situations it is preferable to use an information-theoretic approach (Burnham & Anderson, 1998). Under this approach a limited number of candidate models are selected based on relevant theory and the biologist's knowledge of the system. The model that best explains the data is then selected based on Akaike's Information Criterion (AIC) or similar criteria.

We used the information-theoretic approach to select appropriate models for factors affecting survival and reproduction in each population. Alternative models included factors such as sex, age, annual variation in conditions, population density, season and site. Survival models were fitted to the survey data using MARK (White & Burnham, 1999). Reproduction models were fitted to the data on numbers of fledglings per female per year using general linear modelling in SYSTAT. We also used an information-theoretic approach to obtain appropriate models for the sex ratio of recruits entering each population, the alternative models being: (1) the sex ratio was 1 : 1; (2) the sex ratio was different from 1 : 1 but constant or (3) the sex ratio varied among years. For Tiritiri Matangi robins, we created alternative models for juvenile dispersal and used these to assess whether dispersal was constrained by patch isolation.

Population modelling

After selecting an appropriate model for each process, we combined these into a simulation model. There are many different approaches to population modelling, and there has been considerable discussion about whether 'canned packages' are adequate or whether purpose-built models are needed (e.g. Hamilton & Moller, 1995; Lindenmayer *et al.*, 1995; Lacy, 2000). The aim of modelling is to develop the simplest possible model that captures the key factors affecting the population's dynamics (Starfield, 1997). The issue is not whether a canned or purpose-built model should be used, or whether a simple or complex model should be used, but whether the model reflects our understanding of how the population works (Burgman & Possingham, 2000; White, 2000). We have found the package VORTEX (Lacy, 2000) suitable in some situations. However, we have found it necessary to modify the procedures in VORTEX to incorporate some of our models. Davidson (1999) developed a simulation model in C++ to simulate the Mokoia saddle-back population and we have recently created a similar

model using EXCEL macros to simulate the Tiritiri Matangi robin population (Dimond, 2001).

Our simulation models start by determining the number of offspring produced for each female, picking random numbers based on a mean and standard deviation (which may or may not be affected by age and population density). We have also tried incorporating individual variation in reproduction (White, 2000), but found this to have little effect and to be problematic to estimate. The models then determine the number of adults and juveniles that survive to the next breeding season, based on estimated survival probabilities that may be affected by sex and population density. Sexes are then randomly assigned to the new recruits and the process repeated. The models therefore include demographic stochasticity in reproduction, survival and sex ratios. Annual variation (a form of environmental stochasticity) is incorporated only if the model selected for that process includes it. Our model selection procedures account for sampling variation when estimating process variation (White, 2000), avoiding the 'double dipping' that Brook (2000) notes can inflate estimates of annual variation.

We initially tested each simulation model by comparing the behaviour of the real and simulated populations. We then predicted the population's future dynamics and viability, and assessed the sensitivity of those predictions to uncertainty in parameter estimates and model structure. Finally, we predicted viability under different management scenarios, and if possible, manipulated management to test our predictions.

CASE STUDIES

New Zealand Robins on Tiritiri Matangi

Tiritiri Matangi (36°36'S, 174°53'E) is a 220-ha island in the Hauraki Gulf, 3.5 km east of Whangaparaoa Peninsula and 28 km north of Auckland off the North Island of New Zealand. The island was originally covered by coastal broadleaf forest, and would have had robins and most other bird species found on the North Island. It was first inhabited by Maori who introduced Pacific rats [*kiore*, *Rattus exulans* (Peale)] and cleared the forest for cultivation (Drey *et al.*, 1982). It was then occupied by Europeans, who used the island for grazing and as a lighthouse station. When grazing stopped in 1971, the island was designated a Scientific Reserve and Open Sanctuary (Drey *et al.*, 1982). It was mostly covered by pasture grass, which converted to bracken, but also had several small (0.1–4 ha) forest patches totalling about 13 ha. Most of the grass-bracken matrix was planted with native seedlings during 1983–95, mostly using local seed stock (Mitchell, 1985). Pacific rats were eradicated in 1993 by an aerial drop of brodifacoum cereal pellets.

New Zealand robins are small (*c.* 28 g), ground-feeding insectivorous forest birds in the Australasian flycatcher family (Petroicidae). They are territorial and highly sedentary, rarely moving after settlement (Armstrong *et al.*, 2000). They become sexually mature in their first year, and usually form monogamous pairs that last until one

member dies. The breeding season on Tiritiri Matangi is usually from September to February, with young fledging from October to January (Armstrong *et al.*, 2000). The species has declined considerably, but is still found in some locations on the main islands of New Zealand and on some offshore islands.

Robins were reintroduced to Tiritiri Matangi in 1992 (Armstrong, 1995), 9 years after revegetation started and 18 months before Pacific rats were eradicated. They were the sixth bird species reintroduced to the island. Unlike the first five species, which make extensive use of grassland or newly planted areas, robins are normally confined to the forest remnants. It was initially thought that they would not even cross gaps greater than 100–200 m between forest blocks (Flack, 1979), so could potentially be isolated in the fragments on Tiritiri Matangi, many of which are at least 100 m from the nearest fragment.

The major question for this reintroduction was therefore whether a robin population could be viable in a small amount of fragmented habitat such as that found on Tiritiri Matangi. The planted vegetation was expected to provide fairly continuous habitat for robins within 20–30 years, hence the question was whether the population could survive over this time-scale until the planted vegetation matured. Answering this question would indicate what, if any, management should be considered and whether reintroductions of this species should be conducted in similar situations in the future.

Of forty-four birds released in April 1992, forty-three survived to the start of the first breeding season (September) with a skewed sex ratio of twenty-six males to seven females. They fledged only four young in the first breeding season (0.57 fledglings per female), a rate just sufficient to balance the estimated mortality. Preliminary modelling based on the first 14 months' data suggested the population's viability was marginal, but could be substantially improved by releasing additional females. This conclusion was extremely uncertain given the huge confidence intervals for parameters and numerous assumptions that needed to be made at that stage. Nevertheless, we conducted a second translocation of fourteen robins, mostly females, in June 1993. The population (as estimated at the start of the breeding season) grew to sixty-five birds by September 1996, then stayed at almost exactly that level for the next 2 years. The proportion of females slowly increased, up to 44% (twenty-nine of sixty-six) in October 1998 (Fig. 1).

Analysis of data from the first 6 years showed that the reproductive rate for females in their first year after translocation was substantially lower than the normal rate, and this pattern was consistent for the two translocations. This meant that the preliminary modelling based on the first year's data had underestimated population viability, and that the follow-up translocation conducted in 1993 was unnecessary (Armstrong & Ewen, 2001b). It also showed that survival was unusually low after the September 1993 poison operation to eradicate Pacific rats (Armstrong & Ewen, 2001c). Excluding these factors, the models that best explained our data were: (1) adult survival probability is

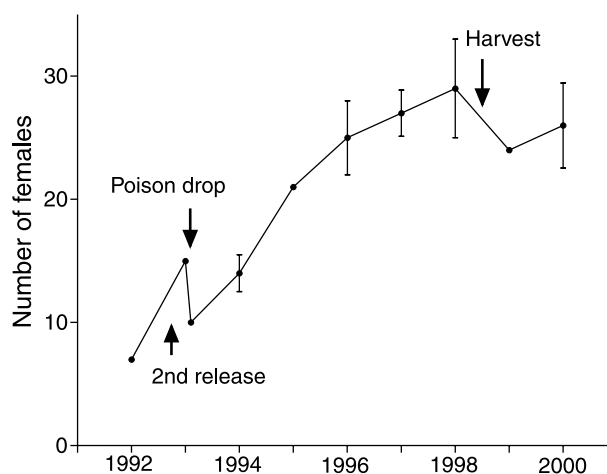


Figure 1 Growth of the New Zealand robin population on Tiritiri Matangi Island following reintroduction in 1992. Data show the estimated number of females (and 95% confidence intervals) at the start of each breeding season. External factors affecting population size included a second release in June 1993, adding seven females to the breeding population, an aerial poison operation on 29 September 1993, causing some mortality, and a harvest of twenty-one birds (twelve males, nine females) in March 1999 for translocation to Wenderholm Regional Park.

constant among years and between sexes; (2) juvenile survival probability declines with population density; (3) the number of fledglings per female varies among forest patches and is lower for first-year birds, but does not vary among years; (4) a recruit has a 0.5 probability of being either sex; (5) isolation among patches does not affect juvenile dispersal, hence the birds could be considered a homogeneous population rather than a metapopulation (Armstrong & Ewen, 2002). A simulation model incorporating these submodels predicted that the population had a negligible chance of extinction over several decades, and this prediction was not sensitive to uncertainty in parameter estimates or model structures. Table 1 gives a summary of these conclusions along with the conclusions for other populations.

The apparent density dependence in juvenile survival further suggested that this small population could be sustainably harvested for further translocations. There are several plausible models of density dependence, and the data for the first 6 years did not allow us to choose between them (Armstrong & Ewen, 2002). We therefore nominated the model best reflecting our intuition about the system. Given that the population had levelled off at 65, we assumed that this was the carrying capacity. We assumed that juvenile survival would be constant until this carrying capacity was reached and would then be truncated to match the number of spaces made available by adult mortality. To test this model, in March 1999, we translocated twenty-one birds (sixteen adults, five juveniles) to Wenderholm Regional Park to reduce population density (Dimond, 2001). Making the additional assumption that juvenile survival was constant

Table 1 Conclusions about dynamics of four populations of forest birds reintroduced to New Zealand islands

Species	Island	Best models			Sex ratio of recruits	Viable	
		Adult survival	Juvenile survival	Reproduction		Unmanaged	Managed
Robin	Tiritiri	Constant	Density-dependent	Patch-dependent, lower age 1	1 : 1	Yes	
Saddleback	Mokoia	Constant	Density-dependent	Density-dependent, lower age 1	1 : 1	Yes	
Stitchbird	Mokoia	Lower in females	Constant	Limited by food supply, nest mites	1 : 1	No	?
Stitchbird	Tiritiri	Limited by food supply	Density-dependent, limited by food supply	Limited by food supply, nest mites?	66% Females	No?	Yes

from the time of fledging until the start of the next breeding season, our model predicted that translocation would result in a compensatory increase in juvenile survival so that the breeding population would be unaffected at the start of the next breeding season.

Further research has allowed us to reject our initial model of density dependence. Dimond (2001) found that there was no increase in juvenile survival after the translocation, and that the population dropped to forty-nine birds (twenty-five males, twenty-four females) for the next breeding season (Fig. 1). Furthermore, fine-grained analysis of survey data collected during 1998–2000 showed that the majority of juvenile mortality occurs in the first 2 months after fledging. This means that translocation, which was conducted more than 2 months after most birds fledged, would not result in an increase in juvenile survival until the following year. A slight increase in juvenile survival was observed in 2000, resulting in an increase in population size (Fig. 1), but smaller than predicted under our original model. A re-analysis of survival data, including data collected up to October 2000, allowed much greater ability to select between models of density dependence in juvenile survival and showed that the truncation model gave a poor fit to the data (Dimond, 2001). The analysis still suggested that juvenile survival was density-dependent, but indicated that the best predictor is the number of pairs at the start of the breeding season. The resulting simulation model still predicted that the population has negligible chance of extinction, and can be sustainably harvested, but predicted subtler and less immediate responses to reductions in density (Dimond, 2001).

Saddlebacks on Mokoia

Mokoia (38°05'S; 176°17' E) is a 135-ha island in Lake Rotorua in the North Island of New Zealand, and is 2.1 km from the mainland at the nearest point. The island would have been originally covered with broadleaf-podocarp forest, and would have had most bird species found in the North Island. Mokoia has had a long history of human use, with several Maori tribes occupying the island for various periods over hundreds of years. The island was cleared, fired and terraced, and the fertile volcanic soil used intensively for

cultivation (Andrews, 1992). European missionaries introduced many species of exotic plants and ungulates starting in the early 1800s, and Norway rats [*Rattus norvegicus* (Berkenhout)] and mice [*Mus musculus* (Linnaeus)] probably arrived at the same time. Cultivation stopped by about 1950, after which the island was designated a Wildlife Refuge and the vegetation allowed to regenerate. The regeneration was influenced by rats, ungulates and fires, resulting in a mosaic of forest, scrub and fernland (Perrott & Armstrong, 2000). The rats and ungulates were eradicated in 1989–90, leaving mice as the only introduced mammals. An aerial drop of brodifacoum cereal pellets was conducted in 1996 to eradicate mice, but this was unsuccessful. A second attempt was made in 2001, and appears to have been successful.

Saddlebacks are medium-sized (*c.* 90 g males, *c.* 70 g females) forest birds, and are one of two extant species of New Zealand wattlebirds (Callaeatidae), a family endemic to New Zealand. Like robins, they are territorial and sedentary, become sexually mature in their first year and usually form monogamous pairs that last until one member dies. They are cavity nesters and typically breed from October through April on Mokoia. Saddlebacks were originally found throughout the North and South Islands. However, they are highly vulnerable to mammalian predators and became extinct everywhere except three small offshore islands following European colonization (Lovegrove, 1996). Their distribution has been increased through translocations to numerous offshore islands (Lovegrove, 1996; Armstrong, 1999–2002), and they may soon be reintroduced to mainland areas with intensive predator control.

Saddlebacks were reintroduced to Mokoia in 1992 (Armstrong & Craig, 1995), creating the first inland population of this species since the nineteenth century. They were the third bird species reintroduced to Mokoia. Previous reintroductions had shown that saddlebacks could survive well in secondary forest and scrub if no ship rats, Norway rats, cats or mustelids were present (Craig, 1994; Lovegrove, 1996). Although they are classified as cavity nesters, saddlebacks are not particular about the cavities they will use and will nest in other protected sites such as bases of New Zealand flax [*Phormium tenax*] (J.R. et G. Forst)] bushes and crevices under tree roots. We placed nest boxes

around the island to aid monitoring, but anticipated that there would be no shortage of natural nest sites on Mokoia. We were, therefore, confident that Mokoia would support a viable population of saddlebacks if it were not reinvaded by rats. However, such an invasion is quite possible given the frequency of uncontrolled boat landings.

Our main objectives in monitoring this population were to: (1) test for density dependence in parameters as the population grew, and use this information to guide strategies for harvesting saddleback populations for further translocation; (2) provide a baseline model for assessing the amount of predation saddlebacks could tolerate if reintroduced to a mainland site with predator control; (3) provide the baseline data to assess the effect of a potential rat invasion on the Mokoia population; and (4) estimate the effect of the poison drop on the saddleback population to assess the feasibility of using poison-based predator control to protect saddlebacks on the mainland.

Of thirty-six birds released in April 1992, thirty-three (nineteen males, fourteen females) survived to the start of the first breeding season in October 1992. The population grew rapidly, reaching approximately 217 birds (120 males, ninety-seven females) in September 1996. The population dropped after the poison drop on 18 September 1996, but had recovered by the following breeding season (Fig. 2). Based on mark-recapture analysis of our survey data, we estimate that about 45% of birds died as a result of the poison drop, presumably because of direct consumption of baits and/or secondary poisoning via invertebrates (Davidson & Armstrong, 2002). Excluding these factors, the models that best explained our data collected up to November 1997 were: (1) adult survival probability is constant among years and between sexes; (2) juvenile survival probability declines with population density; (3) the number of fledglings per female declines with population density and is lower for first-year birds, with no interaction

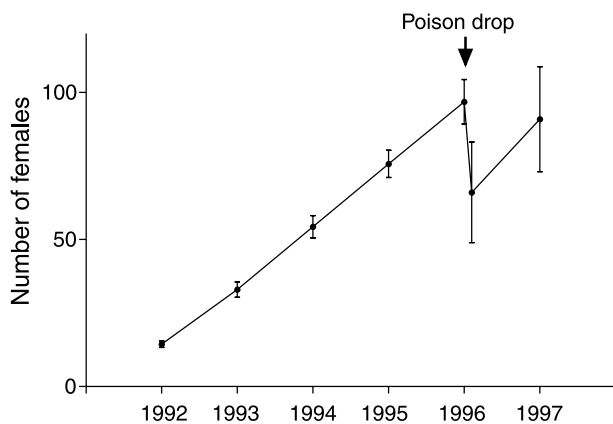


Figure 2 Growth of the saddleback population on Mokoia Island following reintroduction in 1992. Data show the estimated number of females (and 95% confidence intervals) at the start of each breeding season. An aerial poison operation was conducted on 18 September 1996, causing substantial mortality.

between these factors; (4) a recruit has a 0.5 probability of being male (Davidson, 1999). Birds used a mixture of nest boxes and natural sites, and reproductive success was not affected by nest box use, suggesting that nest sites are not a limiting factor. Despite the relatively short time-frame of the data set, there was strong evidence for density-dependence in both survival and reproduction. Models that did not include density as a factor received negligible support. Models assuming that reproduction and juvenile survival declined in relation to the number of pairs at the start of the breeding season gave a good fit to the data, but we did not compare alternative density-dependent models.

A simulation model incorporating these submodels predicted that the population would grow to approximately 250 birds, fluctuating between about 200 and 300 (Davidson, 1999). It predicted that the population could withstand a one-off harvest of up to 139 birds or a sustained harvest of fifty-seven birds annually for 10 years without any risk of extinction. It further predicted that saddleback survival could be reduced as much as 25% with no risk of extinction over a 20-year period if reproduction was not also reduced. We also incorporated the estimated mortality because of the poison drop, along with plausible rates of predator re-invasion, to assess whether this predator control method could be used to maintain saddlebacks on the mainland. The model predicted this was unlikely to be feasible. However, predator control on mainland sites is accomplished using permanent bait stations rather than aerial operations, which should result in much less bykill of saddlebacks. These issues will be explored further when saddlebacks are reintroduced to the first mainland site.

Stitchbirds on Mokoia

Stitchbirds are small (*c.* 40 g males, 32 g females) forest birds in the honeyeater family (Meliphagidae). They are sexually dichromatic, the male having prominent yellow, black, and white markings in comparison with the female's subtle grey-brown plumage. They are cavity nesters, and have a variable mating system that involves frequent extra-pair copulation attempts (Castro *et al.*, 1996; Ewen *et al.*, 1999). They feed on a variety of fruit and nectar sources, as well as invertebrates, but are often displaced from food sources by tui [*Prosthemadera novaeseelandiae* (Gmelin)] or bellbirds [korimako, *Anthornis melanura* (Sparrman)], the other two New Zealand honeyeaters (Rasch & Craig, 1988; Castro & Robertson, 1997). Stitchbirds were originally found throughout the North Island as well as several offshore islands, but became extinct everywhere except Hauturu (Little Barrier Island) following European colonization. Attempts to establish stitchbirds on three other predator-free islands in the 1980s had poor success, the populations slowly declining after release (Rasch *et al.*, 1996). The main hypothesis put forth to explain this was insufficient year-round supply of nectar and fruit, as the new islands had a lower diversity of these food sources, particularly in winter (Lovegrove, 1985; Castro, 1995; Rasch *et al.*, 1996).

Stitchbirds were reintroduced to Mokoia in 1994 (Armstrong *et al.*, 1999), creating the first inland population of this species since the nineteenth century. Given the highly modified nature of Mokoia, it seemed unlikely that it would support a viable stitchbird population without management. Not only was the diversity of fruiting and flowering plants likely to be limited, but also there were no trees large enough to have the types of cavities stitchbirds normally used as nest sites (Rasch, 1985). However, the easy access to Mokoia meant that the population could potentially be intensively managed, and could be used for research to assess factors limiting stitchbird populations in modified habitats. Wooden nest boxes were erected, with small holes to exclude saddlebacks and other species, and feeders were put out, surrounded by plastic mesh cages to exclude tui (Armstrong *et al.*, 1999).

Our initial objectives were to test whether the Mokoia stitchbird population was food limited, using experimental manipulation of feeders, and to test whether the population was viable with or without supplementary food. We did two types of feeder experiments. First, from January to October 1995 we did an 'on-off' supplementation experiment in which sugar water was available for 2 of every 4 weeks. We did this to assess whether survival and/or condition of birds was limited by energy availability at different times of the year, also collecting data on energy availability from natural food sources. Secondly, we compared reproductive success of females with different degrees of access to supplementary food, using a complete supplement (Wombaroo[®] honeyeater and lorikeet mix) or sugar water only. In the first breeding season we erected three stations providing Wombaroo and the distance of feeders from nest boxes varied from 10 to 650 m. In the second and third year, we attempted to place feeders deliberately so that half the females had Wombaroo 10 m from the nestbox and the other half had to travel at least 400 m. In the fourth year, we gave all females access to Wombaroo 10 m away, in the fifth year we did no supplementary feeding, and in the sixth and seventh years we provided sugar water (or jam water) at four feeding stations.

Of forty birds released in September 1994, thirty-three (seventeen males, sixteen females) were known to survive the first 2 months until the start of the first breeding season. The population fluctuated around this number for the next 4 years, but dropped precipitously after the 1998/99 breeding season when no supplementary food was provided (Fig. 3). The on-off experiment in the first year showed stitchbirds never lost weight when food was removed, and survival was similar over periods when food was or was not available (Armstrong & Perrott, 2000). However, annual survival was quite low (*c.* 40%) and has remained at approximately that level over subsequent years. Our results have been equivocal as to whether females produce more fledglings when they have close (10 m) or distant (>200 m) access to food. However, they produced substantially fewer fledglings when no supplementary food was provided at all and this accounts for the population drop from 1998 to 1999. We have also found that broods can be killed by nest

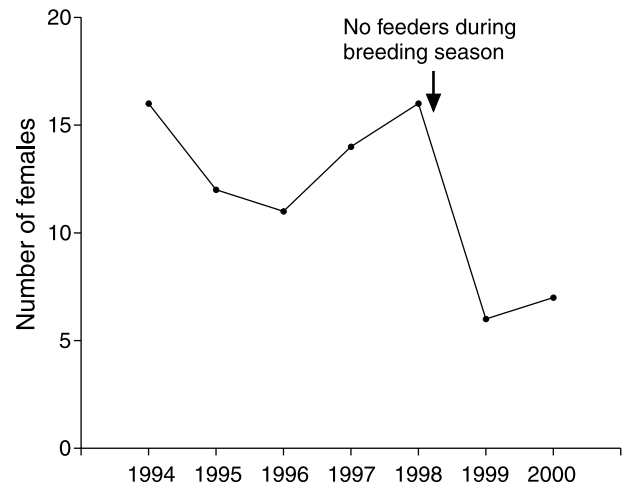


Figure 3 Fluctuation in the stitchbird population on Mokoia Island following reintroduction in 1994. Data show numbers of females at the start of each breeding season. No error bars are shown because detection rates were estimated to be 100%. Supplementary food (either sugar water or a complete supplement) was provided during all breeding seasons except 1998/99. The aerial poison operation in 1996 had no effect on this population.

mites if left unchecked, and have attempted to estimate the likely numbers of young that would have been fledged with and without mite management (providing a new nest part way through brooding). Our best models for this population are: (1) adult survival probability is lower in females than males, but is constant with respect to sex, year or supplementary feeding regime; (2) juvenile survival probability is constant with respect to year and supplementary feeding regime; (3) reproduction is food limited, but does not depend on distribution or type (i.e. sugar water vs. complete supplement) of food, is also limited by nest mites, and is lower in first-year females than older females and (4) a recruit has a 0.5 probability of being either sex.

Simulation modelling predicted that the population would quickly decline to extinction if breeding season management (supplementary food and mite control) were discontinued. Simulations with our best parameter estimates predict that the population has a 65% probability of surviving the next 20 years if breeding season management continues. However, this prediction is highly sensitive to uncertainty in parameter estimates, the population's probability of survival being 0% if parameters are set at the lower limits of their 95% confidence intervals and 99% if parameters are set at the upper limits of those intervals. We conclude that while the population is limited by food supply and nest mites during the breeding season, there must be one or more additional limiting factors to account for its tenuous survival under management.

Post-mortem analysis of dead stitchbirds collected on Mokoia showed birds to have extensive infections of *A. fumigatus* (Alley *et al.*, 1999). Aspergillosis is often a secondary condition associated with factors such as poor nutrition. However, otherwise healthy animals may be killed

by aspergillosis and/or aflatoxicosis if challenged by a high concentration of *A. fumigatus* spores (Bauck, 1994). Consequently, Perrott (2001) studied the ecological factors affecting density of *A. fumigatus* and compared its abundance among islands. Perrott (2001) found that habitat modification and disturbance promote *A. fumigatus* and that densities are substantially higher on Mokoia than on Hauturu, the only island where stitchbirds survived naturally. This suggests that prevalence of *A. fumigatus* could be a key limiting factor on Mokoia and other highly modified habitats.

Stitchbirds on Tiritiri Matangi

Stitchbirds were reintroduced to Tiritiri Matangi in 1995 (Armstrong & Ewen, 2001a), one year after the reintroduction to Mokoia. The situation was very similar to Mokoia in that the island had a highly modified habitat, but allowed opportunities for intensive research and management. Consequently, the research and management conducted on Tiritiri Matangi was very similar to that conducted on Mokoia, with similar objectives. Obvious differences between the two sites were that Tiritiri Matangi had a smaller amount of forest, but a planted matrix composed largely of species that would provide nectar and/or fruit, and that Tiritiri Matangi had bellbirds, a dominant competitor that is absent from Mokoia.

Of thirty-eight birds (twenty males, eighteen females) released in September 1995, the majority disappeared within the first month, leaving an initial population of twelve males and four females. These fledged a total of six young in the first breeding season, and thirteen additional translocated birds (four male, nine female) were released in August 1996. Most of the translocated females disappeared within the first month again, leaving twelve males and six females at the start of the second breeding season. The population grew substantially in the second year, declined slightly in the third, year, then continued to grow, reaching forty-five birds (fifteen males, thirty females) at the start of the sixth breeding season (Fig. 4). In contrast to Mokoia, an on-off feeding experiment in 1996 suggested that stitchbirds showed significant weight loss when supplementary sugar water was removed in some months, and had higher mortality during periods when food was absent (Armstrong & Ewen, 2001a). Supplementary food has been supplied continuously since then, and the adult survival rate has been substantially higher (mean 65%) than on Mokoia. Juvenile survival (mean 36%) has been similar to Mokoia but was higher in the first 2 years, suggesting density dependence. After the first year, when reproduction was atypically low, the number of fledglings per female has been similar to Mokoia, and has been similar when Wombaroo (years 1–2) or sugar water (years 3–6) were provided. In contrast to Mokoia, the sex ratio of recruits has been consistently skewed towards females.

In determining the best models describing the population, we disregarded the die offs of females immediately after the two translocations given that this mortality was substantially

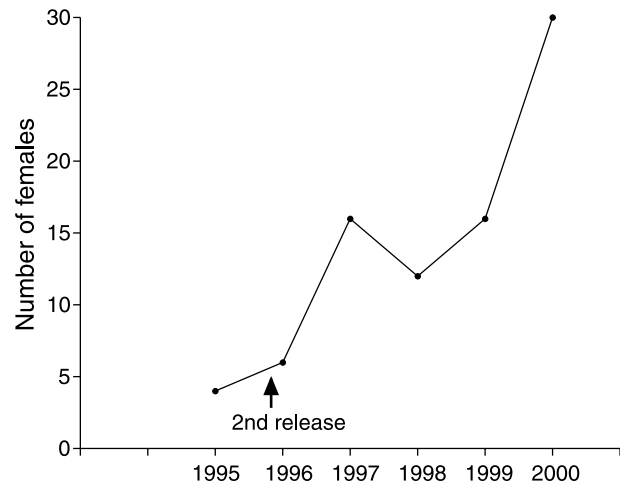


Figure 4 Growth of the stitchbird population on Tiritiri Matangi Island following reintroduction in 1995. Data show numbers of females at the start of each breeding season. No error bars are shown because detection rates were estimated to be 100%. A second release in August 1996 added two females to the breeding population.

higher than anything subsequently observed. We retained the reproductive data for the first year. The atypically low reproduction that year could also be attributable to translocation, as for Tiritiri Matangi robins, but the data are insufficient to assess this. In summary, the best models are: (1) adult survival probability is constant among years and between sexes under supplementary feeding, but is limited by food supply; (2) juvenile survival probability declines with population density under supplementary feeder, but is otherwise limited by food supply; (3) number of fledglings per female is constant among years, but lower for first-year females; and (4) a recruit into the population has a 0.66 probability of being female.

Simulations based on these submodels predicted that the population had a negligible chance of extinction over several decades, and this prediction was not sensitive to uncertainty in parameter estimates or model structure. This population therefore appears to be viable as long as management continues. Future monitoring as the population increases further will give greater capacity to confirm whether juvenile survival is density-dependent. Strong evidence of density dependence will lead to the population being experimentally harvested for translocation elsewhere, similar to the robin population.

The key difference between the Tiritiri Matangi and Mokoia stitchbird populations is the higher adult survival on Tiritiri Matangi. As noted above, the high mortality on Mokoia may be attributable to the high density of the pathogenic fungus *A. fumigatus*. Consequently, in November 2000 we collected soil samples on Tiritiri Matangi for comparison with samples collected from Mokoia and Hauturu at approximately the same time. While levels of *A. fumigatus* in Tiritiri Matangi were higher than on Hauturu, they were substantially lower than on Mokoia,

suggesting that prevalence of *A. fumigatus* may account for the different survival rates on the two islands (Perrott, 2001).

CONCLUSIONS

The four case studies provide a diversity of results concerning factors limiting island populations. The Tiritiri Matangi robins and Mokoia saddlebacks appear to have high growth rates at low density, with subsequent depression of juvenile survival (both populations) and reproduction (Mokoia saddleback) at higher density. This is predicted to result in regulated populations that fluctuate around an equilibrium level, similar to the dynamics observed in the classic lab experiments of Gause (1934) and Frank *et al.* (1957). In contrast, stitchbirds in modified island habitats appear to be limited by a range of ecological factors preventing successful establishment. On Tiritiri Matangi, it appears that the key limiting factors can be removed through provision of supplementary food and management of nest mites, allowing a viable population that will be limited by density dependence in juvenile survival. In contrast, similar management appears insufficient to promote growth in the Mokoia population and its viability remains tenuous at best. We hypothesize that the abundance of *A. fumigatus* on Mokoia creates an additional limiting factor that cannot be easily managed, and that *A. fumigatus* density may be an important factor in determining sites that can potentially support stitchbird populations.

It may appear rash to attempt to understand a population's dynamics from as few as 5 years data and particularly to conclude evidence for density-dependent regulation. There has been a long history of controversy concerning the role of density dependence and methods for detecting it and an increasing emphasis on unpredictable or chaotic dynamics (Turchin, 1999; Elkington, 2000). However, analyses of data from our populations suggest that the relatively minor annual variation can largely be explained by sampling variation and there is no reason to expect these systems to be influenced by rare episodic events or chaos-generating complexities. In addition, the opportunity to observe the populations at a range of densities, combined with intensive monitoring, allows us to make inferences that would otherwise require much longer-term data sets. It would obviously improve our inferences to monitor over longer time frames and obtain more replicates of experimental manipulations. However, inferences about dynamics of reintroduced populations need to be made fairly rapidly to facilitate management of the populations and application to other situations. Our results suggest that it is quite feasible to develop a reasonable working model of a reintroduced population within 5 years, as long as the species reproduces annually and the system is not expected to experience major changes in conditions. The working model then provides a guideline for management, which can be manipulated to further improve understanding of the system.

The management implications from our case studies are strongly interconnected, particularly in their implications for

reintroduction to the mainland. As robins are the least vulnerable of the three species, they are 'leading the charge' of mainland reintroductions, ten such reintroductions having taken place from 1998 to 2001 (Armstrong, 1999–2002). Several of these populations are being monitored and modelled based on our research on Tiritiri Matangi, and the results used to determine the combination of ecological conditions and management needed to maintain this species. As robins are strongly affected by predation (Powlesland *et al.*, 1999), data for reintroduced populations will provide a guideline to the degree of predation expected on saddlebacks when they are reintroduced. This can be used to select appropriate sites for reintroducing saddlebacks to the mainland, and in combination with our model developed from Mokoia saddlebacks, can be used to guide monitoring and management strategies for these reintroductions. In turn, data on reintroduced saddlebacks would be particularly useful for selecting a mainland site to reintroduce stitchbirds. While stitchbirds have never been studied in the presence of mammalian predators because of their extirpation from these areas, they are obligate cavity nesters and consequently expected to be highly vulnerable to predation (O'Donnell, 1996). Interest in reintroducing stitchbirds to the mainland has been spurred on by our research on the likely impacts of *A. fumigatus* in highly modified environments, as well as evidence for food limitation and nest mites in these environments. The more pristine mainland forests in the North Island provide the best opportunity to minimize these limiting factors, shifting the emphasis to mammalian predators which can potentially be controlled more quickly and effectively.

While our research has focused on population dynamics, this research leads to consideration of the broader fields of community ecology and biogeography that are most immediately associated with island systems. The failure of reintroduced stitchbirds to establish self-sustaining populations has led to a research programme considering their interaction with a broad suite of vascular plants (Castro & Robertson, 1997; Perrott & Armstrong, 2000), nest mites and ultimately soil fungi (Perrott, 2001). While single-species studies are now tending to be discouraged in favour of ecosystem monitoring and management, it is ironic that research focused on stitchbird recovery has led to the first research examining the ecological factors affecting soil fungi communities on conservation land. Biogeographical considerations arise when we attempt to apply our research on all three species to mainland reintroductions. The success of these programmes will ultimately depend on a good understanding of the biogeographical factors determining habitat suitability for each species, and the consequences for effective management.

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