Consistency, continuity and creativity: long-term studies of population dynamics on Tiritiri Matangi Island

Doug P. Armstrong[1]*, John G. Ewen[2]

[1]Wildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, Private Bag 11 222, New Zealand
[2]Institute of Zoology, Zoological Society of London, Regents Park, NW1 4RY, London, United Kingdom
*Author for correspondence (Email: D.P.Armstrong@massey.ac.nz)

Abstract: One of the quandaries faced by ecological researchers is whether they should continue to invest in ongoing projects or whether they should shift their attention to new species or systems that may have received less attention. While research on Tiritiri Matangi has touched on a wide range of species and topics, the long-term projects on the reintroduced robin population (20 years) and hihi population (17 years) have accounted for the bulk of the published research, with 57 papers featuring these populations published to the end of 2009. This literature has made contributions to several disciplines (wildlife management, population ecology, behavioural ecology, conservation genetics, ornithology and wildlife disease) at both the local and international level. However, most of these published papers use less than 5 years of data, so most of the results made possible from the long-term data sets have yet to be published. We illustrate how long-term monitoring has allowed us to continually improve our understanding of the dynamics of these populations, and how this has allowed us to interpret and predict the effects of management. This management includes the 1993 poison drop, follow-up translocations to both populations, food provisioning and mite control for hihi, and most importantly, the ongoing harvesting of both populations for reintroduction to other locations. We are now able to detect complex and subtle processes that required many years of data, and present information on the number of years required to obtain various results. These results are now allowing us to develop long-term models integrating factors such as density-dependent regulation, demographic and environmental stochasticity. These models are not only relevant to the long-term viability and management of Tiritiri Matangi populations, but to small populations worldwide.

Keywords: long-term studies; population ecology; population modelling; small population biology; North Island robin; toutouwai; stitchbird; hihi

Introduction

Empirical research in ecology and conservation biology uses a diversity of approaches. It includes field and laboratory studies; experimental, observational and retrospective (e.g. paleontological) studies; studies at several different levels of biological organisation (e.g. individuals, populations and/or ecosystems); and studies at a wide range of spatial and temporal scales. These approaches are complementary, and the diversity essential. Nevertheless, scientists need to make decisions about where they are going to focus their research effort.

One decision that always needs to be made is how long to continue a study. Although projects are often constrained by funding or durations of postgraduate degrees, these constraints still reflect decisions – e.g. whether a researcher encourages another student to continue work on a system, and whether a funding body prioritises the research. The obvious disadvantage of long-term studies (LTS) is that they divert resources, meaning we need to decide whether a LTS is more worthwhile than several smaller studies.

The problem is analogous to the 'SLOSS' problem in reserve design (May 1975), i.e. will a single large reserve have greater conservation value than several small reserves of the same total area? The term 'design' is a misnomer in that reserve systems are rarely planned from the outset, but instead evolve through a stochastic dynamic process involving multiple decisions about whether or not to acquire or expand reserves (Pressey et al. 1993). Similarly, LTS are rarely planned as such from the outset. They usually evolve through decisions about whether or not to continue work on a system. Doing multiple small studies may appear to increase diversity, e.g. by increasing the number of species or taxa focused on, just as having multiple small reserves may increase the diversity of ecosystems covered. However, some aspects of ecosystems (e.g. large carnivore populations and broad-scale disturbance dynamics) can only be conserved in large reserves, and similarly, some aspects of ecology can only be understood through LTS.

On Tiritiri Matangi, there are two research projects that have now had intensive data collection over at least 15 years, and therefore probably qualify as LTS as the term is generally understood in ecology (Likens 1989). These projects involve research on the reintroduced populations of North Island robin (toutouwai, *Petroica longipes*) and hihi (stitchbird, *Notiomystis cincta*). Data have also been collected over periods greater than 15 years on the reintroduced takahe (*Porphyrio hochstetteri*) population, 5-minute bird counts (Graham et al. 2013), invertebrate pitfalls (C. Green, pers. comm.), and vegetation maturation (Mitchell 2013; Myers & Court 2013; West 2008), but at much lower intensity than the other two projects.

This paper focuses on the unique contribution of the two LTS on Tiritiri Matangi. We begin by briefly reviewing the

international literature on LTS, noting some generalities about the characteristics, benefits and challenges of these studies. We then briefly introduce the two LTS on Tiritiri Matangi, outline the contributions of these studies to the international literature and local conservation management, and identify aspects of the research that were only possible with long-term data sets. We conclude by discussing the future internationally significant contributions likely to be made possible by these high-quality long-term data sets.

Long-term studies in ecology

Examination of the ecological literature shows there were several symposia and sets of papers devoted to LTS about 20 years ago (e.g. Likens 1989; Perrins 1991 and accompanying papers; Dunnet 1991 and accompanying papers). These seem to have been motivated by the increased availability of long-term data sets due to many studies starting in the 1960s, increasing realisation of the need for LTS to support ecological management, and the perception that long-term studies were under threat due to increased emphasis on a short-term experimental hypothesis-testing approach. In particular, long-term studies may appear to be 'mere monitoring', and therefore unscientific and unattractive to most funding bodies (Likens 1983; Taylor 1989). Krebs (1991) noted that experiments and LTS were both more effective when the two approaches were combined, and Likens (1983) emphasised the role of LTS in formulating meaningful testable hypotheses in ecology.

Likens (1983) identified four types of processes necessitating long-term data sets: 1) slow processes; 2) rare or episodic phenomena; 3) processes with high annual variability; and 4) complex phenomena. These have been reiterated by many subsequent authors (e.g. Franklin 1989), and several LTS have illustrated the role of rare mortality events in otherwise stable populations (e.g. Brooks et al. 1991; Smith et al. 1991; Pelton & van Manen 1996). Pelton and van Manen (1996) noted that these rare events dramatically shifted interpretations from those formed after 5–10 years. They also noted that their long-term study provided serendipitously useful data (i.e. uses identified later), aided development of field techniques, made it possible to address practical management problems, gave credibility to the research leaders, and provided an excellent training ground for students. Particular challenges included data management, communication, and resolving the joint need for consistency, continuity and creativity. Most authors emphasise the difficulty in funding LTS, and observe that LTS are rarely planned from the outset. Strayer et al. (1986) observed that most successful LTS had the fortuitous combination of a leader (dedicated scientist), an opportunity (site and idea), and funding (often patched together from several sources).

Significant developments in the subsequent 20 years have included major methodological advances for analysing data at both the population (e.g. Nichols 2004; Thomson et al. 2009) and ecosystem level (e.g. Miao et al. 2009). Modern analytical methods allow more complex, but more importantly, much more realistic models to be fitted to data, with emphasis on computationally intensive Bayesian inference. These methods rely on having increased computing power, but also often on having high-quality long-term or broad-scale scale data sets, meaning we are now in a much stronger position than before to take advantage of LTS.

Long-term studies of reintroduced populations on Tiritiri Matangi

Data collection on the robin and hihi populations on Tiritiri Matangi started when the populations were reintroduced to the island in April 1992 and September 1995 respectively (see Armstrong 1995, Armtrong & Ewen 2001 and Armstrong et al. 2002 for information on the reintroductions). Like most LTS, the research was initially conceived and funded as short-term projects. The robin research started as part of DPA's two-year postdoctoral project investigating the effect of pre-translocation familiarity among animals on post-translocation behaviour and vital rates (survival and reproduction). The hihi research started as JGE's two-year MSc project supervised by DPA. While we planned this to be a study of food limitation following research on Mokoia island (Armstrong & Perrott 2000), the poor post-release survival of female hihi on Tiritiri Matangi necessitated an alternative focus on male reproductive strategies (Ewen 1998). Both projects therefore started with a strong behavioural focus, which was partly motivated by scientific curiosity and potential conservation relevance, but mostly necessitated by the need for questions that could be addressed over short time scales, with data from relatively few individuals. However, we also had a strong focus on population ecology from the outset. In both cases we constructed preliminary population models during the first year after reintroduction.

The population focus ensured we adopted monitoring protocols that allowed reliable estimation of survival and reproduction rates (Ewen & Armstrong 2007). Perhaps most importantly, we conducted regular re-sighting surveys where we walked through all forested areas on the island and recorded all individuals seen, giving encounter histories that were analysable using open CMR (capture-mark-recapture) models. Lebreton et al.'s (1992) now-classic monograph on survival modelling was invaluable in designing this monitoring. We initially did these surveys fortnightly or monthly to model post-release survival (e.g. Armstrong & Ewen 2001a), then reduced this to two surveys per year, at the start of the breeding season (September) and near the end of the breeding season (January for robins, February for hihi). We also adopted an intensive breeding-season monitoring protocol that gave data on the number of young fledged by each female. This regime involved finding natural nests of robins (see Armstrong et al. 2000 for methods) and monitoring the nest boxes used by hihi, then checking nests to determine the number of young fledged. We individually colour-banded most chicks while in the nest, and they were considered to enter the CMR encounter history in the January/February survey the year that they fledged.

The basic monitoring protocols have been followed every year since reintroduction, except the 1997/1998 breeding season when robin breeding monitoring was temporarily discontinued. This continuity has been possible due to several factors, including: 1) the island being accessible and having accommodation facilities; 2) the populations being relatively easy to monitor, meaning monitoring could be done by inexperienced personnel; 3) the island and projects being attractive to students and volunteers; and 4) the populations being of conservation relevance and key source populations for other translocations, meaning the research was supported by local conservation bodies. While the two of us undertook most of the initial monitoring ourselves, and have participated to some extent in most years, the bulk of the monitoring has been done by a series of students (MSc, PhD, and undergraduate interns), volunteers, and contractors. Funding has come

from several sources, but most consistently from the New Zealand Department of Conservation, who have employed a hihi contractor each breeding season since 1997/1998, and the Auckland Regional Council, who have supported travel, food and accommodation costs for the robin monitoring for several years.

The basic monitoring has been accompanied by experiments and other data collection designed to address a range of questions (see Thorogood et al. 2013 for an overview of research on the hihi population). This has included food manipulation and harvesting experiments designed to improve our understanding of population dynamics, and therefore our ability to manage the populations, but also fundamental research.

Contribution of long-term studies on Tiritiri Matangi

To analyse the contribution of the LTS, we summarise the papers published in the peer-reviewed scientific literature to date in relation to the overall output from Tiritiri Matangi, outline the population modelling and management made possible by long-term data collection, and discuss the potential future contribution to small-population biology worldwide.

Published literature to date

To assess the contribution of the LTS to the research output from Tiritiri Matangi, we searched the ISI Web of Science for peer-reviewed papers published up to end of 2009 containing the words 'Tiritiri Matangi', and also checked contents of New Zealand journals not covered by ISI Web of Science. We removed papers that mentioned Tiritiri Matangi without reporting any original research from the island, but retained short communications as well as full research papers.

Research from the robin and hihi projects accounts for 57 of the 113 papers found, and 38 of the 56 papers in international journals (Table 1), and higher proportions if short communications are excluded. It is significant that research involving the takahe population contributes the next largest portion of papers (Table 1). That population has been monitored over an even longer time span (22 years), but at much lower intensity and the data have been combined with those from several other populations in most publications. The productivity of these studies partly reflects a huge data collection effort, but nevertheless contributes a surprisingly high proportion of the published research from the island given the number of projects conducted since Tiritiri Matangi was designated a scientific reserve. This at least partially reflects the fact that the robin, hihi and takahe populations are excellent model systems for addressing a range of internationally-significant issues.

Table 1. Focal species or systems in peer-reviewed journal articles featuring Tiritiri Matangi published before 2010.

Species/system	Number of papers		
	NZ/Aust.	International	Total
Hihi (*Notiomystis cincta*)	6	24	30[i]
North Island robin (*Petroica longipes*)	13	16	29[i]
Takahe (*Porphyrio mantelli*)	3	6	9
Bellbird (*Anthornis melanura*)	7	4	11[ii]
Tui (*Prosthemadera novaeseelandiae*)	4	0	4[ii]
Little blue penguin (*Eudyptula minor*)	0	3	3
North Island saddleback (*Philesturnus rufusater*)	3	0	3
Kakariki (*Cyanoramphus novaezelandiae*)	3	0	3
Quail (*Coturnix sp.*)	0	1	1
Fantail (*Rhipidura fuliginosa*)	1	0	1
Grey-faced petrel (*Pterodroma macroptera*)	1	0	1
Little spotted kiwi (*Apteryx owenii*)	1	0	1
North Island kokako (*Callaeus cinerea*)	1	0	1
Pukeko (*Porphyrio porphyrio*)	0	1	1
Whitehead (*Mohoua albicilla*)	0	1	1
Multiple bird species	1	0	1
Kiore (*Rattus exulans*)	3	1	4
Shore skink (*Oligosoma smithi*)	2	0	2[iii]
Duvaucel's gecko (*Hoplodactylus duvaucelii*)	1	0	1[iii]
Argentine ant (*Linepithema humile*)	1	0	1
Scallop (*Pecten novaezelandiae*)	1	0	1
Harakeke (*Phormium tenax*)	2	1	3
Pohutukawa (*Metrosideros excelsa*)	0	1	1
Kokekohe (*Dysoxylum spectabile*)	1	0	1
Multiple plant species or flora/vegetation	3	0	3

[i] two papers involve both species
[ii] three papers involve both species
[iii] one paper involves both species

Table 2. Main contributions of peer-reviewed journal articles featuring research on Tiritiri Matangi published before 2010.

	Number of papers				
	Robin	Hihi	Takahe	Other	Total
Anatomy/development	1	4	0	1	6
Physiology	0	2	0	0	2
Parasitology/pathology	3	3	0	3	9
Longevity	0	0	0	1	1
Breeding biology	3	0	1	9	13
Behaviour observations	2	1	2	7	12
Behavioural ecology	2	10	0	7	19
Systematics	1	1	0	1	3
Species composition	NA	NA	NA	1	1
Spatiotemporal distribution	0	0	0	2	2
Methodology	7	3	0	5	14[i]
Description of restoration procedures	0	0	0	3	3
Population ecology & management	10	6	6	7	28[i]

[i] includes one paper focusing on both robins and hihi

Research published from Tiritiri Matangi has covered a diversity of topics (Table 2), but when robin, hihi and takahe are excluded, most of the research can be described as 'basic biology' of species, descriptions of flora, or description of management procedures. The LTS also contribute to these areas, but their strength lies elsewhere. They have generated significant bodies of fundamental research in behavioural ecology and applied research in population ecology and management (Table 2). Most of the papers in these areas are published in highly-ranked international journals, and constitute the major contribution of Tiritiri Matangi to international research. The papers listed as 'population ecology and management' all include some analysis of vital rates, hence are classified as population ecology, but most of the papers involving robins and hihi also include population projections and/or evaluation of management actions. These management actions include alternative translocation strategies (Armstrong 1995), the 1993 poison drop (Armstrong & Ewen 2001b), follow-up translocations (Armstrong & Ewen 2001c), food provisioning and mite control (Armstrong & Ewen 2001a; Ewen et al. 2009), and the ongoing harvesting of both populations for reintroduction to other locations (Dimond & Armstrong 2007).

Projecting the trajectory and fate of a population requires construction of models of how that population works. Such models reflect our understanding based on analysis of the available data. Population analysis is famously 'data hungry' (Possingham et al. 1993), so this is a key area where long-term data sets can contribute. We therefore review population analyses involving the LTS on Tiritiri Matangi.

Population modelling and management

As noted above, we constructed population models within one year of both robins and hihi being reintroduced. These were used to obtain preliminary population projections, and to help decide whether to proceed with follow-up translocations of additional birds the year after reintroduction. These follow-up translocations both took place, and Armstrong & Ewen (2001c) give a retrospective analysis of this decision for the robin population. Initial population models consisted of three estimated parameters: mean number of young fledged per female, annual adult survival probability, and juvenile survival probability (probability of surviving from fledging to the following breeding season). The mean sex ratio of recruits (juveniles surviving to breeding age) was 50:50. We always included demographic stochasticity in survival, reproduction and sex ratio of recruits, but did not explicitly include uncertainty in parameter estimation in initial models. This was a major flaw given that our subsequent modelling has shown that initial parameter uncertainty translated to huge variance in population projections. That effect overwhelmed the effects of demographic stochasticity. Another limitation of initial projections was that female robins had substantially lower reproductive success in the first year after reintroduction than in subsequent years (Armstrong & Ewen 2001c, 2002). Indeed, it is important when modelling any reintroduced population to estimate the extent to which both survival and reproduction rates were reduced immediately after translocation, and discount these effects when making long-term projections. In later analyses, we discounted the first breeding season after release from reproduction analyses, and discounted at least the first month after release from survival analyses. We were able to discount post-translocation effects because we had large multi-year data sets.

The main advantages of such data sets go beyond the discounting issue, however. They open the way for improved precision in estimates of vital rates such as survival probability (Fig. 1), and an ability to weight alternative models for factors affecting those vital rates using Akaike's Information Criterion (AIC) or other criteria (Burnham & Anderson 2002). When we had about five years of data, we had good power to assess effects of sex and season on survival probability, assess effects of age on reproductive success, and assess whether any parameters varied over time and showed density dependence (Table 3). The key results of model comparison at this stage (Armstrong et al. 2002) were that: 1) mean reproductive success was lower for first-year females than older females in hihi, but appeared unaffected by the age of either the male or female or the pair in robins, and was not density-dependent in either species; 2) juvenile survival probability declined with increasing population density in robins but not in hihi; 3) there was an approximately 50% chance of recruits being
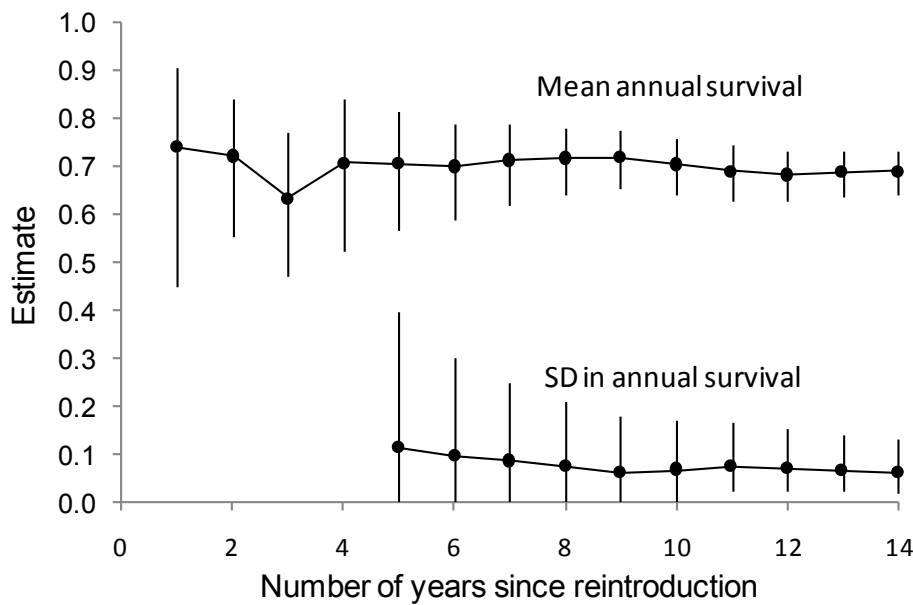
Figure 1. Improvement over time in estimation of mean annual survival and annual variation in survival of adult hihi on Tiritiri Matangi. Dots and vertical bars show estimates and 95% confidence limits obtained from Program MARK, using variance components output from model $\phi_t P_t$ when ≥ 3 years data were available and model $\phi_t P_t$ for the first two years. Comparison of alternative models for this population shows adult survival is similar for males and females, and there is significant annual variation in survival but no trend over time.

Table 3. Approximate number of years of monitoring data for reintroduced robin and hihi populations on Tiritiri Matangi needed to obtain reliable estimates of key parameters affecting viability of small populations.

Population process	Years	Comment
Mean vital rates[i]	5	adult & juvenile survival, reproduction
Demographic stochasticity[ii]	5	
Age effects[iii]	5+	hihi reproduction
Individual variation[iii]	5+	hihi & robin reproduction
Density dependence[iii]	8+	robin juvenile survival, hihi sex ratio
Environmental stochasticity[iii]	11+	hihi adult survival
Inbreeding depression[iii]	12+	robin juvenile survival
Long-term trends[iii]	14+	robin adult & juvenile survival

[i] considered reliable when S.E. < 10% of estimate
[ii] depends on mean vital rates so time frame the same
[iii] considered reliable when the confidence limits for effect sizes do not include zero

male or female; and 4) adult survival probability was similar for males and females and fairly constant over time in both populations. The best models for the different vital rates were then combined into stochastic population models that were used to predict long-term viability (Armstrong & Ewen 2002; Armstrong et al. 2002).

The main application of these models has been to guide the subsequent harvesting of the populations for reintroductions to new sites, with four translocations of robins and five translocations of hihi having taken place (Fig. 2). Tiritiri Matangi has been extremely valuable as a source population, as it had the only accessible robin population in the Auckland region, and the growing hihi population provided an alternative to ongoing harvesting of the single remnant population on Hauturu (Little Barrier Island). It has also been a source population for reintroductions of North Island saddlebacks (*Philesturnus rufusater*), whiteheads (*Mohoua albicilla*), and bellbirds (*Anthornis melanura*). It is important to consider impacts on source populations in all translocations, and essential when repeatedly harvesting small populations. The high-quality data available for the robin and hihi populations has not only made it possible to make pre-harvest projections

of impacts on these populations, but to provide information that can be used worldwide.

The key to prudent harvesting of any population is to have not only reliable estimates of demographic rates but to be able to predict density-dependent responses to harvesting (Holt & Talbot 1978). When robins were first harvested from Tiritiri Matangi in 1999, the fact that juvenile survival had declined since reintroduction (Fig. 3) while adult survival and reproduction had stayed relatively constant, suggested that the population was regulated by density dependence in juvenile survival. However, we had poor ability at that stage to choose among plausible models of density dependence. Our approach at the time was to adopt a single plausible model, that juvenile survival was limited by the population having a fixed carrying capacity of about 65 breeding adults, and to harvest the minimum number allowing the population to stay at carrying capacity. This turned out to be a poor model (Dimond & Armstrong 2007). The observed population drop the next breeding season was inconsistent with the model's projections (Fig. 2). We subsequently compared six models using data collected up to 2000, and found that juvenile survival was best predicted by the number of pairs at the start of the
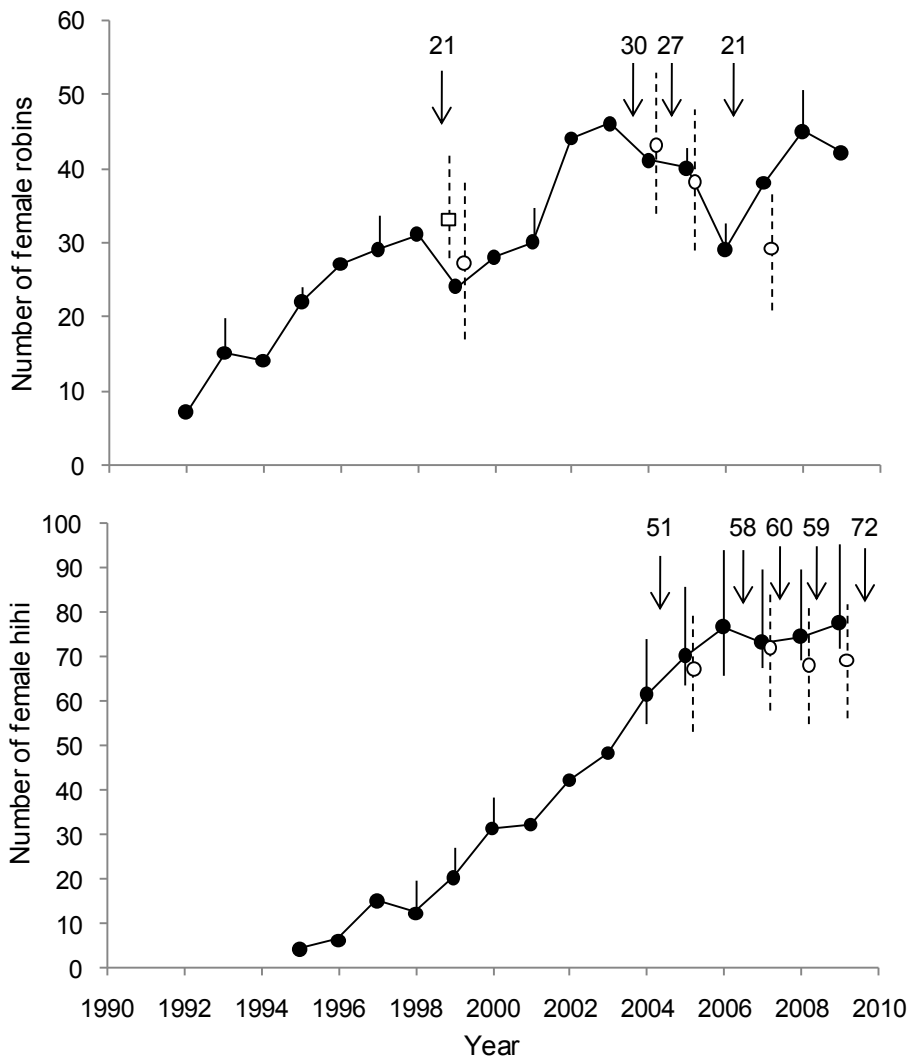
Figure 2. Application of population models for guiding harvesting of North Island robin and hihi populations on Tiritiri Matangi for translocation to other sites. Lines and filled circles show the estimated numbers of females at the start of each breeding season, arrows show numbers harvested, and open symbols show median pre-harvest projections from population models, with error bars showing 95% confidence intervals. For robins in 1999, the square and associated error bars show the distribution of projections obtained from the model of juvenile survival assumed at the time, and the open circle shows the distribution of projects that would have been obtained through model averaging with six plausible models considered.
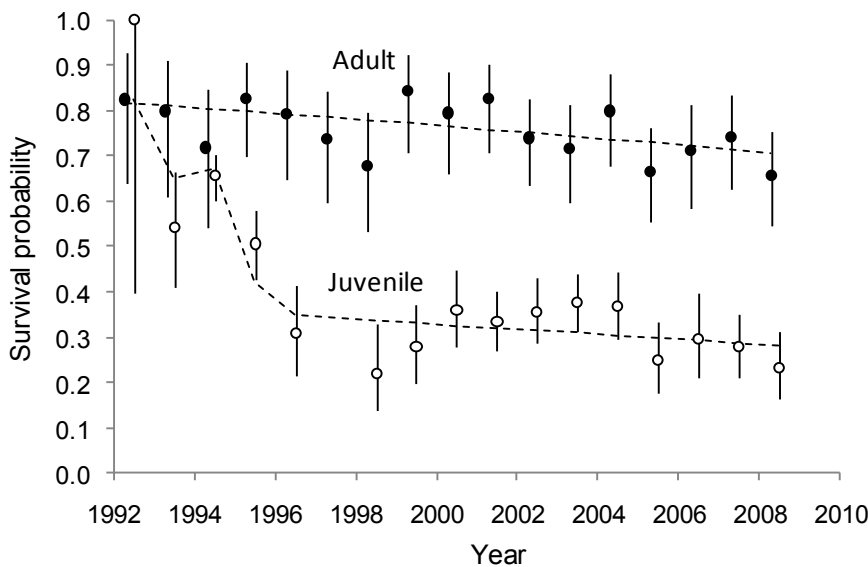
Figure 3. Annual estimates of survival probability for adult and juvenile robins on Tiritiri Matangi each year from 1992–93 to 2008–09, with years running from September to September. Dots and vertical bars show estimates and 95% confidence limits obtained, and the dotted line shows expected survival rates under the models that best explain the data. The best model for adult survival is a logit-linear decline in survival probability over time, with similar survival for males and females. Under the best model for juveniles, survival declines with density until the population reaches 24 females, and also declines over time.

breeding season (Dimond & Armstrong 2007). In hindsight, we should have considered this set of models before the 1999 harvest and made projections using model averaging (Buckland et al. 1997), a procedure that would have given projections consistent with the observed decline (Fig. 2). We followed this approach with subsequent harvests, in each case using data collected up to the time of the harvest. However, we added two additional models to the set due to none of the existing models giving satisfactory fit to the data after the population increased markedly in 2002. The new preferred model was that juvenile survival probability declined with density until above a critical number of females (estimated to be about 24), then remained constant (at an equilibrium level determined by adult mortality and number of fledglings per female). This model has received near 100% of the weight in all subsequent comparisons, so has dominated subsequent projections (Fig. 2).

Harvesting projections for hihi have been somewhat simpler due a lack of apparent density dependence (although more recent modelling has detected subtle density-dependence in reproductive success; Ewen et al. 2011). The harvesting model was constructed using data collected from 1996–2004. It has given accurate projections (Fig. 2) so has not been updated. Data collected to that stage showed no density dependence in adult survival, juvenile survival or reproduction, and the population trajectory approximated exponential growth (Fig. 2), with minor deviations attributable to shifts in age and sex ratio. Subsequent harvests were designed to maintain the population near 70 females, because this gave good numbers for harvests and prevented the ongoing management (maintenance of nest boxes and sugar water feeders) from being overwhelming.

Continuing data collection from both populations has made it possible to detect additional complexities in each population's dynamics (Table 3). After 11 years it became possible to estimate annual variation in adult survival of hihi, indicating subtle fluctuation in conditions over time (Fig. 1). After 12 years it became possible to detect subtle effects of density and sex ratio on reproductive success of hihi, using models that also accounted for individual variation in reproduction. After 14 years we were able to detect subtle long-term declines in survival of both adult and juvenile robins that were not attributable to density dependence, suggesting either a decline in individual quality or a decline in conditions.

Contributions to small-population biology

Making reliable short-term population projections depends mainly on having accurate estimates for vital rates, and the key factors affecting those rates such as age, sex and management regime (Beissinger & Westfall 1998; White 2000). Focusing on these factors can be seen as following the 'declining population paradigm', which Caughley (1994) described as the process of understanding why populations declined, but can be applied equally well to understanding why populations are growing or stable. The declining population paradigm may also be sufficient over longer time frames if populations are large. However, making reliable projections over long time frames for small populations requires expanding our focus to include the 'small population paradigm', i.e. threats to populations through loss of genetic diversity, inbreeding depression, demographic stochasticity and environmental stochasticity (Shaffer 1981). Demographic and environmental stochasticity can also threaten very small populations over short time frames, and could potentially have been important in the initial years of the robin and hihi populations on Tiritiri Matangi when

there were fewer than 10 females of each species.

Projecting potential impacts of demographic stochasticity only requires incorporating it into population models, and the accuracy of the projections depend only on the accuracy of estimates for the vital rates affected. In contrast, addressing the other small population issues requires additional data. Estimating environmental stochasticity requires large data sets in order to separate the 'process variance' in vital rates due to changing environmental conditions from 'sampling variance' that also causes year to year variation in estimates (White 2000b). As noted above, 11 years of data were required to estimate annual variation in survival of adult hihi. Measuring loss of genetic diversity does not require continual data collection but does need several generations to have taken place between the start and end points. The loss of genetic diversity over the first 13 years since reintroduction has recently been estimated for Tiritiri Matangi hihi (Brekke et al. 2011). Estimating inbreeding depression requires construction of pedigrees using molecular or other means, and samples from sufficient individuals of known pedigree to distinguish effects of inbreeding from other factors that affect vital rates. We had sufficient data after 12 years to estimate inbreeding depression in Tiritiri Matangi robins (Jamieson et al. 2007; Armstrong & Cassey 2007), and increased inbreeding could potentially account for the gradual declines in survival probability over time in that population (Fig. 3). Similarly, long-term data from the hihi made it possible to estimate inbreeding depression in hihi embryos and nestings using inbreeding coefficients based on microsatellite markers (Brekke et al. 2010).

So far, we have not attempted to incorporate environmental stochasticity or inbreeding depression into population projections, nor have we attempted to assess the effects of other complexities detected only after many years of data were collected (Table 3). A goal of our ongoing research will be to assess the relevance of these complexities to the viability and management requirements of these populations in the long term. Given the difficulty of obtaining such extensive data sets for small populations, we anticipate that the results will make a major international contribution to the biology and management of small populations.

Discussion

Our long-term research with robin and hihi populations on Tiritiri Matangi shares many of the general characteristics of LTS identified by previous authors (Strayer et al. 1986; Likens 1983; Franklin 1989; Pelton & van Manen 1996). As is usually the case, we did not plan to undertake LTS at the outset, and have progressively addressed new questions that we had not previously considered. The long-term data sets have certainly aided our ability to guide practical management. The projects have also provided an excellent training ground for students at a range of levels, and the combination of well established relatively straight forward protocols has made it possible to involve relatively inexperienced students and volunteers. In fact, the ability of enthusiastic but previously inexperienced people to participate with minimal supervision has been critical, especially for the robin project. Funding the projects has been a challenge, as is always the case with LTS, but has been facilitated by many factors, including conservation relevance, opportunity to address a series of novel scientific questions, and perhaps most importantly, the ability to do some research quite cheaply due to the support

of enthusiastic volunteers, the New Zealand Department of Conservation, and the Supporters of Tiritiri Matangi Inc. We concur with Pelton & van Manen (1996) that challenges have included data management, communication, and resolving the joint need for consistency, continuity and creativity. Maintaining relatively error-free data sets has been especially challenging, mainly due to colour band combinations being mis-recorded or changing due to band loss. All data need to be checked line-by-line each year by someone with long-term involvement in the project, and this is probably a key reason why long-term studies usually require a dedicated leader, as noted by Strayer et al. (1986).

Unlike some other LTS (e.g. Brooks et al. 1991; Smith et al. 1991; Pelton & van Manen 1996), we have not yet observed any rare mortality events that dramatically changed our interpretation of the populations' dynamics. We did record a significant mortality rate in hihi when about 25% of the adult population was killed by a *Salmonella* outbreak in 2006 (Ewen et al. 2007), but this can be considered a fairly minor event in the population's history, given that the population still grew that year (Fig. 2). The relatively minor impact of the event largely reflects the species' fast life history (i.e. breed in first year, high reproductive rate). For example, a similar mortality event in a common snapping turtle (*Chelydra serpentina*) population at the northern edge of its range in Canada caused a major impact due to extremely slow maturation and negligible reproductive success of the turtles (Brooks et al. 1991).

Of the four types of processes that Likens (1983) identified as requiring long-term data sets, the only category that really fits our situation is 'complex phenomena', which we interpret as processes that occur consistently but require large multi-year data sets to detect or discern. Examples cited above include adult survival of hihi, where significant annual variation was detected after 11 years, and density-dependent juvenile survival in robins, which was apparent within five years but required 12 years of records before we could develop a satisfactory model. The benefit of hindsight has emphasised the importance of incorporating uncertainty in model projections, particularly uncertainty in parameter estimation (Taylor et al. 2002; Wade 2002), but also uncertainty in model selection (Burnham & Anderson 2002). For example, our attempts to understand density dependence in juvenile survival of robins (Fig. 3) illustrate the usefulness of considering plausible alternative models and using a model averaging approach when making projections (Burnham & Anderson 2002). The inherent uncertainties of population ecology raise the question of how to make management decisions in the absence of long-term data sets. As well as emphasising the need to fully acknowledge uncertainty, we also note there is strong potential to adopt a Bayesian approach (McCarthy 2007; Link & Barker 2010) where long-term data from other systems is used to create prior distributions for parameters and prior weighting of candidate models. Indeed we hope our research will be used in this way to improve management of other populations with fewer data.

We wish to conclude by returning to the contribution of our LTS on Tiritiri Matangi to the local and international literature. We noted above that 57 papers had been published from the robin and hihi projects up to the start of 2010, and that these account for the majority of published research from Tiritiri Matangi. We subsequently outlined several results that have been made possible by having > 10 years of data. However, at this stage most of these long-term results are unpublished; of the 57 publications to date, only 12 have used > 5 years of data and only 3 have used > 10 years data. Therefore, while

the LTS have already been very productive, the full benefits to the local and international literature have yet to be realised. This is a situation we aim to rectify in coming years.

Acknowledgements

References

Armstrong DP, Cassey P 2007. Estimating the effect of inbreeding on survival. Animal Conservation 10: 487–492.

Armstrong DP 1995. Effects of familiarity on the outcome of translocations. II. A test using New Zealand robins. Biological Conservation 71: 281–288.

Armstrong DP, Davidson RS, Dimond WJ, Perrott JK, Castro I, Ewen JG, Griffiths R, Taylor J 2002. Population dynamics of reintroduced forest birds on New Zealand islands. Journal of Biogeography 29: 609–621.

Armstrong DP, Ewen JG 2001a. Testing for food limitation in reintroduced hihi populations: contrasting results for two islands. Pacific Conservation Biology 7: 87–92.

Armstrong DP, Ewen JG 2001b. Estimating impacts of poison operations using mark-recapture analysis and population viability analysis: an example with New Zealand robins (*Petroica australis*). New Zealand Journal of Ecology 25: 29–38.

Armstrong DP, Ewen JG 2001c. Assessing the value of follow-up translocations: a case study using New Zealand robins. Biological Conservation 101: 239–247.

Armstrong DP, Ewen JG, Dimond W, Lovegrove TG, Bergström A, Walter B 2000. Breeding biology of North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island. Notornis 47: 106–118.

Armstrong DP, Ewen JG 2002. Dynamics and viability of a New Zealand robin population reintroduced to regenerating fragmented habitat. Conservation Biology 16: 1074–1085.

Armstrong DP, Perrott JK 2000. An experiment testing whether condition and survival are limited by food supply in a translocated hihi population. Conservation Biology 14:

1171–1181.

Beissinger SR, Westphal MI 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62: 821–841.

Brekke P, Bennett PM, Santure AW, Ewen JG 2011. High genetic diversity in the remnant island population of hihi and the genetic consequences of re-introduction. Molecular Ecology 20: 29–45.

Brekke P, Bennett PM, Wang J, Pettorelli N, Ewen JG 2010. Sensitive males: inbreeding depression in an endangered bird. Proceedings of the Royal Society of London B 277: 3677–3684.

Brooks RJ, Brown GP, Galbraith DA 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69: 1314–1320.

Buckland ST, Burnham KP, Augustin NH 1997. Model selection: an integral part of inference. Biometrics 53: 603–618.

Burnham KP, Anderson DR 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. New York, Springer Verlag.

Dimond WJ, Armstrong DP 2007. Adaptive harvesting of source populations for translocation: a case study using New Zealand robins. Conservation Biology 21: 114–124.

Dunnet G 1991. Long-term studies of birds. Ibis 133 s1: 1–2.

Ewen JG 1998. A genetic and behavioural investigation of extra-pair copulation in stitchbirds (*Notiomystis cincta)* breeding on Tiritiri Matangi Island. MSc thesis, Massey University, New Zealand.

Ewen JG, Armstrong DP 2007. Strategic monitoring of re-introductions in ecological restoration programs. Ecoscience 14: 401–409.

Ewen JG, Thorogood R, Brekke P, Cassey P, Karadas F, Armstrong DP 2009. Maternally invested carotenoids compensate costly ectoparasitism in the hihi. Proceedings of the National Academy of Sciences U.S.A. 106: 12798–12802.

Ewen JG, Thorogood R, Armstrong DP 2011. Demographic consequences of adult sex ratio in a reintroduced hihi population. Journal of Animal Ecology 80: 448–455.

Ewen JG, Thorogood R, Nicol C, Armstrong DP, Alley MR 2007. *Salmonella* Typhimurium in hihi, New Zealand. Emerging Infectious Diseases 13: 788–790.

Graham M, Veitch CR, Aguilar G, Galbraith, M 2013. Monitoring terrestrial bird populations on Tiritiri Matangi Island, Hauraki Gulf, New Zealand: 1987–2010. New Zealand Journal of Ecology 37: 359–369.

Holt SJ, Talbot, LM 1978. New principles for the conservation of natural living resources. Wildlife Monographs 59: 1–33.

Jamieson IG, Tracy LN, Fletcher D, Armstrong DP 2007. Moderate inbreeding depression in a reintroduced population of North Island robins. Animal Conservation 10: 95–102.

Krebs CJ 1991. The experimental paradigm and long-term population studies. Ibis 133 s1: 3–9.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR 1992. Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. Ecological Monographs 62: 67–118.

Likens GE 1983. A priority for ecological research. Bulletin of the Ecological Society of America 64: 234–243.

Likens GE, ed. 1989. Long-term studies in ecology: approaches and alternatives. New York, Springer Verlag.

Link WA, Barker RJ 2010. Bayesian inference with ecological applications. Amsterdam, Academic Press.

May RM 1975. Island biogeography and the design of wildlife preserves. Nature 254: 177–178.

McCarthy MA 2007. Bayesian methods for ecology. New York, Cambridge University Press.

Miao SL, Carstenn S, Nungesser M, eds. 2009. Real world ecology: large-scale and long-term case studies and methods. New York, Springer.

Mitchell N 2013. Tiritiri Matangi Island: What if nothing had been done? New Zealand Journal of Ecology 37: 261–265.

Myers SC, Court AJ 2013. Regeneration of taraire (*Beilschmiedia tarairi*) and kohekohe (*Dysoxylum spectabile*) in a forest remnant on Tiritiri Matangi Island, northern New Zealand. New Zealand Journal of Ecology 37: 353–358.

Nichols JD 2004. Evolution of quantitative methods for the study and management of avian populations: on the importance of individual contributions. Animal Biodversity and Conservation 27: 3–19.

Pelton MR, van Manen FT 1996. Benefits and pitfalls of long-term research: a case study of black bears in Great Smoky Mountains National Park. Wildlife Society Bulletin 24: 443–450.

Perrins CM 1991. Introductory remarks: long-term population studies of birds. Acta XX Congressus Internationalis Ornithologici: 1499.

Possingham HP, Lindenmayer DB, Norton TW 1993. A framework for the improved management of threatened species based on population viability analysis (PVA). Pacific Conservation Biology 1: 39–45.

Pressey RL, Humphries CJ, Margules CR, Vane-Wright RI, Williams PH 1993. Beyond opportunism: key principles for systematic reserve selection. Trends in Ecology and Evolution 8: 124–128.

Shaffer ML 1981. Minimum population sizes for species conservation. Bioscience 31: 131–134.

Smith JNM, Arcese P, Hochachka W, Cassidy ALEU, Rogers CM 1991. Determinants of abundance in an island song sparrow population. Acta XX Congressus Internationalis Ornithologici: 1514–1521.

Strayer D, Glizenstein JS, Jones CG, Kolasa J, Likens GE, McDonnell MJ, Parker GG, Picket STA 1986. Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. Millbrook, New York, USA, Occasional Publication of the Institute of Ecosystem Studies, Number 2.

Taylor LR 1989. Objective and experiment in long-term research. In: Likens, GE, ed. Long-term studies in ecology: approaches and alternatives. New York, Springer Verlag. Pp. 20–70.

Taylor BL, Wade PR, Ramakrishnan U, Gilpin M, Akcakaya HR 2002. Incorporating uncertainty in population viability analyses for the purpose of classifying species by risk. In: Beissinger SR, McCullough GM, eds. Population viability analysis. Chicago, USA, University of Chicago Press. Pp. 239–256

Thomson DL, Cooch EG, Conroy MJ, eds. 2009. Modeling demographic processes in marked populations. Springer.

Thorogood R, Armstrong DP, Low M, Brekke P, Ewen JG 2013. The value of long-term ecological research: integrating knowledge for conservation of hihi on Tiritiri Matangi Island. New Zealand Journal of Ecology 37: 298–306.

Wade PR 2002. Bayesian population viability analysis. In: Beissinger SR, McCullough GM, eds. Population viability analysis. Chicago, USA, University of Chicago Press. Pp. 213–238

West C 2008. Unanticipated successional patterns in ungrazed grasslands on Tiritiri Mātangi Island, northern New Zealand. Unpub. paper presented to the 2008 NZ Ecological Society Conference, Unitec Institute of Technology, Auckland.

White GC 2000b. Population viability analysis: data requirements and essential analyses. In: Boitani I, Fuller K, eds. Research techniques in animal ecology: controversies and consequences. New York, USA, Columbia University Press. Pp. 288–331.

White GC 2000a. Modelling population dynamics. In: Demarais S, Krausman PR, eds. Ecology and management of large mammals in North America. New Jersey, USA, Prentice-Hall. Pp. 85–107.