Modelling the Dynamics of Translocated Populations

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Author’s Declaration

The work presented in this thesis is my own and all else is referenced appropriately.

I am the first author for all chapters that are published, accepted for publication or in preparation. A list of co-authors, and their respective contributions, is included at the beginning of each chapter. People who provided less formal advice are named in the acknowledgments.

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Copyright Declaration

Abstract

Climate change is widely accepted as one of the worst threat to the world's biodiversity. A recently proposed solution to help species survive climate change is "assisted colonisation", i.e. translocations of species to more suitable sites. Although assisted colonisation could be a powerful conservation tool, translocations are known to have a low success rate despite being commonly-used. Before promoting assisted colonisation as a solution, we need to make two major advances: first, understand how translocated species will respond to a changing climate and if their population viability will be compromised and, second, develop a quantitative framework to improve the success rates of conservation translocation under global environmental change. Those were the two aims of my thesis. The hihi (stitchbird; *Notiomystis cincta*) was used as a study species. It has been the subject of several translocations in the past few decades and every translocated population is intensely monitored, yielding long-term demographic datasets.

Climate was found to be a key factor in the dynamics of translocated population, and thus viability. However, it may also interact with other intrinsic factors like density and age to influence species' long-term persistence. A stochastic population model built to quantify the potential impacts of future climate change on translocated populations' long-term persistence showed the importance of taking into account the impact of longer and more frequent extreme weather on translocated population's viability. Moreover, MaxEnt was found to be a good habitat suitability model for translocated populations and used to identify future translocation sites for the hihi under climate change. Finally, quantitative guidelines for the planning and implementation of assisted colonisations were developed. They address the known issues impeding translocation success, and, if used, will maximise the success of assisted colonisations.

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Aims and Outline of Thesis

In this thesis entitled "Modelling the dynamics of translocated populations", I aim to:

(1) Understand how translocated species will respond to climate change and if their population viability will be comprised.

(2) Develop a quantitative framework to improve the success rates of conservation translocation under global environmental change.

This thesis is divided into six chapters.

In Chapter 1, I present a review of the literature on conservation-oriented species translocation with a particular focus on the new concept of assisted colonisation, i.e., translocations to help species adapt to climate change. This chapter culminates with quantitative guidelines for the planning and implementation of assisted colonisations that address known issues impeding translocation success.

In Chapter 2 and 3 I improve our understanding of the factors, both intrinsic and extrinsic, that influence the long-term dynamics of a translocated population. In Chapter 2, I use the hihi population on Tiritiri Matangi Island to study the impact of age, density, climate and their interactions on hihi survival rate and reproductive success. In Chapter 3, I quantify the impact of management on the viability of the translocated hihi population on Kapiti Island. Although management is implemented in all translocated hihi populations it is only on Kapiti that there has been a period of monitoring and no management allowing direct quantification of the benefits of intensive management actions on hihi recovery.

In Chapter 4, I develop a modelling framework to project translocated populations into the future, quantifying the potential impacts of climate change on their long-term persistence. The stochastic density-dependent population model presented measures the impact of increases in mean and variance of weather variables, as well as changes in temporal autocorrelation patterns, on future dynamics of the hihi population on Tiritiri Matangi. It is the first of its kind for threatened species.

In Chapter 5, I investigate how habitat suitability models (SDM) can be used to select translocation sites that will remain suitable in the future under climate change. I test two SDM, presence-absence GLM and presence-only MaxEnt, to find the best modelling approach for species surviving in artificial and isolated populations like the hihi. I also identify the distribution of future suitable habitat for the hihi, guiding the selection of future translocation sites.

Finally, Chapter 6 is the overall discussion. I summarise key findings and limitations of my approach, and I suggest future avenues of research in translocation science and for hihi management.

Male hihi (photo credit: Eric Wilson)

CHAPTER 1

Maximising the success of assisted colonisations

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Co-author contributions: I was responsible for the research, design and writing of this chapter. All co-authors commented on the different versions of this chapter, providing advice on how to improve the content and the writing.

ABSTRACT

Climate change is causing spatio-temporal shifts in environmental conditions, and species that are not able to track suitable environments may face increased risks of extinction. Assisted colonisation, a form of translocation, has been proposed as a tool to help species survive the impacts of climate change. Unfortunately, translocations generally have a low success rate, a well-documented fact that is not considered in most of the recent literature on assisted colonisation. One of the main impediments to translocation success is inadequate planning. In this review, we argue that by using well known analytical tools such as species distribution models and population dynamics modelling we can maximise the success of assisted colonisation. In particular, we present guidelines as to which questions should be investigated when planning assisted colonisation, and suggest methods for answering them. Finally, we also highlight further implementation and research issues that remain to be solved for assisted colonisations to be efficient climate change adaptation tools.

INTRODUCTION

Global biodiversity is under increasing threat from anthropogenic impact, and the unprecedented rate of species loss is a major concern to ecologists and wildlife managers (Secretariat of the Convention on Biological Diversity, 2010). One of these impacts is climate change, which has already affected the Earth's biota and is expected to have a profound effect on individuals and populations for years to come (Pejchar and Mooney, 2009). While climate change is often perceived as being synonymous with global warming, an increased average temperature on Earth is not the only expected consequence. Changes in seasonal patterns of rainfall and temperature, frequencies of extreme events, and greenhouse gas concentrations are also to be expected (Foden et al., 2008). All of these consequences pose a threat to species globally. As environmental conditions are altered through climate change, spatial mismatches will develop between species locations and their optimal environments (Atkins and Travis, 2010). Responses of species to change in environmental conditions are expected to fall into one of the following four categories: (1) thrive, i.e., species able to remain extant under the new set of conditions without having to change their ecology, (2) adapt, i.e., species able to remain extant under the new set of conditions by changing their ecology, (3) shift range, i.e., species whose range will contract or shift to remain under suitable conditions or (4) go extinct, i.e., species not able to remain extant under changing conditions, nor adapting or shifting distribution (Pettorelli, 2012).

Numerous species could fall into category (4), and many of these expected extinctions may be driven by topographic, physiological, behavioural or ecological constraints to dispersal (Foden et al., 2008). This is the case for species confined to offshore islands, isolated patches of habitats separated from suitable environments by physical barriers, and species that are not mobile or disperse too slowly. To counteract the impact of climate change, human intervention, in the form of translocation, may be a solution. Translocation outside a species' historic range for conservation purposes is traditionally called "conservation introduction" (IUCN, 1998), but the term "assisted colonisation" has recently been coined in the literature (Seddon, 2010).

Assisted colonisation is a controversial tool for reasons that are discussed below. However, in cases where it is the conservation action of choice, it makes sense to ensure that it succeeds. In this review, we highlight how assisted colonisation can be planned to efficiently counteract the impact of climate change on biodiversity. To do so, we review the state of translocation as a conservation action and highlight its existing shortcomings, review the current state of knowledge on assisted colonisation, and propose a way to improve the overall chance of success of translocations, and thus assisted colonisations.

TRANSLOCATIONS

Translocations are defined as "any movement of living organisms from one area to another" (IUCN, 1987), and have been part of the conservation toolkit for decades (Seddon et al., 2007). Conservation orientated translocations have historically been poorly planned and monitored (Armstrong and Seddon, 2008) as they were likely to be a last resort solution, and decision-makers often did not have the time or training to predict possible outcomes or plan necessary management beforehand. Guidelines for reintroduction that were published by the IUCN (1998) and several papers in the late 1980s and 1990s emphasised the need for an increase in research-oriented planning and monitoring (Scott and Carpenter, 1987; Griffith et al., 1989). Although the situation improved, a recent review suggests that the success rate of translocations is still generally low, with many attempts having resulted in either failure or partial success (see Box 1.1; Seddon et al., 2007). Moreover, Seddon et al. (2007) still found that more than half of the literature published in peer-reviewed journals on wildlife reintroduction were the result of retrospective evaluation, i.e., analysis is done because data were generated as a by-product of a reintroduction instead of being generated as one of the aims of the project, thus highlighting the current need for better planning and more targeted monitoring (Ewen and Armstrong, 2007; Armstrong and Seddon, 2008).

Box 1.1: Measuring the success of translocation projects

One issue with evaluating translocation projects is that what constitutes a successful translocation is still not clear (see Table 1.1 for examples). A popular metric of success is whether or not the translocated population is self-sustaining. The term "self-sustaining" is however vague and has not been properly defined even when used as a metric for success (Griffith et al., 1989; Dickens et al., 2010). It could, for example, imply that a translocation attempt is considered successful when the new population persists without needing further translocations or that it persists without any human intervention at all. Either of these definitions are probably a commendable aim for any translocation attempt. Unfortunately, translocated populations that are not subject to management actions, such as feeding or supplementation of individuals, at least for some years after translocation, are rare (see e.g., Chauvenet et al., 2012; Soorae, 2012), making this measure of success inadequate on the shorter term. One proposed solution to the lack of agreement about how to measure translocation success is to work within a decision-making framework (Rout et al., 2009). This means establishing explicit conservation objectives for the translocation against which success can be measured on the short- and medium-term using targeted monitoring (Nichols and Armstrong, 2012). Structured decision making provides such a framework. By identifying objectives, available actions and incorporating the best knowledge about the species to be translocated, structured decision making allows decisions to be logical and transparent (Nichols and Armstrong 2012). A well known subset of structured decision making is adaptive management (AM). AM is an iterative process that allows decisions to be recurrent while taking into account the uncertainty surrounding the system's parameters (McCarthy et al., 2012). It is particularly relevant to translocation as they are long-term endeavours and objectives may have to be revised every few years based on monitoring and management results (McCarthy and Possingham, 2007; Seddon et al., 2007). Eventually, after short- and medium-term goals have been reached, managers should find themselves in a position where a self-sustaining population is achievable. Hence, the long-term goal can still be to establish a population that requires no intervention to persist, but using AM would ensure adequate decision-making throughout the process and a regular assessment of progress towards this ultimate goal.

Table 1.1. Example of measure of success of species translocation

Measure against which success is assessed	**Reference**
Establishment of a self-sustaining population	Griffith et al. (1989); Dickens et al. (2010)
Surviving capture, transport and release, and breeding and settling in new area	Letty et al. (2007)
Persistence time of population	Sheller et al. (2006)
Individuals survive and do as well or better in new area	Strum (2005)
Survival of released individuals, recruitment and dispersal	Oro et al. (2011)
Yearly survival, number of individuals attempting to breed and fledgling success over 2 years	Reynolds et al. (2008)

ASSISTED COLONISATION

Definition

The term “assisted migration” was used by McLachlan et al. (2007) to describe conservation introduction in response to climate change, with specific reference to the translocation of Florida torreya (*Torreya taxifolia*) seedlings from Florida to North Carolina. The alternative terms “assisted colonisation” (Hoegh-guldberg et al., 2008) and “managed relocation” (Richardson et al., 2009) have also been used in subsequent literature. Seddon (2010) proposed that the term “assisted colonisation” be adopted for describing conservation introductions carried out to address threats to species, as opposed to those carried out for the purpose of ecosystem restoration; this usage is currently being adopted in the revised IUCN reintroduction guidelines. Seddon (2010) also argued that Ricciardi and Simberloff (2009a) proposed the most sensible definition of assisted colonisation as “translocation of a species to favourable habitat beyond their native range to protect them from human-induced threats, such as climate change”. The advantage of this definition is that it includes climate change explicitly, but acknowledges the fact that assisted colonisation can also be used to counteract other threats (Seddon, 2010) thus eliminating the need for more terminology.

In this paper, we focus on the use of assisted colonisation as an adaptation tool to climate change. Following Fussel and Klein (2006), we define an “adaptation tool” as a strategy for “moderating the adverse effects of unavoided climate change through a wide range of actions that are targeted at the vulnerable system”.

Concerns about assisted colonisation

McLachlan et al. (2007) sparked a debate on the usefulness of assisted colonisation as an adaptation tool for climate change. This debate has so far mainly focused on three points: ecological risks, costs and uncertainties (Hewitt et al., 2011). The main ecological risk associated with assisted colonisation is the introduction of invasive alien species. Invasive alien species are introduced species (i.e., species occurring outside their native range due to human intervention) that cause damage to the environment, the economy and, ultimately human well-being (Hulme et al., 2009). Invasive alien species are a significant threat to biodiversity (Mueller and Hellmann, 2008). It is therefore not surprising that conservationists, decision-makers, managers and the public have grown wary of species introductions, including those associated with assisted colonisations (Ricciardi and Simberloff, 2009b). Mueller and Hellman (2008) argued that the risk of invasion due to assisted colonisation is small, but also found that if any species were to become invasive, it would have a large negative impact on biodiversity. Moreover, it is difficult to predict which species will become invasive. All introduced species will have an impact on their recipient ecosystem but that impact can span from positive, to neutral, to negative, with invasiveness being the extreme (Blackburn et al., 2011). Not only is the probability of a species becoming invasive species-specific, but this probability may also depend on the composition of the recipient community. In addition, the invasive behaviour may be difficult to detect, especially in the beginning when the invasive species is in low numbers (Mehta et al., 2007). Nonetheless, the risk of losing species through not doing assisted colonisation needs to be balanced against the risk of invasion. Those risks will be dependent, among other things, on how close the species is to extinction (Schlaepfer et al., 2009).

The precautionary principle, defined as “when an activity raises threats of harm to human health or the environment, precautionary measures should be taken even if some cause and effect relationships are not fully established scientifically" (Raffensperger and Tickner, 1999), has been invoked as an argument against assisted colonisation. Indeed, Ricciardi and Simberloff (2009b) argue that assisted colonisation is not a viable management action because the risks to biodiversity cannot be entirely anticipated and consequences may be more damaging than inaction. Yet this reasoning has been declared as a weak argument by others (Sax et al., 2009; Thomas, 2011). Being precautionary might mean not using assisted colonisation to prevent a potential invasion, but might also mean using assisted colonisation before the extinction of a given species due to other threats (Sax et al., 2009). Considering that the threat of climate change is global and that its effects are widely believed to be inevitable, and considering that the risk of translocated species becoming invasive is small (Mueller and Hellmann, 2008; Thomas, 2011), it is likely that many species will need assisted colonisation, and that some of them may have benign enough impacts following translocation to be good candidates for it.

A step toward safe and efficient assisted colonisation

One way to minimise the risks of negative ecological impacts, and maximise the net benefit of assisted colonisation, is to work within a well-defined and, ideally, widely accepted decision framework. Three laudable attempts have been made at devising decision-frameworks for assisted colonisation. First, Hoegh-Guldberg et al. (2008) proposed a linear decision tree for deciding whether or not to perform assisted colonisation. This decision tree's main advantage is that it is extremely simple to use and therefore may appeal to many stakeholders. However, one of its downfalls is the vagueness of several questions. For example, the first question is 'Is there a high risk of decline or extinction under climate change?' and the possible answers are 'low', 'moderate' or 'high'. To answer this question, relevant stakeholders would have to decide what a high risk is, know the climate change projections under all different scenarios and decide which one is most likely, and assess threats to the species or habitat of interest under chosen projections. Subsequently, Richardson et al. (2009) proposed a decision framework for assisted colonisation that is much more complex than that proposed by Hoegh-Guldberg and colleagues (2008). Described by the authors as a "multivariate framework" that can be "conceptualized as *N*-dimensional set of criteria" (Richardson et al., 2009), it is based on the concept of scoring and/or ranking different ecological (e.g., likelihood of extinction, potential for reversibility or the likelihood native species may go extinct in the recipient range) and social attributes (e.g., cultural importance of the target species and its community, financial loss if the focal species goes extinct) used to evaluate the need for, and feasibility of, assisted colonisation from both the donor and recipient communities point of view. This decision framework's advantage is that it reflects the complexity of natural systems and the impact of such a level of complexity on how to make decisions. In addition, it is designed to be used by all categories of stakeholders, including the recipient community. However, Richardson et al. (2009) do not provide guidance on how to score attributes or even offer an exhaustive list of attributes to use. Therefore, it is difficult to see how this framework can or will be used by stakeholders and how it guarantees decisions to be transparent and repeatable. Most recently, McDonald-Madden et al. (2011) published a framework that attempts to optimise the decision of when to move a population if the aim is to maximise its size. They used an optimisation algorithm whereby decisions are made based on the size of the candidate population for assisted colonisation (i.e., source), the cost of translocation in terms of individual lives (i.e., survival rate of translocated individuals) and the dynamic state of the carrying capacity at both source and target sites (e.g., increasing or decreasing). The main drawback is the current lack of flexibility as the framework was designed to answer one specific question: what is the optimal timing of assisted colonisation? However, it is arguably the most transparent of the set, as it is not only quantitative but also explicitly accounts for the uncertainty about the impact of climate change on the candidate population.

The core issue

Overall, the debate on assisted colonisation has focused on questions about ethical issues (Minteer and Collins, 2010), feasibility (Hoegh-Guldberg et al., 2008; Richardson et al., 2009) and potential negative impact (Mueller and Hellman 2008). However, assisted colonisation is first and foremost a type of translocation (Seddon 2010) and, as pointed out before, translocations are suffering from overall poor planning and implementation. Thus, some of the issues that have been contributing to poor success rates in translocations (Seddon, 1999) will also reduce the success of assisted colonisation. Yet, the question of how to achieve success and avoid problems associated with translocations has been largely absent from the assisted colonisation debate. Moreover, published literature on translocation projects show that climate change has seldom been taken into account, even though it is bound to influence future translocation success. A search in 'ISI Web of Knowledge' (up to July 2010) for any paper combining conservation-oriented translocations (any kind) and climate change (even just a mention) revealed 142 published articles (Appendix 1A). Within those 142 articles, only 5 (3.5%) mention climate change as a possible correlate of success/failure of a translocation after it took place, while only 11 (7.8%) mention climate change in the process of planning a conservation translocation (Appendix 1B). The remainder (88.7%) mention conservation-oriented translocation and climate change in the same paper, but without linking an actual translocation outcome or planning to changes associated with climate.

We thus propose that the key to maximising the success of assisted colonisation in the face of climate change is to draw from the knowledge garnered from translocation research, as well as experience from past successes and failures, in order to address issues that can impede success.

ASSISTED COLONISATION AS AN ADAPTATION TOOL TO CLIMATE CHANGE

Research on translocation, and particularly reintroduction, is extensive. As a result, there is much knowledge to be drawn from the literature for assisted colonisation.

For example, Osborne and Seddon (2012) focus on the use and issues of habitat suitability models for reintroduction. They argue that habitat suitability modelling (also known as Species Distribution Models or SDM) is an important tool for planning translocation but raise several issues regarding our ability to correctly identify and define suitable and unsuitable habitat. While these issues apply to reintroduction, selecting a translocation site that is, and will remain, suitable in the future is paramount to the success of assisted colonisation. Therefore being able to identify what makes habitat suitable is an issue that is at the heart of assisted colonisation. Armstrong and Reynolds (2012) argue for the systematic use of population models when planning reintroductions and provide a detailed step-by-step guide for building them. Using population models when planning reintroduction can yield invaluable knowledge on how to plan and implement a translocation project. The benefits that using population models for reintroduction projects yield (e.g., investigating release and management strategies on the population's viability before taking action) are equally valuable in assisted colonisation projects. In particular, as assisted colonisation is introduction, rather than reintroduction, and by definition riskier, using population models before translocation may prevent irreparable mistakes. McCarthy et al. (2012) and Nichols and Armstrong (2012) focus on explaining and promoting structured decision making (including adaptive management: see Box 1.1) in the context of reintroduction. Whether for reintroduction or assisted colonisation projects, structured decision making guarantees those decisions are transparent and accountable. Furthermore, structured decision making ensures that the actions implemented are chosen based on the best available knowledge and that uncertainties in this knowledge are made explicit.

In the following section, we present and discuss guidelines on how to plan and implement assisted colonisation as an adaptation tool to climate change. By relying on concepts that have been developed for reintroduction or translocation, we bridge the gap between our knowledge of translocation and performing successful assisted colonisation.

Recommendations on planning and implementing assisted colonisation

The guidelines for planning and implementing successful assisted colonisation under climate change take the form of a list of questions along with a list of methods to answer them (Table 1.2). At the planning phase, the first priority is to identify whether a species is threatened by climate change and is thus a candidate for assisted colonisation (Q1 in Table 1.2). The decision frameworks proposed by Hoegh-Guldberg and colleagues (2008) and Richardson and colleagues (2009) have been partly designed to address this issue by suggesting questions to investigate, but do not explicitly propose a method to do so. To assess whether or not a species is a candidate for assisted colonisation, we suggest exploring whether the species is experiencing (or is projected to experience) an increased extinction risk associated with range contraction driven by climate change. Habitat suitability models (Hirzel and Le Lay, 2008; McRae et al., 2008; Elith and Leathwick, 2009; Osborne and Seddon, 2012) have been put forward as a way to identify conditions promoting species' survival and project changes in their distribution under different climate change scenarios (obtained from sources like the IPCC 2007 or other global or regional climate models; Wolf et al., 2010; Barbraud et al., 2011). To quantitatively assess changes in species' risk of extinction associated with likely range contraction, habitat suitability models can be combined with a spatially-explicit Population Viability Analysis (PVA; see e.g., Keith et al., 2008; Brook et al., 2009). Habitat suitability models will also highlight populations that are not immediately threatened and could potentially be used as source populations for translocations (Q2 in Table 1.2), as well as potential translocation sites where the environmental conditions are projected to remain stable as climate changes (Q3 in Table 1.2). However, once potential translocation sites have been identified, the risk of the introduced species becoming invasive should be assessed (Q3 in Table 1.2). A risk assessment could be based on which of the traits known to promote invasiveness the species possesses (see, e.g., Sakai et al., 2001; van Kleunen et al., 2010). Loss et al. (2011) suggested using laboratory and field tests as a way to assess invasiveness likelihood. Quantitative models of community interactions could also be designed on a case-by-case basis to predict the impact of a new species assemblage on the introduced species' behaviour.

Table 1.2. Table summarising the questions that need to be answered, and the methods that can be used to do so, to maximise the success of assisted colonisation under climate change. SDM stands for Species Distribution Model; PVA stands for Population Viability Analysis.

When?	What?	How?
Planning	*Q1. Is the species threatened by the impact of climate change?*	• Decision frameworks • SDM identifying future range contraction potentially followed by a spatially-explicit PVA
	Q2. Which population (if n>1) can be the source for the translocated individuals?	• SDM identifying populations not threatened by the range contraction • Scenario-based population dynamics modelling to project the source population's abundance under different harvesting scenario (scenarios are defined by numbers of individual harvested e.g., 0, 10, 20, etc.…)

	Q3. Where can the species be translocated?	• SDM to locate where the identified suitable environmental conditions will be spatially distributed in the future • Risk assessment of the likelihood the introduced species will become invasive using knowledge on intrinsic traits that promote invasiveness, laboratory and field tests, or community-based modelling
	Q4. How many individuals and what sex-ratio should be translocated?	• Scenario-based population dynamics modelling to project the translocated population's dynamics under different founder population scenarios (scenarios are defined by e.g., founding numbers, sex- and age-composition, genetic composition, etc.…)
	Q5.What management should be applied to the translocated population?	• Scenario-based population dynamics modelling to predict the abundance under different management scenario (scenarios are defined by different management options, e.g., supplemental feeding, vaccination, doing nothing, etc.…)
Implementation	*Q6. Is the source population negatively affected by the removal of individuals?*	• Monitoring to determine source population's abundance and demographic parameters • Population dynamics modelling to project the source population in the future

	Q7. Are the projections made for the translocated population correct?	• Monitoring of the translocated population's abundance and demographic parameters • Comparison between projection and observed abundance • Population dynamics modelling to project the source population in the future
	Q8. What adaptive management decision, if any, should be made?	• Scenario-based population dynamics modelling to predict the abundance under new management scenario (scenarios are defined by different management options, e.g., supplemental feeding, vaccination, doing nothing, etc.…)

The second priority at the planning stage is defining the logistics of the translocation by identifying the best source population (Q2 in Table 1.2), the optimal founder population (e.g., size, age composition, sex ratio, genetic composition; Q4 in Table 1.2) and the best management, if any, to be applied to the newly translocated population (Q5 in Table 1.2). We recommend a scenario-based approach in order to find the optimal answer to these questions. This involves building a population model, and investigating the impact of different management decisions (i.e., the scenarios) on the population trajectory (Armstrong and Reynolds, 2012). The outcomes of the different runs are assessed against a specific objective set for the population. For example, managers may want to know the optimal founding population in order to maximise the growth rate of the translocated population and minimise costs. When implementing the translocation, they would select the strategy given by the scenario that performed best against that objective, i.e., which gave the most cost-efficient strategy. This scenario-based approach allows the identification of a case-specific optimal translocation strategy for both the source and translocated populations. In addition, it can yield predictions for the future dynamics of both populations if this optimal strategy is implemented. One caveat to this approach is the amount of data required to parameterise the models. In some cases, it may be possible to obtain estimates of expected demographic parameters from published meta-analyses (Brawn et al., 1995; Falster et al., 2008; McCarthy et al., 2008).

Once the initial assisted colonisation has taken place, in-situ monitoring becomes the backbone of future decisions (Ewen and Armstrong 2007; Armstrong and Seddon 2008; Nichols and Armstrong 2012). It should be done for both the source and the translocated populations. A key requirement, however, is that monitoring programs should be designed with specific questions in mind (Armstrong and Seddon 2008). The monitoring data collected from the source population can, for example, be used to verify that the initial conclusion that the source population would not be negatively affected by the removal of individuals was correct (Q6 in Table 1.2). Similarly, the monitoring data collected for the translocated population can be used to match the projected population trajectory with the actual translocated population growth (Q7 in Table 1.2) and to increase the understanding of the translocated population dynamics to support future management decisions through adaptive management (Q8 in Table 1.2; McCarthy et al., 2012; Nichols and Armstrong 2012).

By following the proposed systematic guidelines in Table 1.2, decision-makers could be one step closer to securing the future of biodiversity with assisted colonisation. Nevertheless, we have identified several issues at the implementation and research levels that have to be resolved before assisted colonisation can become the most cost-efficient adaptation tool for species threatened by climate change.

Issues regarding implementation

There is an untold number of species that will be potential candidates for assisted colonisation, i.e., for which the answer to Q1 (Table 1.2) is "yes" because they are projected to have an increased extinction risk due to climate-change related range contraction. One pressing question is how to choose which species to move first? There are several prioritisation schemes and methods that currently attempt to guide conservation choices, e.g., cost-benefit analysis (Bottrill et al., 2008), biodiversity hotspots (Joppa et al., 2011), and phylogenetic uniqueness (Isaac et al., 2007). These could all be useful to prioritise species for assisted colonisation. However, once assisted colonisation has been implemented (i.e., a species has been introduced to a new area), undoing this action and its consequences is very difficult, thus leaving little room for error when making decisions. As a result, concerns like the risks associated with species introduction, such as diseases or potential for invasiveness for example, could play a large role in deciding for which species to take action first.

Second, one of the possible future impediments to implementing assisted colonisation will be the question of who will make the critical decisions of prioritization and implementation. Today, depending on the project, conservation decisions are made by various groups, from small organized groups of people (e.g., the Torreya Guardians; McLachlan et al., 2007), to NGOs (e.g., Durrell Conservation Trust, BirdLife International; Corry et al., 2010) and governments (e.g., New Zealand Department of Conservation; Cromarty et al., 2002). However, the need for assisted colonisation will grow alongside the impact of climate change on everything else, increasing the chance of conflicts between groups. While no one entity can be in charge of making decisions regarding all assisted colonisation projects, we hope that by using the same decision-making framework at least the decisions made will be transparent.

Further research required

There are also a number of challenging issues for research. First, there are the issues of the accuracy and scale of climate change projections that are to be used in habitat suitability models (e.g., to answer Q1-3 in Table 1.2). There are several models that can be used to project climate change ('the multi-model dataset at PCMDI'; www-pcmdi.llnl.gov/ipcc/data_status_tables.pdf); these are mostly global climate models (GCMs) that originally had coarse resolution but have been downscaled to resolutions as small as 30 arc-second (www.worldclim.org). The issue is that GCMs do not always agree on predictions at the global scale, let alone at the scale needed for conservation, which is often much smaller than a country and can be sometimes as restricted as a field.

Second, there are four possible responses of species to climate change: thrive, adapt, shift or die. Although they are clear-cut, little is known of the true potential of species to tolerate or adapt to climate change. Often, the problem will lie in identifying which alternative outcome the species are moving towards, e.g., species with long generation time and limited dispersal like the Florida torreya (McLachlan et al., 2007) will be both unable to adapt and unable to shift range. Unless there is evidence for range-shifting, the only way to be really sure about the species' fate would be to wait and observe. However, this is not an option for those species that are declining rapidly. Because conservation money is limited, it is inefficient to move species that would have survived had they been left in their original range. On the other hand, some species could be saved with assisted colonisation but may be ignored because the skills necessary to identify their lack of adaptation are missing (Hill et al., 2011). Although studies have started investigating the problem for plants (see Jump and Penuelas 2005 for a review), one of the biggest challenges yet is to learn to predict plasticity and adaptation capacity for all species.

Third, the relationship between environmental conditions and species' demography is still not fully understood. So far, most published research has focused on identifying the relationship between some climate variables and the survival and reproduction of species based on current or past conditions (see e.g., Borrego et al., 2008; Frederiksen et al., 2008). However, our ability to predict how changes in baseline environmental conditions will affect future demographic rates is still limited. For example, difficulties arise when the future environmental conditions are outside the range of conditions experienced by species in the past, and models based on current conditions cannot be trusted to be informative (Berteaux et al., 2006). As a result, the quality and accuracy of predictive population models in the face of climate change, such as those that would be built to answer Q2 (Table 1.2), may be compromised. Lessons from historical introductions for reasons other than conservation may help in these circumstances (c.f. Cassey et al., 2008).

Finally, Armstrong and Reynolds (2012) suggest 5 topics related to population modelling that warrant further research. While those are offered in the context of reintroduction, advances on those subjects would benefit assisted colonisation, or indeed any form of translocation. In particular, they suggest focusing on the long-term genetic effect of translocating populations. Inbreeding and loss of genetic diversity could have a significant impact on the long-term viability of any population, but especially those established through translocation, as they are generally small. However, genetic issues are seldom included into predictive population models (Armstrong and Reynolds 2012), which may be an impediment to our ability to accurately predict the dynamics of translocated populations.

CHAPTER 2

Climate interacts with age and density to determine the dynamics of a translocated bird population

This chapter will be submitted for publication under the authorship of Aliénor L. M. Chauvenet, John G. Ewen, Doug P. Armstrong and Nathalie Pettorelli.

Co-author contributions: I was responsible for partly-designing and performing all analyses and the writing of this chapter. Nathalie Pettorelli provided advice and help when designing the analyses. John G. Ewen and Doug P. Armstrong provided knowledge on the life-history of the hihi, giving valuable insight on how its dynamics should be modelled. Doug P. Armstrong helped with the capture-mark-recapture analysis. All co-authors read and commented on all versions of this chapter.

ABSTRACT

Climate change is considered as one of the largest threats to biodiversity. Changes in climatic conditions can be expected to affect species' demographic rates (survival and reproduction), thus impacting their population dynamics and long-term chance of persistence. Optimal decision-making for species conservation in the face of climate change requires being able to predict how changes in environmental conditions will affect the future dynamics of species. One key step towards this is to understand the impact of recent climate fluctuations on species' vital rates. Climate variables have been used to explain observed population dynamics patterns in the past, but the approach taken has often ignored the potential interactions between climate and intrinsic factors. Here we investigated how weather interacted with the age-structure, as well as the density, of a translocated bird population of stitchbirds (or hihi). We modelled hihi survival using a capture-mark-recapture framework and found significant interactions of rainfall with age, and temperature with density. Then, we estimated female reproductive success using generalised linear mixed modelling and found that age, temperature, and density all contributed to shape reproductive success. Our findings highlighted that the impact of climate changes on species' vital rates will depend on populations' intrinsic characteristics; a fact that should be taken into account when planning future conservation actions.

INTRODUCTION

Climate change is one of the most severe threats to biodiversity (Parmesan and Yohe, 2003; IPCC, 2007). Environmental conditions such as averages and extremes of temperature and precipitation, seasonality, and primary production dynamics are changing at the global scale (Foden et al., 2008). This trend is expected to continue in the future (Parmesan, 2006; IPCC, 2007) and consequences on species have already been observed (see e.g. Thomas et al., 2001; Wilson et al., 2007; Hoegh-Guldberg and Bruno, 2010). Ultimately, changes in environmental conditions impact species' demographic rates (i.e., survival and reproductive rates), either directly (e.g., thermoregulation) or indirectly (e.g., decrease in food availability), altering their population dynamics and thus their future risk of extinction (Kéry et al., 2006). Large uncertainties regarding how species' extinction probability will be affected by climate change still remain (Thomas et al., 2004). As a result, making optimal conservation decisions in the face of future environmental change is difficult. One key step towards predicting the impact of climate change on biodiversity is thus to understand the impact of past climate on species' population dynamics (Grosbois et al., 2006).

Studying the impact of climate on population dynamics is complicated as climate itself is a complex process, comprised of a multitude of components. In addition, there is a lack of understanding about how some climate components will affect different taxa (Grosbois et al., 2006). There are, nevertheless, two broad types of climate variables that can be linked to patterns of population dynamics; direct climate attributes which are single measures such as mean temperature, number of rain days or amount of precipitation; climate indices, measuring large scale fluctuation in the atmospheric pressure which can be related to temperature and rainfall patterns such as the North Atlantic Oscillation index (NOA index; Hurrell et al., 2001) or the Southern Oscillation Index (SOI or ENSO; Allan et al., 1996). Population dynamics studies have sometimes used only one type (Frick et al., 2010; Glenn et al., 2010; Oro et al., 2010; Wolf et al.,

2010) or combined both in the same analysis (Grosbois et al., 2006). While both approaches are valid and have advantages and disadvantages, choosing a type of climate variable may incur a trade-off. Hallett et al. (2004) showed that large-scale climate indices may better correlate with patterns of survival and reproduction but indices can also be difficult to relate back to local climate patterns (Stenseth et al., 2003), which is the scale of most ecological data. The key may be to choose variables that have a biological meaning for the species of interest, i.e., for which hypotheses can be formulated, and to keep that list as restricted as possible (Grosbois et al., 2006).

When studying population dynamics, however, considering extrinsic influences such as climate is not enough. Intrinsic variables, e.g., age and sex, or density are also known to directly impact species' survival and reproduction rates (Björsntad et al., 1998; Coulson et al., 2001; Bonenfant et al., 2009). Several studies have included both intrinsic and extrinsic factors when investigating patterns of survival (Farand et al., 2002; Frederiksen et al., 2008), population growth rate (Kruger and Lindstrom, 2001; Long et al., 2007; Piha et al., 2007) or reproduction (Solberg et al., 2001; Bunnell et al., 2006). Yet, the interaction between both types of factors has seldom been taken into account explicitly. When it has, the interaction between density and weather (e.g., Svalbard reindeer *Rangifer tarandus platyrhynchus*, Solberg et al., 2001; Alpine Ibex *Capra ibex*, Jacobson et al., 2004; American elk *Cervus canadensis*, Hebblewhite, 2005) and the interactions between age or sex and weather (e.g., Soay sheep *Ovis aries*, Coulson et al., 2001; Asp viper *Vipera aspis*, Altwegg et al., 2005) were tested but not always found significant. Most of these examples are found in the ungulate literature, but few studies have explored how intrinsic and extrinsic variables shape demographic parameters in other taxa. Yet, a broader understanding of the impact of the interactions between intrinsic and extrinsic variables may be paramount for efficient conservation planning in the face of climate change.

With this study, we explored the impact of the interaction between intrinsic and extrinsic variables on the vital rates of a small, passerine bird from New Zealand, the hihi (or stitchbird; *Notiomystis cincta*), on the island of Tiritiri Matangi. After almost going extinct in the late 19th century (Taylor et al., 2005), reintroductions have resulted in five wild populations across the North Island and offshore islands as well as one remnant population. However, the long-term fate of all populations is unclear, and the hihi is classified as Vulnerable on the IUCN Red List (IUCN, 2011). In most translocated hihi populations, survival and breeding are monitored at the individual level, creating detailed records of their population dynamics and an ideal dataset for in depth demographic studies. Previous studies have estimated the impact of several factors on hihi demographic rates. Those shown to matter were age (survival and reproduction; Armstrong et al., 2007; Low et al., 2007; Low and Pärt, 2009), density (reproduction; Ewen et al., 2011; Chauvenet et al., 2012), sex ratio (survival and reproduction; Ewen et al., 2011), and management (survival and reproduction; Armstrong et al., 2002, 2007; Chauvenet et al., 2012). Moreover Low and Pärt (2009) investigated the impact of ambient temperature on the survival of different age classes, and found that temperature was particularly important for nestling survival. The impact of variations in precipitation, however, has not been investigated.

We predicted that the survival and reproduction rates of the hihi population would decrease as environmental harshness increases. It is well known that environmental harshness can constrain population growth in species by acting on survival and reproduction rates (Price, 1974; Hobbs et al., 2006). However, as there is no general definition, for the hihi population, we defined environmental harshness as a departure from average climatic conditions, making the assumption that the conditions they currently encounter are optimal. Specifically, hihi demographic rates should have been negatively affected by: (1) an above average temperature during the breeding season (spring/summer, i.e., drier and warmer) and a below average temperature during the non-breeding season (autumn/winter, i.e., wetter and colder), and (2) a below average amount of rainfall during the breeding season and an above average amount of rainfall during the non-breeding season. Based on previous studies carried out on other taxa, we then hypothesised that the effect of environmental harshness would manifest itself through the following interactions with intrinsic variables:

H1: The interaction between density and the weather covariates: at high density, environmental harshness should have a greater impact on hihi survival and reproduction than at low density (Sauer and Boyce, 1983; Barbraud and Weimerskirch, 2003; Sæther and Sutherland, 2004).

H2: The interaction between age and the weather covariates: environmental harshness should have a greater impact on the survival of juveniles, and the survival and reproduction of first-year hihi than older ones (Caughley, 1966; Sullivan, 1989; Solberg et al., 1999; Oppel and Powell, 2010).

MATERIAL AND METHODS

Study species and data collection

Study species

Hihi are small, sexually dimorphic, forest-dwelling passerine birds (Ewen et al., 1999, 2011; Armstrong and Ewen, 2001). Their mean life expectancy is 4 years but they have been known to live up to 9 years old (Low and Pärt 2009). Hihi breed annually between September and February. While they are territorial and form breeding pairs, the rate of extra-pair copulation (males forcing females to mate with them) is extremely high (Brekke et al., 2012).

Once found throughout the North Island, hihi declined to one single offshore population on Little Barrier Island (Hauturu; LBI) following European colonisation and the consequent habitat loss and introduction of mammalian predators and diseases (Taylor et al., 2005). Since the early 1980s, there have been several attempts at reintroducing hihi on offshore islands and ecological sanctuaries on the mainland of the North Island. Today, hihi persist in 6 wild populations (5 translocated and LBI; Chauvenet et al., 2012).

Hihi on Tiritiri Matangi Island

Tiritiri Matangi Island (Tiri) is a 220ha scientific reserve located 3.5 km from the mainland, north of Auckland city, New Zealand (36°36'S, 174°53'E; Armstrong and Ewen, 2001). It has been free of mammalian predators since 1993, when Pacific rats (*Rattus exulans*) were eradicated. Most of the native vegetation on Tiri was modified by clearing and burning for farming, but it is now mostly covered by regenerating forest following a revegetation program which started in 1983 (Mitchell, 1985).

The hihi population on Tiri was established through two translocation events (Ewen et al., 1999; Armstrong and Ewen 2001). In 1995, 20 males and 18 female hihi were released on the island but high female mortality following release prompted a second translocation event in 1996 of 4 males and 9 females. Due to evidence that hihi were food limited (Armstrong and Ewen 2001; Armstrong et al., 2007), the translocated hihi population have been provided with *ad libitum* supplemental food (i.e., sugar water) through feeders at fixed locations since 1996. In addition, hihi are also provided with nest boxes because of the scarcity of natural nesting cavities. The intensity of the management effort on Tiri has been consistent throughout the years, meaning the availability of supplementary food and nest boxes to individual hihi has been fairly constant.

Hihi survival was monitored through bi-annual surveys (February and September) between September 1995 and September 2010. During surveys, birds were “sighted” via a direct observation survey during systematic searches of the entire forest habitat on the island and dedicated time spent the feeders. Hihi were individually identifiable from a combination of coloured rings placed on their legs as nestlings or when captured as adults for translocation to the island. In addition, nests throughout the island were checked regularly during the breeding seasons between September 1995 and February 2011. Information on the female at the nest, the numbers of eggs laid, number of eggs that hatched, number of dead chicks, and number of chicks that fledged, were recorded for every clutch laid by every female during that time.

Climate data

The mean monthly temperature and total monthly precipitation for the 1995-2011 period were downloaded from the New Zealand’s National Climate Database (http://cliflo.niwa.co.nz). The weather station selected was “Tiritiri Matangi lighthouse”, which is situated on the island itself. We calculated the average mean monthly temperature and the total sum of precipitation for the March to August (non-breeding) and the September to February (breeding) periods of each year between 1995 and 2011. We also acquired data for the Southern Oscillation Index (SOI; The National Centre for Atmospheric Research http://www.cgd.ucar.edu/cas/catalog/climind/soiAnnual.html) for the 1995-2011 period. However, we elected not to use the SOI, as there was no significant correlation with local temperature or rainfall patterns; this was concurrent with previous findings (Zheng and Renwick, 2003).

The average temperature and the average total rainfall during the non-breeding season were 15.3˚C and 526 mm respectively (SD 1.4˚C and 96 mm). During the breeding season they were 17°C and 393 mm respectively (SD 0.4°C and 84 mm). There was no trend in either climate variable for either season (Mann-Kendall trend tests, $p>0.5$).

Analysis

Survival and Recapture

We used Cormack-Jolly-Seber (CJS; Cormack, 1964; Jolly, 1965; Seber, 1965) models in MARK (White and Burnham, 1999) to estimate the survival, φ, and recapture probabilities, p, of the hihi on Tiritiri Matangi Island. Because surveys were conducted each year in February and September, uneven time-intervals were implemented. The over-dispersion (c-hat or $\hat{c}$) was estimated using the median $\hat{c}$ test implemented in MARK. Moreover, the sighting record of hihi on Tiri contained 125 birds that were translocated away from the island during various events between 2004 and 2010. To prevent an over-inflation of the mortality rates estimated by MARK, we added a '1' in the survey immediately after the translocation, e.g., if they were removed in April, we replaced the 0 in the September survey that was due to their absence by a 1. Moreover, '-1' was added to the capture histories of removed birds (White and Burnham 1999) to indicate they were harvested after their last sighting. Although this method may introduce some bias in the survival estimates of juveniles, we believe it is very limited.

Survival during the breeding and non-breeding season was modelled separately because the former occurs during the spring/summer time and the latter autumn/winter time, thus weather patterns were different and environmental harshness defined differently.

Table 2.1. List and description of covariates used in survival and/or reproduction analysis. 'B' stands for breeding season; 'NB' stands for non-breeding season.

Name	**Description**	**Survival analysis**		**Reproduction analysis**
		B	**NB**	
Intrinsic factors				
Age	Indicating the age of individuals at each time-step; was tested as both continuous and categorical.	Yes	Yes	Yes
Clutch Number	Number of clutches laid by females during the breeding season.	No	No	Yes
Density	The total number of individuals at the beginning of each breeding and non-breeding season.	Yes	No	Yes
Sex	Distinguishing between males and females.	Yes	No	No
Extrinsic factors				
Rainfall	The total precipitation across each breeding and non-breeding seasons.	Yes	Yes	Yes
Temperature	The average monthly temperature across each breeding and non-breeding seasons.	Yes	Yes	Yes

a. Survival during the breeding season

The variables used to analyse hihi survival during the breeding season (i.e., September to February) and test H1 and H2 are described in Table 2.1. Age, density, sex, rainfall and temperature were modelled as additive effects alone and in combination. The interactions age x rainfall, age x temperature, density x rainfall, density x temperature were tested alone and in combination. Age was modelled as a categorical variable for which hihi were distributed into two age-classes: 'first-year' for first-year adults, and 'older' for the others (there are no juveniles during the breeding season). This age structure was chosen after it was contrasted with others (i.e., age as a categorical factor, linear, quadratic and a 3rd degree polynomial) and found best. Recapture probabilities were modelled as time-dependent and constant across the seasons.

b. Survival during the non-breeding season

The variables used to analyse hihi survival during the non-breeding season (i.e., March to August) are described in Table 2.1. Because there was limited knowledge on the behaviour and ecology of hihi during the non-breeding seasons, we were unable to make predictions on the interaction between density and weather variables. As a result, a restricted set of survival models was run and only H2 was tested. Age, rainfall and temperature were modelled as additive effects and the interactions age x rainfall, age x temperature were also tested alone and in combination. Age was modelled as a categorical variable for which hihi could be either: 'juveniles' for individuals that entered the dataset in February, 'first-year' for first-year adults and 'older' for the older birds. This age-structure was chosen after it was contrasted with others (i.e., age as a factor, linear, quadratic and a 3rd degree polynomial) and found best. Recapture probabilities were modelled as time-dependent and constant across the seasons.

For both analyses, the best model of the candidate set was selected using the corrected Akaike Information Criterion for small datasets (AICc; Burnham and Anderson, 2002). Finally, a variance component analysis was run in MARK on the survival beta estimates. This was used to separate process from sampling variance to give more accurate survival estimates (White et al., 2001).

Reproduction

Modelling reproduction can be difficult as breeding success may be defined by different parameters depending on the species. For example, hihi reproduction has been modelled as the number of eggs that hatched, the number of nestlings that fledged, or other clutch-specific measure of breeding success (Low et al., 2007). The potential issue with this approach is knowing which measure of breeding success is most appropriate and, if several are, how to combine them so that results are meaningful. Here, hihi reproductive success was measured as the total number of fledglings produced during the whole breeding season, T_f, divided by the total number of eggs laid during that season, T_e. We called this measure of reproduction the overall breeding success (OBS) with OBS= T_f/T_e (see Appendix 2A for rationale). Using OBS amounted to calculating the probability that an egg laid survived to the fledgling stage. It was calculated for every female in every season in which they bred. Because OBS measured breeding success across the entire breeding season, reflecting on the breeding process from start to finish, it was well adapted to correlation with climate data that spanned the entire season.

To analyse OBS, we used generalized linear mixed models with a binomial error structure and a logit link function implemented in R (lmer; package 'lme4'). As measures were repeated across females and years, female identity and breeding year were set as random effects. Age-specific reproduction is common in birds (Forslund and Part, 1995; Reid et al., 2003) and Low et al. (2007) found similar patterns for the hihi (age as a quadratic function). However we found that using three age categories: 'first-year' for females reproducing for the first time, 'prime-age' for females between the age of 2 and 6, and 'senescent' for older females performed best. The covariates used in the breeding analysis to test H1 and H2 are described in Table 2.1. Age, density, rainfall, temperature and number of clutched were modelled as additive effects alone and in combination. The interactions age x rainfall, age x temperature, density x rainfall, density x temperature were tested alone and in combination. Moreover, the continuous covariates (i.e., density, temperature and rainfall) were all standardised to mean 0 and variance 1 to avoid convergence problems in lmer. The decision tree suggested in Bolker et al. (2009) was used to guide the model selection process. As there was no overdispersion in the data, models were compared and selected using the AICc (Burnham and Anderson 2002).

RESULTS

Survival and Recapture

The total number of capture occasions was 31 and the total number of individuals in the record n=1773. There was very little overdispersion in the data $\hat{c}$=1.2 and the $\hat{c}$ adjustment option in MARK was used to correct for it. Model selection was thus based on QAICc rather than AICc*.* Density, temperature or rainfall during either season were not correlated (Spearman's rank correlation, p>0.1).

Regardless of the season, models where recapture probabilities were time-dependent always performed better than those where they were constant across seasons and recapture probability on Tiri was high: 0.77 on average between 1996 and 2010 (SD ± 0.15).

a. Survival during the breeding season

There were a number of models that plausibly fitted the data for hihi survival during the breeding season (Table 2.2). The two models with the lowest QAICc had almost identical weights and the same number of parameters. Therefore, the one with the lowest QAICc was chosen as best (Table 2.2 and 2.3). It contained age and rainfall as additive effects and the interaction between density and temperature (H1). There was no significant interaction between density and rainfall or between age and either weather covariates (H2). Results, however, showed that during the breeding season, individuals that were older had an overall higher probability of survival than first-year ones. Moreover, while we expected rainfall to positively correlate with survival, rainfall had a slight negative impact (Table 2.3). Graphical examination of the results showed that, as expected, when density was low, the temperature had little effect of the survival of hihi (Figure 2.1). However, when density was high, environmental harshness in the form of above average temperature had a significant negative impact of the survival of hihi of both age classes (H1).

Table 2.2. Analysis of hihi survival during the breeding season. Shown is the set of models within 2 ΔQAICc. The most parsimonious model is in bold. Recapture probabilities were always time-dependent. Parameters estimates were adjusted for ĉ=1.2. 'Age' was a categorical variable separating first-year individuals (1-2) from older ones (2+).

	Model	K	QAICc	ΔQAICc	Weight	Cumul. W	QDeviance
1	**Age + Density x Temperature + Rainfall**	**21**	**5802.294**	**0.000**	**0.127**	**0.127**	**2049.816**
2	Age x Temperature + Rainfall	21	5802.542	0.248	0.112	0.238	2050.064
3	Age x Temperature	20	5803.198	0.905	0.081	0.319	2052.743
4	Age x Temperature + Density x Temperature	21	5803.262	0.968	0.078	0.397	2050.784
5	Age x Rainfall	20	5803.443	1.150	0.071	0.468	2052.988
6	Age x Rainfall + Age x Temperature	23	5803.533	1.239	0.068	0.536	2047.008
7	Age + Density x Temperature	20	5803.988	1.694	0.054	0.591	2053.532
8	Age + Density x Rainfall + Density x Temperature	22	5804.025	1.731	0.053	0.644	2049.524
9	Age x Temperature + Sex + Rainfall	22	5804.206	1.912	0.049	0.693	2049.705
10	Age x Temperature + Rainfall + Density	22	5804.244	1.951	0.048	0.740	2049.744

Table 2.3. MARK estimates for the most parsimonious model of hihi survival during the breeding season. The estimates presented are the shrinkage beta estimates and their standard error (SE) obtained using the variance component analysis in MARK (logit-link used).

Parameter	Estimate	SE
Intercept	-0.219	0.055
Age (1-2)	-1.041	0.398
Age (2+)	0.578	0.400
Density	0.264	0.077
Temperature	0.181	0.065
Rainfall	-0.004	0.002
Density x Temperature	-0.016	0.005

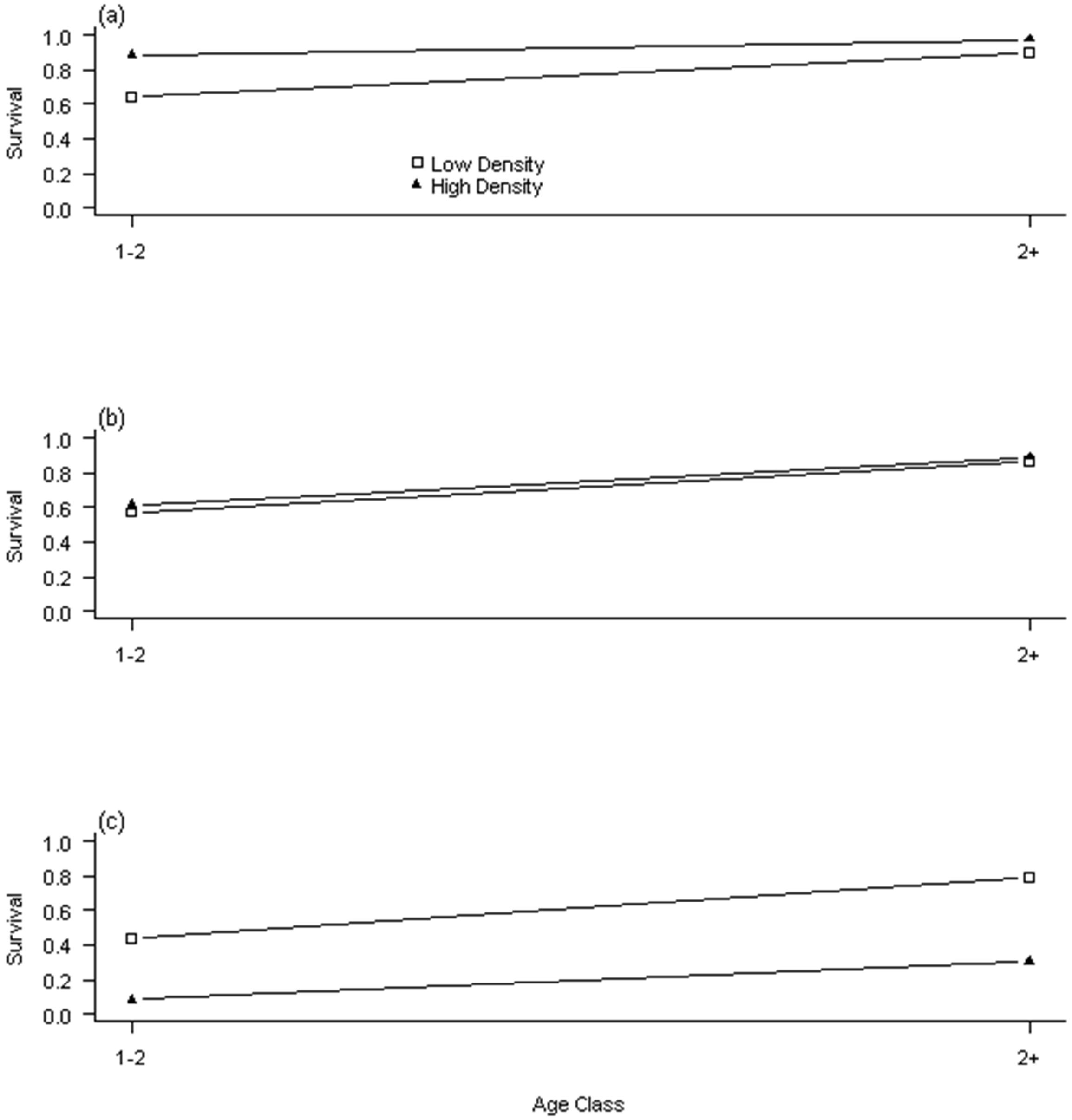

Figure 2.1. Hihi survival during the breeding season, when temperature was (a) below average, (b) average, and (c) above average. Two age classes are shown, “1-2” representing adult in their first year, and “2+” representing older individuals. There are no juveniles during the breeding season. Rainfall was set as the average between 1995 and 2010.

b. Survival during the non-breeding season

There were also a number of models that plausibly fitted the data for hihi survival during the non-breeding season (Table 2.4). However, of the top two models with the lowest QAICc and almost equal weights, one had a much lower number of parameters and it was thus chosen as the best model (Table 2.4). It contained an interaction between age and rainfall (H2) but no interaction between age and temperature or between density and either weather covariates (H1; Table 2.5). Graphical examination of the results showed that, as expected, an increase in environmental harshness in the form of above average rainfall decreased juvenile survival compared to when the environmental conditions were clement (Figure 2.2). Although we expected first-year adults to also have a lower survival than older ones when environmental harshness increased, both adult age classes seemed to be little affected by environmental harshness.

Table 2.4. Analysis of hihi survival during the non-breeding season**.** Shown is the set of models within 2 ΔQAICc. The most parsimonious, and thus best, model is in bold. Recapture probabilities were always time-dependent. Parameters estimates were adjusted for ĉ=1.2. 'Age' was a categorical variable separating juveniles (Juv), first-year individuals (1-2) and older ones (2+).

	Model	K	QAICc	ΔQAICc	Weight	Cumul. W	QDev.
1	Age x Temperature + Age x Rainfall	21	5666.834	0.000	0.356	0.356	1914.356
2	**Age x Rainfall**	**18**	**5667.046**	**0.212**	**0.320**	**0.676**	**1920.631**
3	Age x Rainfall + Temperature	18	5667.695	0.861	0.231	0.907	1921.280

'Cumul. W' is the cumulative sum of a model's weight and the weight of all the models that have a lower QAICc, 'QDev.' is the deviance.

Table 2.5. MARK estimates for the most parsimonious model of hihi survival during the non-breeding season. The estimates presented are the shrinkage beta estimates and their standard error (SE) obtained using the variance component analysis in MARK.

Parameter	Estimate	SE
Intercept	0.498	0.100
Age (Juv)	0.318	0.185
Age (1-2)	0.115	0.201
Age (2+)	0.264	0.200
Rainfall	-0.003	4E-4
Age (1-2) x Rainfall	0.003	6E-4
Age (2+) x Rainfall	0.004	6E-4

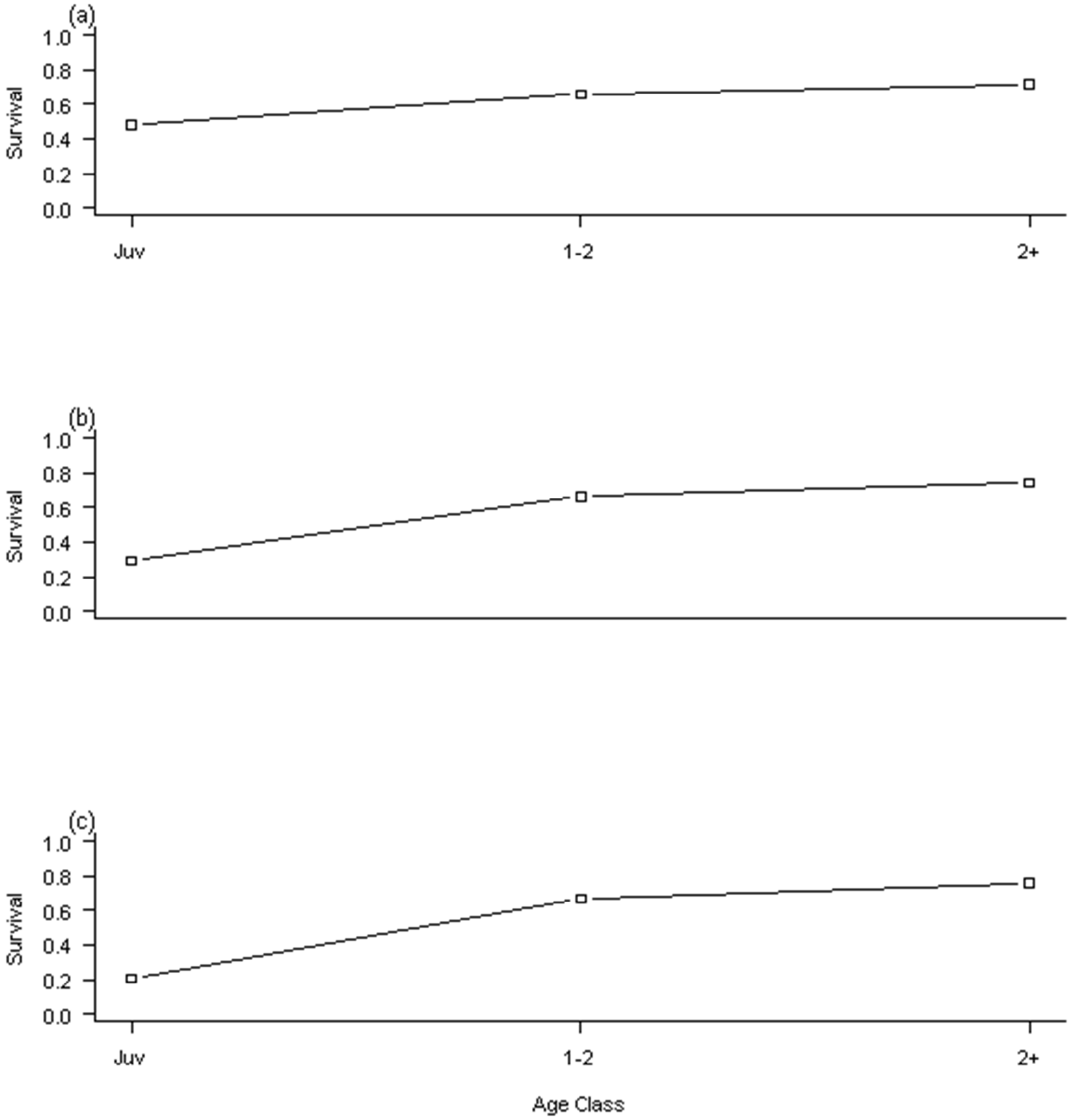

Figure 2.2. Hihi survival during the non-breeding season, when rainfall was (a) below average, (b) average, and (c) above average. Three age classes are shown, “Juv” representing fledglings, “1-2” representing adult in their first year, and “2+” representing older individuals.

Reproduction

The breeding record contained information for 212 female hihi and 562 breeding events (defined as a breeding season per female). On Tiri, females laid on average 1.6 clutches per breeding seasons (SD 0.6) but there were instances when they laid 3 or 4 clutches. Because there were only four events when females were recorded to have laid 4 clutches, those were pooled together with instances of 3 clutches. The average number of eggs laid across a breeding season per female was 6.5 (SD 2.6) and the average number of fledglings produced was 3 (SD 1.9).

There was evidence that the model with the lowest AICc was unequivocally the best fit as it had more than twice the weight of the next best model (Table 2.6 and 2.7). It was one where the overall breeding success, OBS, was a function of age, density, temperature and clutch number as additive effects. Surprisingly, there was no interaction between age or density and either weather covariates (H1 and H2) in the most parsimonious model. Graphical examination of the results showed that we were able to detect senescence in hihi female reproduction with older individuals having a significantly lower reproductive success than females in their prime (Figure 2.3). Moreover, first-time breeders also had a lower OBS than older, prime-aged females. Overall, an increase in the average temperature and an increase in density both led to a lower OBS. Although not shown on Figure 2.3, laying more than one clutch reduced females' overall breeding success. On average, laying two clutches during the breeding season reduced OBS by 15% and laying three (or four) clutches by 35%.

Table 2.6. Analysis of female hihi reproductive success (OBS). Shown is the set of models within 2 ΔAICc. The best model is in bold. ‘Age’ was a categorical variable separating first-time breeders (1), prime-age females (2-6) and older females (6+).

	Model	K	AICc	ΔAICc	Weight	Cumul. W	LL
1	**Age + Density + Temperature + Clutch Number**	**9**	**1166.070**	**0.000**	**0.370**	**0.370**	**573.890**
2	Age + Density + Rainfall + Temperature + Clutch Number	10	1167.870	1.790	0.150	0.520	573.750

‘Cumul. W’ was the cumulative sum of a model’s weight and the weight of all the models that have a lower AICc.

Table 2.7. Fixed effects estimates for the most parsimonious model of female hihi reproductive success (OBS; generalised linear mixed effect model).

Parameter	Estimate	SE
Intercept	-0.091	0.085
Age (2-6)	0.582	0.088
Age (6+)	-0.088	0.171
Density	-0.185	0.053
Temperature	-0.103	0.039
Clutch Number (2)	-0.671	0.892
Clutch Number (3)	-1.715	0.188

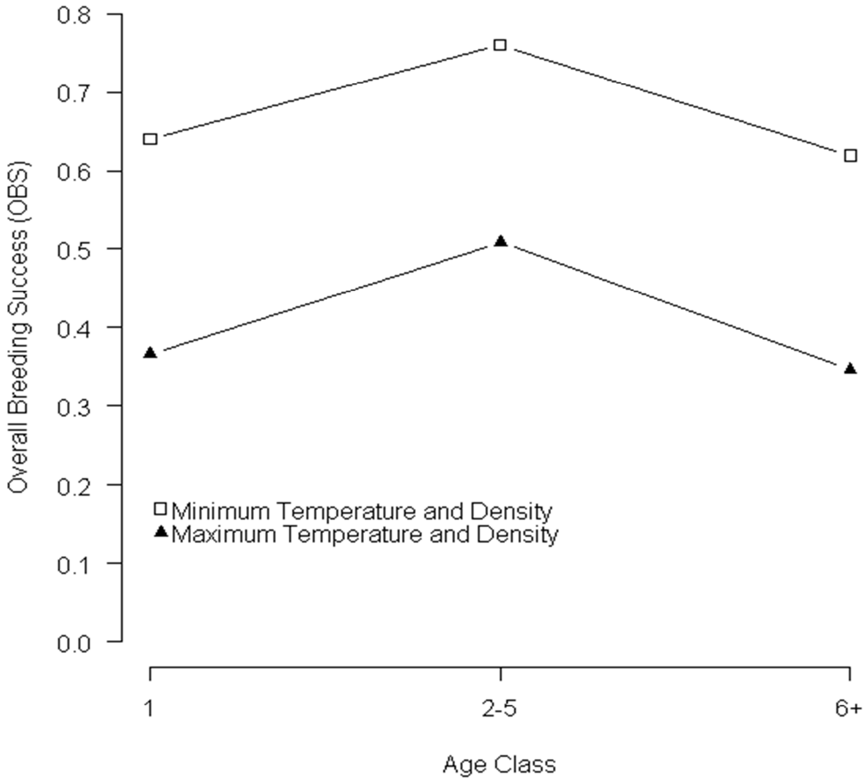

Figure 2.3. Overall breeding success of female hihi for three ages classes: “1” or first time breeders, “2-6” or prime-age individuals, “6+” or older/senescent individuals. Shown is OBS when temperature and density were set to the minimum and maximum values experienced by the hihi during the breeding seasons between 1995 and 2011.

DISCUSSION

This study explored how the interactions between intrinsic and climate factors impacted the dynamics of a threatened translocated bird population, the hihi on Tiritiri Matangi Island. Both survival and female reproductive success were found to be age-dependent.

While we detected differences between juveniles, first-year individuals and older ones for both survival and reproduction, senescence was only found in reproductive success. Significant findings were (1) the interactive effect of climatic harshness (i.e., high temperature) and density on hihi survival during the breeding season, (2) the interactive effect of climatic harshness (i.e., high rainfall) and age on hihi survival during the non-breeding season, (3) the negative impact of climatic harshness (i.e., high temperature) on reproductive success (OBS), and (4) finding that laying more clutches during the breeding season decreased female OBS.

By analysing hihi survival during the breeding and non-breeding seasons separately, we uncovered two significant interactions between intrinsic and climatic factors. First, during the breeding season, environmental harshness, in this case increased temperature, affected survival when density was high but not when it was low. This finding was anticipated because, at this time of year, both sexes are already under pressure due to males competing with each other to pair with a mate, but also attempting to force copulation with extra-pair females (Ewen et al., 2011). Therefore, an increase in density would have lead to an even greater pressure on both male and female hihi, especially if the adult sex-ratio was skewed as it was observed on Tiri (Ewen et al., 2011). This increased pressure meant that hihi had a lower ability to cope with environmental harshness, reflected in the drop in survival rates.

Second, during the non-breeding season, environmental harshness, in this case increased rainfall, significantly decreased juvenile survival. Because exposure to rainfall can facilitate body heat loss (Merola-Zwartjes, 1998), and the non-breeding season was naturally wet and cold, it made sense that increased rainfall reduced survival. The finding that only juveniles appeared to be affected could be explained by the fact that across many taxa, including birds, juveniles are naturally expected to have a lower survival than adults (Caughley, 1966; Sullivan, 1989; Oppel and Powell, 2010). Here, juvenile survival corresponded to the period between birds fledging and becoming adults. These were months of transition to independence, when hihi were the least experienced and during which they moulted into their adult plumage. These factors could all have contributed to making juveniles more vulnerable to environmental harshness than adults. However, unless the gap in knowledge regarding hihi behaviour during the non-breeding season is filled, there are still uncertainties as to why adults seemed unaffected by environmental harshness.

As far as the reproduction analysis was concerned, we also found that environmental harshness (i.e., high temperature) and increased density, decreased overall reproductive success (OBS). However there was no significant interaction between the two variables. There were two potential mechanisms through which increased temperature could lower OBS. First, because OBS represented the average survival of eggs to fledglings, which itself was influenced by the survival of eggs to nestlings and nestling to fledglings, temperature may have directly affected nestlings' survival. This was corroborated by Low and Pärt (2009) who showed that nestling survival was negatively correlated to temperature. Alternatively environmental harshness could have impacted the mothers' ability to successfully 'convert' eggs into fledglings. Indeed, studies suggest that long-lived species, like the hihi, tend to adopt risk-sensitive reproductive strategies where individuals divert resources toward survival to the detriment of reproductive output when conditions are harsh (Linden and Møller, 1989; Ricklefs, 2000). During the breeding season, the impact of increased temperature on survival was marginal when density was low, but significant when density was high which could suggest that female hihi indeed may be risk-sensitive when it comes to reproduction, at least when other additional pressure such as density are present.

Finally, female OBS was also significantly affected by the number of clutches laid during the breeding season. Laying one clutch led to higher OBS than two or three (or four) clutches. This was slightly counter-intuitive as it could be expected that a greater effort (i.e., three or four clutches) would yield a greater return (i.e., higher OBS). One explanation was that females had a limited amount of resources to invest into reproduction across one breeding season. When more than one clutch were laid, each clutch was more likely to receive too little investment, leading females to overall raise fewer fledglings. Alternatively, females who laid more than one clutch may often have only done so when the first one had failed, thus reflecting the poor ability of some female hihi to raise young.

The values of temperature and precipitation used to illustrate hihi survival and OBS were within the current climatic range experienced by the hihi. Our results therefore demonstrated how current climate variations impacted the population on Tiri, allowing us to understand their population dynamics in detail. However, they also hinted at the impact predicted changes could have on hihi persistence. Indeed, the average temperature is expected to rise by *c.* 2°C in this region by 2100 (IPCC 2007). Because this hihi population is currently growing (Ewen et al., 2011), and we found that density and temperature negatively affected both adult survival during the breeding season and reproduction, those two demographic parameters can be expected to decrease in the coming decades. However, precipitations are predicted to decrease by as much as 20% by 2100, especially during the non-breeding season (IPCC 2007) and juvenile survival could therefore benefit from future predicted change.

There are two main caveats to this analysis. First, to model the impact of climate on hihi dynamics, we used two simple measures: average temperature and total rainfall across seasons. Other studies have sometimes used larger numbers and/or more complex climate variables in their analyses of population dynamics (Newton et al., 1993; Peach et al., 1994;

Franklin et al., 2000). While it can be beneficial to increase the scope of the analysis, there are two issues associated with this method. First, the number of models tested increases exponentially as more covariates are added to the list and it can lead to testing any and all possible climate variables. Second, results of complex models or models containing less obvious climate variables may be harder to interpret, thus decreasing the understanding of the process behind the results.

Second, the modelling approach used was correlative. This meant simplifying complex interactions (i.e., pathway between climate and population dynamics), assuming linear relationships between various factors and hihi survival or breeding success. While models are meant to be simpler representations of reality, oversimplification may yield meaningless results. However, there was sufficient general knowledge regarding the impact of temperature and rainfall on bird survival and breeding success to be confident our results would be biologically meaningful. In addition, correlative approaches are also known to have two major problems: spatial autocorrelation and temporal autocorrelation (Araújo et al., 2005). The former does not apply here because Tiri was treated as one geographic unit as opposed to a set of pixels for which there are individual measurements. There was little point in dividing Tiri in smaller units as it is a small area in which hihi travel freely and climate data were not available at a smaller scale than the one used. The latter, however may be a problem for the results presented. It relates to the fact that observations in a time-series (e.g., temperature and precipitation) can be non-random because of non-independence between observations close in time (Araújo et al., 2005). As a consequence, the models of survival and reproduction may have a lower predictive power than expected because they did not account for potential temporal autocorrelation.

Our findings, nevertheless, highlighted that small variations in average temperature and total rainfall, which are simple climate variables, can have large impacts on population dynamics. Therefore, even if the realised impact of climate change corresponds to the most optimistic IPCC scenario (IPCC 2007), we could expect species such as the hihi to show altered population dynamics. Importantly, we also found evidence that changes in environmental conditions are likely to have an age-specific and/or density-related impact. One of the consequence of the interaction between intrinsic and climate factors is that species may be precipitated towards extinction faster than expected if climate change impacted all individuals in the population equally or if its effect was not interacting with intrinsic factors.

While our work focused on the hihi, our findings have direct implications for biodiversity conservation. They suggested that (1) conservation efforts could sometimes be better directed at age classes that are most sensitive to climate rather than evenly distributed across all demographics, (2) accurately forecasting the impact of climate on species will requires knowledge of species' intrinsic characteristics, and (3) optimal conservation decision-making in the face of climate change needs to explicitly take into account the possible interactions between climate and other biotic variables.

CHAPTER 3

Does supplemental feeding affect the viability of translocated populations? The example of the hihi

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Co-author contributions: I was responsible for partly-designing and performing both statistical and quantitative modelling, as well as the writing of this chapter. John G. Ewen and Doug P. Armstrong provided advice relating hihi life-history traits and how they should be modelled. Nathalie Pettorelli, Doug P. Armstrong and Tim Coulson provided advice on the design and performing of statistical and quantitative modelling. Leila K. Walker collected the data used in the capture-mark-recapture analysis and Lynn Adams provided access to it. Tim M. Blackburn provided editorial advice. All co-authors read and commented on versions of this chapter.

ABSTRACT

Translocations are commonly-used conservation actions that aim at establishing new, self-sustaining populations of threatened species. However, many translocated populations are not self-sustaining but managed through supplemental feeding from the onset. Often the decision to start managing is *ad hoc*, but managers will eventually have to make decisions for the future, e.g., stop intervening, continue as it is or change the quantity of food provided. Such a decision requires managers to quantify the importance of supplemental feeding in determining the performance and population dynamics of translocated populations, information that is rarely available in the published literature. Using the hihi as a case study, we examined the importance of supplemental feeding for the viability of a translocated population in New Zealand. We found that supplemental feeding positively affected the survival and abundance of translocated adult hihi but also found evidence of negative density-dependence on recruitment. We present two stochastic population models, which project the hihi population under different management scenarios, quantitatively assessing the impact supplemental feeding has had on the population. Our results illustrate how important long-term targeted monitoring is for robust decision-making about adaptive management.

INTRODUCTION

The ultimate goal of conservation translocations is to establish self-sustaining populations to increase the overall chance of survival of a species (Bright and Morris, 1994; Guerrant, 1996). In practice, not all translocated populations can maintain themselves (i.e., are self-sustaining) without management actions such as predator control or supplemental feeding (Robertson et al., 2006; Soorae, 2012). For example, it is quite common in bird translocations to provide translocated individuals with supplemental food during, and/or after translocation e.g., red-necked ostrich (*Struthio camelus camelus*) in Saudi Arabia, Southern Ground-hornbill (*Bucorvus leadbeateri*) in South Africa, Hawai'i creeper (*Oreomystis mana*) in Hawaii and red kite (*Milvus milvus*) in Ireland and England (Soorae 2008). If the population increases while supplemental food is provided, because management is costly and funding is limited, managers will eventually have to choose between four options: continue as is, increase the amount provided, decrease the amount or stop providing any. There is a likely trade-off as, on one hand, managers risk spending money on a management action that is not necessary but on the other hand, minimising costs could end up negatively impacting survival and/or reproductive rates.

In-situ food experiments (on-off or temporal and/or spatial variation in quantity) can help assess the consequences of altering management actions (Armstrong and Perrott, 2000). However, managers rarely take this risk as translocated populations are generally small (Shaffer, 1981) and such experiments could result in the loss of precious translocated individuals. Alternatively, models can be used to study past and future variation in management regimes and assess the importance of such variation on a species' survival and/or reproductive rates. The goal of this type of modelling exercise is to inform and update management decisions as an iterative process, i.e., perform adaptive management (Holling, 1978; Walters and Hilborn, 1978; Walters, 1986). Ideally, adaptive management requires an *a priori* development of possible management options, which are evaluated and refined following targeted monitoring (Ewen and Armstrong, 2007). In many cases, however, new management options arise well into a project. If relevant monitoring has been on-going, then population modelling can inform the likely response of populations based on past data, and new management can be incorporated into the adaptive management framework (Williams, 2011). Long-term monitoring datasets are rare, but one of the species for which relevant information is available is the New Zealand endemic hihi (or stitchbird *Notiomystis cincta*).

The hihi is a cavity-nesting passerine bird (Castro et al., 2003) native to the North Island of New Zealand, and classified as vulnerable on the IUCN Red List (BirdLife International 2007). Following European colonization of New Zealand, this species was driven to quasi-extinction by introduced mammal predators (mainly rats *Rattus rattus*), habitat loss and diseases (Rasch et al., 1996). Hihi declined to one remnant population on Little Barrier (Hauturu) Island (LBI; Figure 3.1). They have been the subjects of several successful and unsuccessful translocations in the past few decades. Today, they persist in six wild populations (LBI and five translocated populations; Figure 3.1). As hihi are mainly nectar-feeders, they rely on native vegetation for food, which is often limiting in their translocated habitat, and every translocated population is managed by provision of various amounts of supplemental food in the form of sugar water. Originally, the decision was made to provide supplemental food to the translocated hihi because of (1) a difference in vegetation on the new sites compared to LBI, i.e., less rich in nectar and fruits (Armstrong, Castro and Griffith 2007) and (2) food competition with other species such as bellbirds *Anthornis melanura* and tui *Prosthemadera novaeseelandiae* (Angehr, 1984) for natural and supplemental food sources, which are limited in those modified environments.

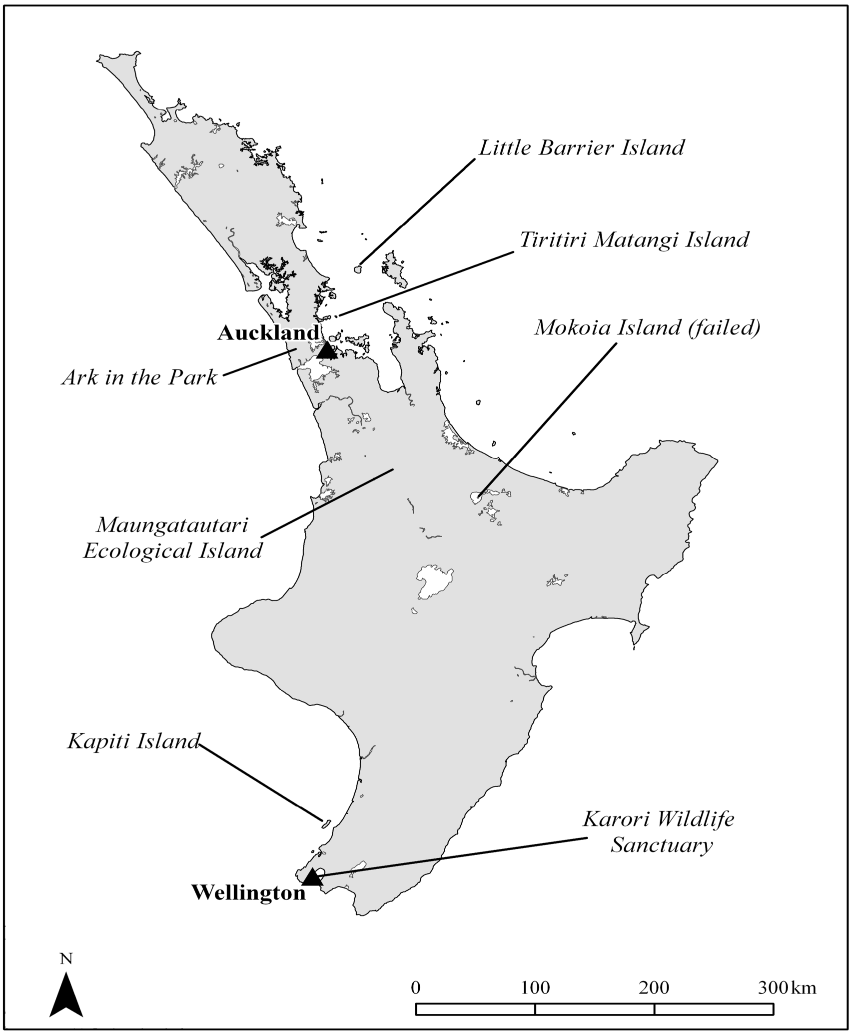

Figure 3.1. Populations of hihi on North Island, New Zealand. All the populations shown are currently extant, except for the one on Mokoia Island.

The effect of supplemental feeding on translocated hihi has been studied for two island populations in the past: the extinct population of Mokoia Island and the extant population on Tiritiri Matangi Island. On Mokoia, 40 birds were released in 1994 and up until 2001 they were the subject of in-situ feeding experiments and adaptive management (Armstrong and Perrott 2000; Castro et al., 2003; Armstrong et al., 2007). Supplemental feeding regimes on Mokoia Island varied between no supplemental food provided, supplemental food provided during the breeding season only, and supplemental food provided all year round (Castro et al., 2003). When there was no supplemental food available to the population, the number of fledglings decreased, which led to the conclusion that food was necessary, at least during the breeding season. However, juvenile survival did not appear to be highly improved by supplemental feeding and adult female survival showed no response at all (Armstrong et al., 2007). From 2000, supplemental food was provided all year round, but the population continued to decrease. In 2002, the 12 remaining Mokoia hihi were moved to another translocated population (Armstrong et al., 2007) in an attempt to rescue them. Conclusions from Mokoia were thus ambiguous, and although changes in the amount of supplemental food may have contributed to the ultimate fate of the population, other unidentified factors were likely to have been limiting population viability (Armstrong et al., 2007).

On Tiritiri Matangi Island, 38 hihi were released in 1995 (Armstrong and Ewen, 2001; Armstrong et al., 2002). However, due to a high rate of post-release mortality, with only 12 males and 4 females surviving, 13 birds were added to supplement the population in 1996 (Armstrong et al., 2002). An on-off food experiment in 1996 showed that, unlike hihi on Mokoia, those on Tiritiri Matangi were more dependent on supplemental food, as they lost a significant amount of weight during periods without food, and adult and juvenile survival rates were lower (Armstrong and Ewen 2001). Since this experiment, food has been provided on the island *ad libitum*, i.e. the amount increases as the population increases.

While results from Tiritiri Matangi highlighted the importance of supplemental feeding for the survival of translocated populations of hihi, conclusions for Mokoia Island did not entirely support that hypothesis. Yet, supplemental feeding is still carried out for every population of translocated hihi, and much time and effort goes into such management. Here, the dynamics of another reintroduced population of hihi, on Kapiti Island, is presented (Figure 3.1). This population was the ideal candidate for this study as the amount of management received by the population over the years has been variable (Figure 3.2). In the first 10 years or so after translocation, a very limited amount of food was provided during the breeding season, except in 1999 when there was no food given at all. From 2000, a new strategy was implemented: food was given all year round and the amount, being provided *ad libitum,* has grown from 107 litres in 2000 to 3,648 litres in 2009.

The hihi population on Kapiti has been monitored since 1993, which allowed us to use statistical models to assess the importance of supplemental food on the population, specifically on three demographic parameters: adult survival, recruitment (i.e., the average number of recruits per breeding adults the year before) and adult abundance. We hypothesised that:

H1: If supplemental feeding benefited hihi on Kapiti, survival, recruitment and abundance should be higher when supplemental food was *ad libitum* (Armstrong et al., 2002; Armstrong et al., 2007).

H2: If supplemental feeding benefited hihi on Kapiti, abundance should also show an increasing trend post-2000.

H3: Previous studies of hihi have shown no difference in survival between males and females (Armstrong et al., 2002; Ewen et al, 2011) so there should be similar patterns for the survival of the Kapiti population.

H4: Ewen et al. (2011) found that the average number of recruits and adult survival on Tiritiri Matangi also tended to be negatively affected by increasing female density so we should find similar results on Kapiti Island.

Two population models were built to project the population under the little-to-no feeding regime and under the *ad libitum* feeding management regime.

MATERIAL AND METHODS

Study site and data collection

The current hihi population on Kapiti Island was established by two successful translocation events in 1991 and 1992 (Figure 3.2; Taylor et al, 2005). There had been three previous translocation attempts (1983, 1985 and 1990 with a total of 74 individuals moved; Castro et al., 1994) but only four individual hihi were surviving on Kapiti in 1991. In 1996, rats were eradicated from the island (Sinclair et al., 2005) and, in 2002, 12 additional hihi were also translocated from Mokoia to Kapiti. Hihi do not disperse to or from Kapiti Island and this is essentially an isolated population. Since the establishment of hihi on the island, the birds have been supplemental fed under different regimes (Figure 3.2). Two periods are distinguishable; pre-2000 when there was little-to-no food given and post-2000 when supplemental feeding was *ad libitum.*

Translocated hihi are individually monitored. Surveys were conducted once a year from 1993 to 2001 (in October) and twice a year between 2002 and 2010 (in March and in October; Figure 3.2). The total number of capture occasions was 27. Hihi breed between September and February and thus, March surveys correspond to the end of the breeding season while October surveys correspond to the beginning of the breeding season. All birds that are "captured" at the October survey are either young adults that have just been recruited into the population and are breeding for the first time, or older birds breeding for another year. There are two main types of surveys: observation surveys (feeder watches and walked transects near feeders), and direct capture (traps and mist-nets at feeder sites).

Sighting or physical capture of banded hihi are recorded as a “recapture event” on the individual sighting database. Un-banded hihi that are caught, are ringed, and their sighting recorded as first capture (i.e., they are added to the database). The intensity of monitoring effort of Kapiti Island is such that individuals caught for the first time are almost always fledglings (when caught in March) or adults starting their first breeding season (when caught in October). Older adults are easily distinguishable from younger birds as fledglings (and young adults) have a distinctive plumage. Little information is available on clutch size or numbers of nestlings and fledglings on the island.

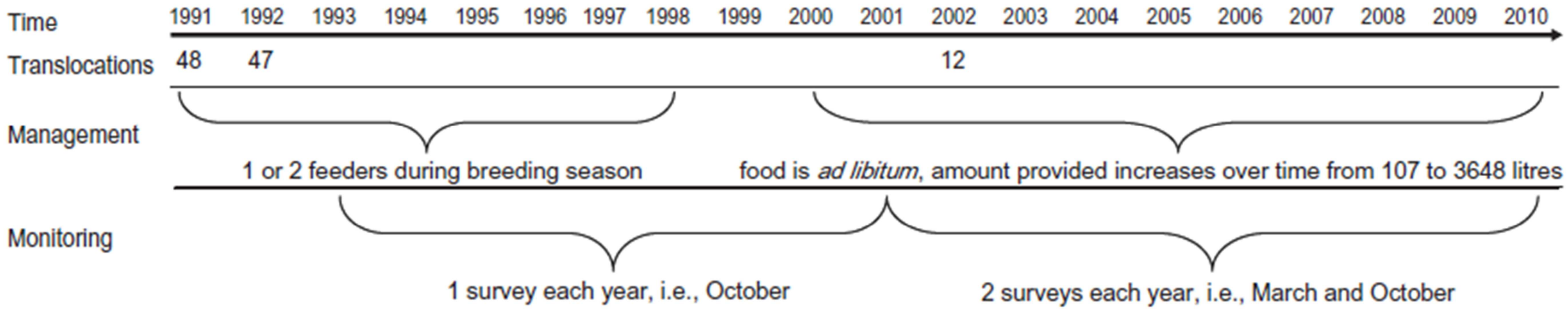

Figure 3.2. Hihi timeline on Kapiti Island. Translocation events in 1991 and 1992 were to establish the population; the event in 2002 was to rescue 12 birds from the island of Mokoia.

Estimating demographic parameters

We used the software MARK (Cooch and White, 2009) to estimate (1) adult abundance and recruitment with the POPAN Jolly-Seber parameterisation and (2) adult survival and recapture probabilities using Cormack-Jolly-Seber models (CJS; Cormack 1964; Jolly 1965; Seber 1965). We aimed to generate abundance estimates (with POPAN) that could be used as covariates of survival (in CJS). Both the POPAN formulation and CJS models were used to minimise circularity problems and obtain abundance estimates with standard errors.

As monitoring effort on the island of Kapiti has varied over time (Figure 3.2), time-intervals between sampling occasions from 2002 onward were uneven. Therefore, to analyse the data, there were two options: (1) implement uneven time-intervals in MARK, or (2) only use data from October surveys which have been consistent since the beginning of monitoring. Based on simple observation of the data structure and estimating data over-dispersion for both options in MARK (tests implemented in RELEASE run in MARK), we found that the best solution was to focus solely on October surveys.

All models were built using RMark as an interface (White and Burnham 1999; Cooch and White 2009), i.e., MARK was run from R (R Development Core Team, 2011). The best models within the POPAN and CJS candidate sets were selected using the corrected Akaike Information Criterion for small datasets (AICc; Burnham and Anderson 2002; Cooch and White 2009). For the best CJS model, which yielded survival and recapture estimates, the variance components procedure in MARK was used to separate sampling variance from process variance. Therefore, the estimates of survival presented (and used in further analyses) include process variance only and correspond to the ‘shrinkages’ estimates known as S-tilde (White et al., 2001).

Abundance and Recruitment: POPAN formulation

Because the goal was to estimate abundance and recruitment, as opposed to survival and recapture, a restricted number of models were run. Survival and probability of capture were modelled as either time-dependent or as time- and sex-dependent (H1, H2). The 'probability of entrance' parameter, or *pent*, was constrained as being time- and sex-dependent to estimate sex-specific recruitment. Because of parameter identifiability issues (Cooch and White 2009), we were only able to estimate abundance between 1994 and 2009 and recruitment, defined as the number of new individuals (i.e., detected for the first time) at time t divided by total number of individuals in the population at time $t-1$, between 1995 and 2009.

Survival and Recapture: CJS models

CJS models were used to estimate adult survival, φ, and recapture probabilities, p. According to (H3), there should be no difference in survival between the sexes, so we allowed for models with and without sex-dependent survival. In addition, survival was modelled as being time-dependent as, according to (H1), survival should have increased when management regime changed. However, hihi survival has been shown to be constant over time in another population under an *ad libitum* feeding regime (Armstrong et al., 2002; Ewen et al., 2011) so it was also constrained to be time-independent over the two management periods by using a 'treatment' covariate set to 0 before 2000 and 1 after 2000. Finally, we also looked for density-dependence on survival by using the abundance estimates generated with the POPAN formulation, as covariates. Recapture probability was modelled as being fully time-dependent but independent of sex, as sex was not found to influence re-sighting probabilities for two other populations of hihi (Armstrong et al., 2001; Ewen et al., 2011).

Looking for density-dependence

To investigate if there were density-dependent effects on the hihi population of Kapiti, we used the test for statistically significant density-dependence developed by Dennis and Taper (1994) on abundance estimates during the two feeding periods, i.e., pre 2000 and post 2000. It is a parametric bootstrapping likelihood ratio test that tests for $b = 0$ (the null hypothesis, i.e., density-independence) against $b < 0$ (alternative hypothesis, i.e., density-dependence). If the null hypothesis is rejected, we can conclude that there is evidence for density-dependence in the data (Dennis and Taper, 1994; Meyer et al., 1998). In addition, we plotted the population growth rate $r_t = log(N_t + 1/N_t)$ (where N_t and N_{t+1} are population abundance at time t and $t + 1$), against the log of abundance and visually assessed the island carrying capacity under the two management regimes.

We found evidence of negative density-dependence of the abundance during the *ad libitum* feeding period and thus looked for density-dependence in both recruitment and survival (H4). Density-dependence on survival was investigated in MARK (see previous section). To assess effects of density-dependence on recruitment, we plotted male recruitment (defined as average number of new males in the population at time t per breeding adult at time $t - 1$) and female recruitment (average number of new females in the population at time t per breeding adult at time $t - 1$) as a function of total abundance and tested for significant linear relationships using linear regression.

Population models

Stochastic population models were built to model hihi abundance under two different management scenarios. We looked at what would have happened if *ad libitum* management had never started and the population had been left to grow with very little or no supplemental feeding (hereafter scenario 1) and what would be the future of the population under *ad libitum* feeding (hereafter scenario 2). The aim was to quantify the long-term impact of both feeding regimes, to demonstrate the importance of supplemental feeding on the population on Kapiti but also, potentially, for other translocated hihi populations.

The two models were discrete stochastic population models as only adult survival was known (based on current data collection protocol) and a matrix model requires at least two classes of individuals (Caswell, 2001). Moreover, an individual-based model (Grimm and Railsback, 2005) would have been too complex for the amount of data available. They are described below.

Scenario 1

Between 1993 and 1999, there was little-to-no supplemental food given to the hihi on Kapiti Island. Thus, to answer the question of the fate of the population if managers had not started providing *ad libitum* feeding, we modelled the population as if the conditions between 1993 and 1999 remained true past 2000. As we found no significant effect of density on either survival or recruitment (see results), to investigate scenario 1, we built a model in which annual population size was a function of (1) population size at the previous time-step and (2) the annual population growth rate λ:

$$N_{t+1} = \lambda \times N_t$$

where $\lambda = e^{r_{Nt}}$.

N_t and N_{t+1} were population size at time t and $t + 1$.To model the intrinsic growth rate r_{Nt}, we regressed the Kapiti population growth rate r_t against log(abundance) for the 1993-1999 period and used the resulting linear model ($y = 4.5 - 1.442x$) to calculate r_{Nt} as function of log(Nt) at each time-step. The overall model was made stochastic by adding an error term ε to the estimation of r_{Nt}. Each time r_{Nt} was estimated, a value for ε was sampled on a normal distribution of mean=0 and standard deviation equal to the residual s.d. (0.46) of the linear model mentioned above.

Scenario 2

During the *ad libitum* feeding period, 2000-2009, we found a significant and sex-specific effect of density on recruitment but not on survival (see results). Thus, to model the future of the population under *ad libitum* feeding, we built a model with explicit density-dependent sex-specific recruitment. Annual population size was a function of (1) population size at the previous time-step, (2) the average adult survival during the period of *ad libitum* feeding and (3) density-dependent recruitment:

$$N_{t+1} = N_t \times S_t + R_{N_t}$$

where N_t and N_{t+1} were population size at time t and $t + 1$; survival S_t was the annual adult survival. To make S_t stochastic between years but constrained between 0 and 1, the mean S-tilde and its standard deviation for the 2000-2009 period were logit-transformed (μ_{LT}=logit-transformed(mean) and σ^2_{LT}=logit-transformed(s.d.)). At each time-step, an estimate of survival was drawn from a normal distribution logit(S_t) ~ N(μ_{LT}, σ^2_{LT}) and back-transformed such that $S_t = e^{logit(S_t)}/(1 + e^{logit(S_t)})$. The number of new individuals in the population R_{N_t}, was density-dependent and calculated as follow:

$$R_{N_t} = N_t \times (R_{N_t(m)} + R_{N_t(f)})$$

$R_{N_t(m)}$ and $R_{N_t(f)}$ were the number of male and female recruits per adult (N_t) at time t. At each time step, the value of $R_{N_t(m)}$ was calculated using the linear model of male recruitment as a function of total abundance and the value for $R_{N_t(f)}$ was calculated using the linear model of female recruitment as a function of total abundance (for the post-2000 period). In order to make the recruitment stochastic, error terms, ε_m and ε_f, were added to both sex-specific linear models. At each time-step a value for $\varepsilon_m$was sampled on a normal distribution of mean=0 and standard deviation corresponding to the residual s.d. of the linear model of male recruitment as a function of abundance. A value for $\varepsilon_f$was sampled on a normal distribution of mean=0 and standard deviation corresponding the residual s.d. of the linear model of female recruitment as a function of abundance. Because of the nature of the data (i.e., breeding is not monitored on Kapiti and thus there is no information available on reproduction at the individual level), we were not able to distinguish between demographic stochasticity, environmental stochasticity and parameter uncertainty in our measure of recruitment stochasticity (ε_m and ε_f). Therefore, the two error terms represent a mix of all three.

For both scenarios, simulations were run in R on a twenty-year timeframe and for 100,000 iterations. For each run of scenario 1, the initial population size was the observed population size in 1993, i.e., 20 individuals. For scenario 2, it was the population size in 2000, i.e., 10 individuals. We calculated the average r-squared value between simulated abundance under each scenario and estimated true abundance for 1993-1999 and 2000-

2009 respectively and the probability of extinction of the population over 100,000 simulation iterations. In addition, we also performed a standard deviate test, which is one method for validating stochastic population models (McCarthy and Broome, 2000). It involves calculating a "standard deviate" value for every simulation iteration, creating a standard deviate distribution. Standard deviates are calculated by subtracting the mean observed population size to the mean modelled population size and then dividing by the standard deviation of modelled population size (Sokal and Rohlf, 2001). If the model predicts the observed population size and variance accurately, the mean standard deviate and the variance of standard deviates should not be significantly different from 0 and 1 respectively (McCarthy and Broome 2000; Sokal and Rohlf 2001). Two tests were performed to assess whether the mean and variance of the standard deviates were different from the expected values, a *t*-test and χ^2-test respectively (McCarthy and Broome 2000; Sokal and Rohlf 2001).

RESULTS

Estimating demographic parameters

By only using the information from October surveys (18 out of the 27 capture events), there was no overdispersion in the data (χ^2=44.05, df=51, p>0.1). The total number of individuals captured was n=393.

Abundance and Recruitment: POPAN formulation

The POPAN formulation yielded one unequivocal best model from the restricted list tested (i.e., ΔAICc between the first and second model was >2; Burnham and Anderson 2002). In this best model survival and capture were both time-dependent (Appendix 3A). Abundance and recruitment estimates were extracted from the derived parameters list. The estimates of abundance (Figure 3.3 (a)), showed a clear distinction before and after 2000. During the period when there was little-to-no supplemental food on the island (1993-1999) abundance remained low and stable. From 2000, as the amount of supplemental food started increasing, abundance steadily increased as well. Those results were in accordance with H1 and H2.

Results for recruitment, however, did not entirely follow the expected pattern (H1). Recruitment remained quite low before *ad libitum* feeding and even dropped to 0 in 2000 following the entire removal of supplemental food in 1999. After the switch in management in 2000, recruitment started increasing rapidly but since 2005 it has been steadily decreasing to the point of reaching pre-2000 levels (Figure 3.3 (b)). This pattern is characteristic of a density-dependence response in the population, showing that hihi on Kapiti Island reached their habitat carrying capacity *c.* 2005.

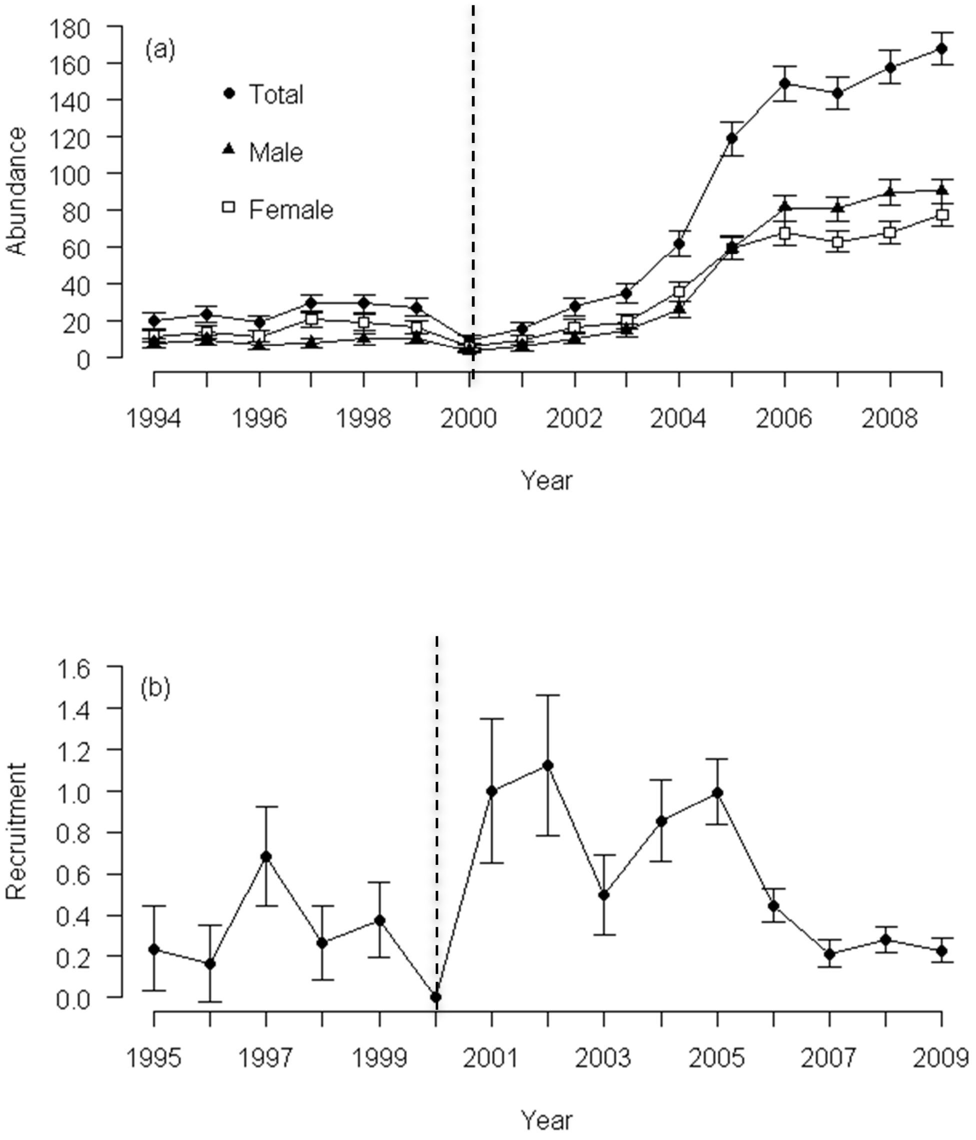

Figure 3.3. Estimates of (a) abundance (total, female and male) and (b) recruitment. Abundance and recruitment estimates were obtained through the use of the POPAN Jolly-Seber formulation in MARK. The dashed lines represent the start of *ad libitum* feeding. Error bars represent standard errors.

Survival and Recapture: CJS models

The ΔAICc between the first and second CJS models was >2. The model with the lowest AICc, i.e., with time-dependent survival and recapture, was thus chosen as the unequivocal best model (Burnham and Anderson 2002; Table 3.1; H3).

While survival varies between years (Figure 3.4 (a)), a pattern can still be distinguished. During the first management regime period (1993-1999), survival was quite unpredictable, being 0.65 one year and close to 1 the next, but it ended up decreasing to its lowest value ever recorded in 2000, *c.* 0.45. When *ad libitum* feeding started, however, survival steadily increased for the first few years and remained high. Overall, survival was higher and more stable when food was *ad libitum,* which was consistent with (H1). Interestingly, density-dependent models were not among the best suggesting that adult survival was not affected by density. The 'treatment' covariate, which constrained the survival to be constant within the two management regimes but different between them, was also not a good predictor of survival on its own (Table 3.1). Nonetheless, the second best model was one where survival was time-dependent and included 'treatment' as a covariate. However, this model had little support compared to the one with the lowest AICc where survival was time-dependent only.

Recapture rates on Kapiti Island were very high (Figure 3.4 (b)). Estimates were always above 0.9 except in 2008 highlighting the intensity of the monitoring. However, MARK encountered estimability problems for some years, as demonstrated by the 1 ± 0 recapture estimates.

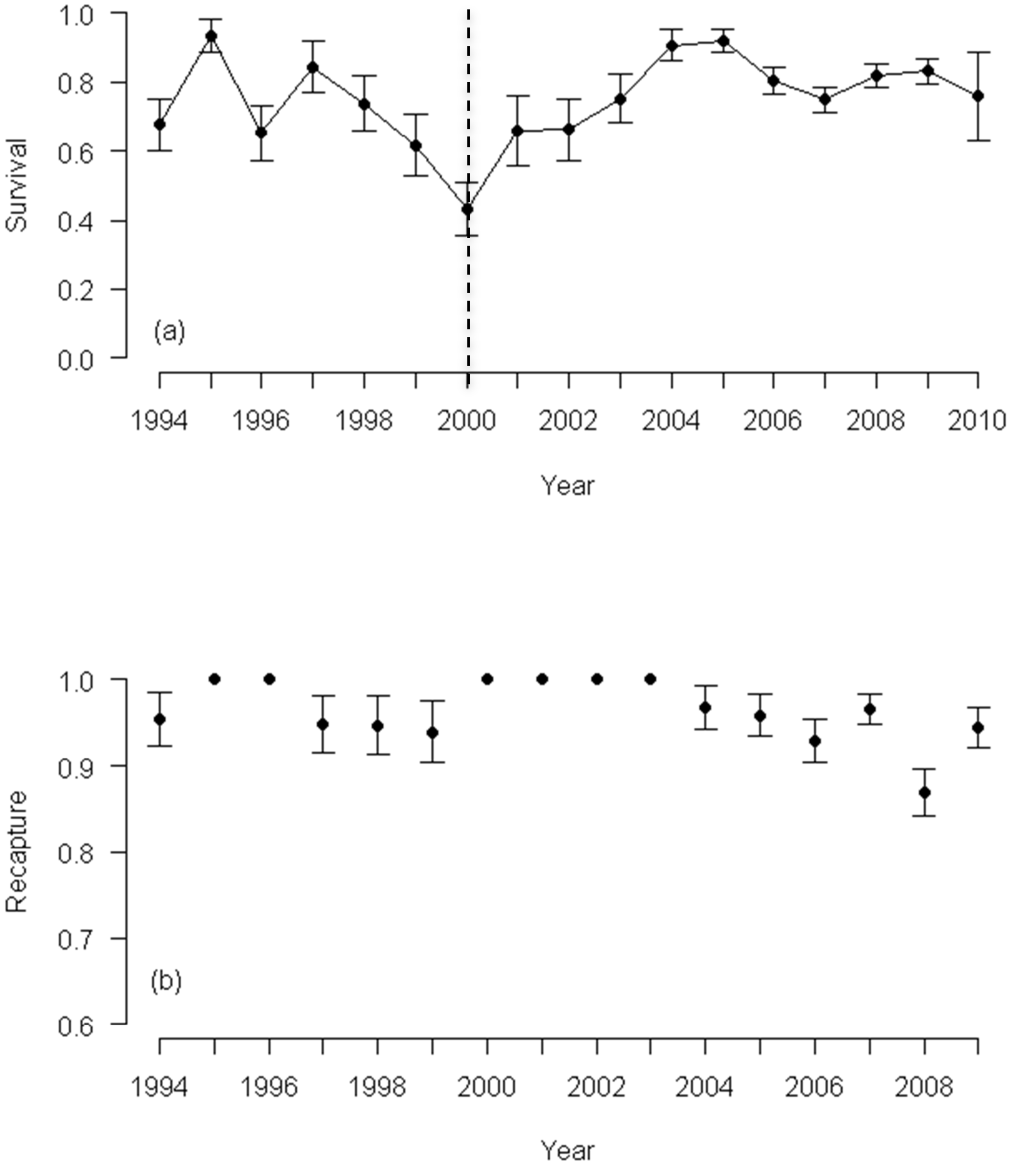

Figure 3.4. Estimates of (a) adult survival (S-tilde) and (b) recapture probability. The dashed line in Figure 3.4(a) represents the start of *ad libitum* feeding. Error bars represent standard errors.

Table 3.1. Results of the CJS analysis in MARK (implemented in RMark). For every model, φ, or survival, is a measure of adult survival and p represents recapture probability. Models can be time-dependent ('time'), sex-dependent ('sex'), density-dependent ('density') and/or treatment-dependent ('treatment', coded as '0' before 2000 and '1' after 2000). The models are organised from the most likely (in bold) to least likely.

Model	Num. Par	AICc	ΔAICc	Weight	Deviance
φ(time) p(time)	**32**	**1400.765**	**0**	**0.6990**	**346.1828**
φ(time + treatment) p(time)	33	1402.904	2.139	0.2399	344.6445
φ(sex + time) p(time)	35	1405.659	4.894	0.0605	346.1828
φ(treatment) p(time)	19	1416.381	15.616	0.0003	389.2169
φ(treatment + density) p(time)	20	1417.568	16.803	0.0002	388.3202
φ(treatment + sex) p(time)	20	1418.114	17.349	0.0001	388.8663
φ(treatment + sex + density) p(time)	21	1419.116	18.351	0.0001	387.781
φ(density) p(time)	19	1421.993	21.228	0.0000	394.8283
φ(time * treatment) p(time)	42	1422.365	21.6	0.0000	394.5401
φ(sex + density) p(time)	20	1423.788	23.023	0.0000	346.1828

Looking for density-dependence

There was no density-dependence in the population before 2000 ($p=0.44$). However, we found evidence of negative density-dependence during the *ad libitum* feeding period ($p<0.05$) (Appendix 3B). In addition, we also found that following the change in feeding regime, the carrying capacity of the island increased. Before 2000, it was at *c.* 30 individuals but during the post-2000 period, the carrying capacity went through a ten-fold increase (Appendix 3C).

While the analysis in MARK showed no evidence of density-dependence on survival, there was evidence of negative density-dependent effects on male and female recruitment during *ad libitum* feeding. In accordance with (H4), we found a significant negative relationship between abundance and both female recruitment and male recruitment (Figure 3.5). For males, the linear relationship was $y=0.4363 - 0.00215x$ ($r^2=0.61$, $F(1,6)=9.176$, $p<0.05$, residual s.d.=0.1093), and for females, it was $y=0.5038 - 0.0030x$ ($r^2=0.62$, $F(1,6)=9.609$, $p<0.05$, residual s.d.=0.1472).

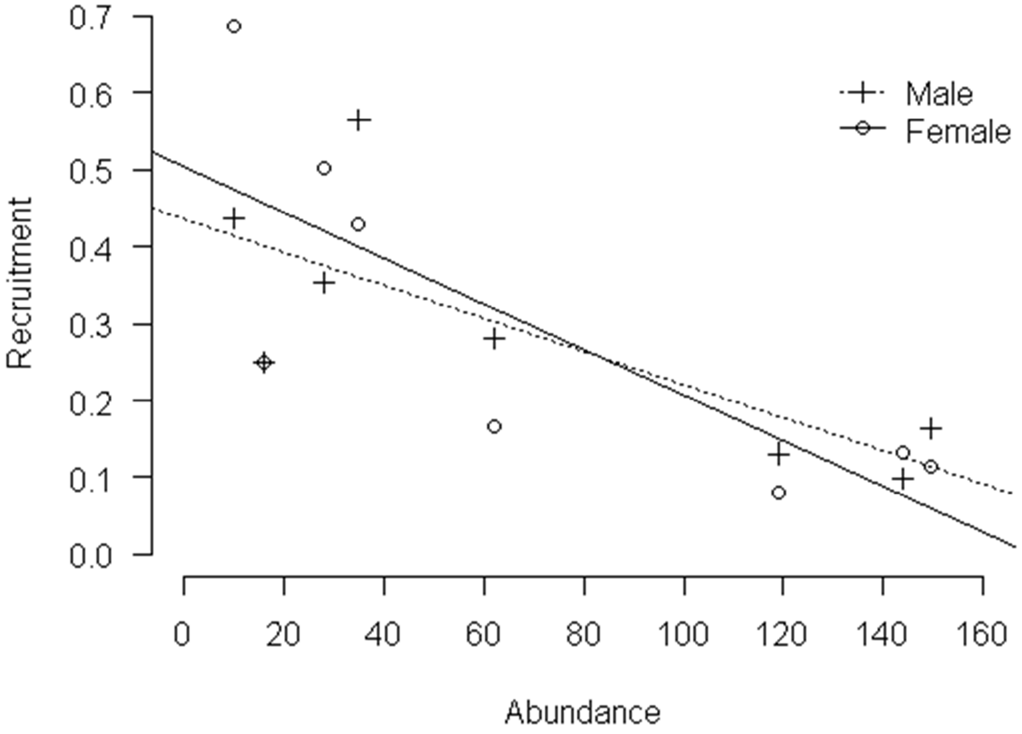

Figure 3.5. Density-dependence on sex-specific recruitment. Shown are the significant linear relationships between abundance and both female (circles) and male (crosses) recruitment. Female recruitment is more strongly affected by density-dependence than male recruitment.

Population models

Scenario 1

The simulation model for scenario 1 predicted that if *ad libitum* feeding had never started the population would have stabilised at ~22 individuals for the time-frame considered (Figure 3.6(a)). In addition, it yielded a probability of extinction over 20 years of 2.5%. The r-squared between observed abundance between 1993 and 1999 and modelled abundance was only 0.19 (s.d.=0.15), showing high variability between each model output. Nonetheless, the observed abundances remained well within the 95% confidence interval of the simulations

The standard deviate test for the model of scenario 1 showed that it under-predicted population size (the mean of the standard deviates was significantly different from, and smaller than 0) but captured population variation well (the variance of the standard deviates did not differ significantly from 1; Appendix 3D).

Scenario 2

The stochastic model for scenario 2 yielded a much higher average r-squared between modelled abundance and observed abundance between 2000 and 2009 (0.89 ± 0.063; Figure 3.6 (b)) and, the observed abundance was also within the 95% confidence interval of the model. Simulations predicted that under *ad libitum* feeding regime, the population should stabilize *c.* 135 individuals. The probability of extinction of the population over the time-frame considered was 0.

The standard deviate test for the model of scenario 2 showed that this model also under-predicted population size (the mean of the standard deviates was significantly different from, and smaller than 0). However, contrary to the model of scenario 1, it was not very good at capturing variations in abundance as the variance of the standard deviates significantly differed from 1; Appendix 3D).

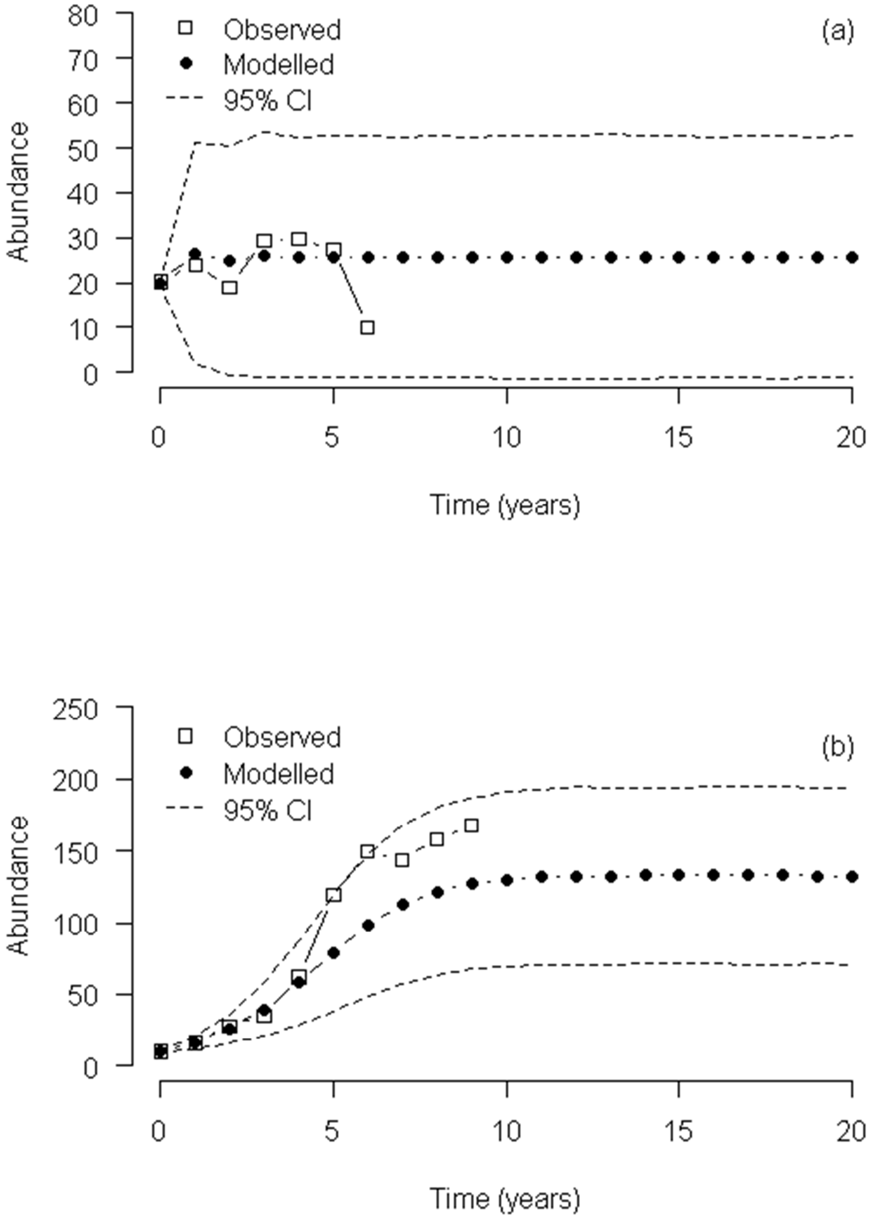

Figure 3.6. Stochastic population model results for the (a) little-to-no feeding and (b) *ad libitum* feeding scenarios shown on a twenty-year timeframe. Simulations were run for 100,000 iterations. The yearly average abundance, 95% confidence intervals and the true observed abundance are shown.

DISCUSSION

The published literature contains several examples of animal translocations where supplemental food was provided and its impact assessed. Some confirm that supplemental feeding benefits populations: for example, kakapo (*Strigops habroptila*) showed an increased chick survival (Elliott et al., 2001), wild European rabbits (*Oryctolagus cuniculus*) an increased abundance (Cabezas and Moreno, 2007) and Florida Scrub-Jay (*Aphelocoma coerulescens*) an increased reproductive output (Schoech et al., 2008). Other studies show no effect of supplemental food: Meek et al (2003) found no increase in adult or fledgling survival in barn owls (*Tyto alba*). However most published studies present either mixed or uncertain results. For example, the conclusion of the effect of supplemental feeding on Eastern wild turkey (*Meleagris gallopavo silvestris*) is that it could help survival under some weather conditions (Kane et al., 2007) and supplemental feeding increased the survival of pre-adult bearded vultures (*Gypaetus barbatus*) but not that of adults (Oro et al., 2008). In addition, while supplemental feeding increases kakapo chick survival, it does not increase adult productivity (Elliott et al., 2001). Overall, while supplemental feeding or management in general, is a common practice in animal translocations, it seems to lack integration into a decision-making framework, which could result in efforts being misdirected.

Hihi, which now persist in several translocated populations, have been provided with various amounts of supplemental food for years. The effects of feeding management have already been studied in two populations, one extant and one extinct. However, the conclusions reached for these two populations relating to the importance of supplemental feeding were contradictory (Armstrong and Ewen, 2001; Armstrong et al., 2007, 2010). By studying another of the translocated hihi populations, we were able to draw conclusions on the management and monitoring of the species across its range and make recommendations for the hihi on Kapiti Island. Our results indeed showed clear patterns in abundance and survival, which confirmed that *ad libitum* supplemental feeding, was an important and useful management action for the population. Moreover, finding similar results for two translocated populations out of three studied (i.e., Tiritiri Matangi Island and Kapiti Island) reinforced the idea that supplemental feeding was beneficial for all translocated hihi population dynamics (Armstrong and Ewen 2001; Armstrong et al., 2002). Finally, as conclusions for Tiritiri Matangi were reached based on only one year of observation (Armstrong and Ewen 2001), this study has provided the best support for supplemental feeding of hihi yet.

The dynamics of hihi on Kapiti Island showed some similarities to the dynamics of hihi on Tiritiri Matangi Island. On the latter, adult survival rate was found to be constant over time and independent of sex (*c.* 0.67; Ewen et al., 2011). According to the best CJS model, we found analogous results in that sex did not affect adult survival on Kapiti. However, survival was time-dependent with distinct patterns between both feeding periods. On Tiritiri Matangi, food was *ad libitum* from the onset (i.e., since 1996) whereas, on Kapiti, it took almost ten years before a similar feeding regime started. The survival of adult hihi on Kapiti has been quite high and stable since 2004 and it is possible that five or ten more years of the *ad libitum* regime, could lead to constant survival on Kapiti as well.

A worrying aspect of the hihi dynamics on Kapiti Island is the clear sex-specific density-dependence on recruitment. The current level of recruitment is very low and models predicted that unless abundance lowers, not only will recruitment stay low but also more males than females will be recruited into the population. The switch in recruitment from female to male-biased appeared to be *c.* 90 individuals. This threshold was reached between 2004 and 2005, which translated into a switch in sex-bias in the population abundance from female- to male-biased. The mating system of hihi involves frequent male-initiated forced copulation, and the consequences of such behaviour include reduced paternal investment (Ewen and Armstrong, 2000). Having a male-biased population could thus further reduce the number of female hihi and/or recruitment on Kapiti Island (Ewen et al., 2011). Alternatively, the sex-bias could also be explained by a monitoring bias towards male hihi. While it is possible that males are recorded more often than females, this bias is unlikely because (1) survey methods have remained the same since the beginning of monitoring and (2) recapture rates have been consistently high, indicating that most animals within the population are captured. Interestingly, similar sex-bias has also been observed for the population on Tiritiri Matangi Island (Ewen et al., 2011). Ewen et al. (2011) investigated the direct effect of biased sex-ratio on hihi dynamics on Tiritiri Matangi Island but did not find any effect for that population.

We expected both 'treatment' (little-to-no food versus *ad libitum*) and density to be good predictors of adult hihi survival. However, the CJS model with time-dependent only survival was the best. The way the 'treatment' covariate was implemented constrained survival to be constant within feeding regimes but different between them. In hindsight, since the best model was time-dependent, it makes sense that a model forcing survival to be constant over time did not perform well. The absence of density-dependence on survival was, however, more surprising since we found evidence of it on the intrinsic population growth rate, r_t. If there was no evidence of density-dependence on recruitment, we could conclude that the population had not reached its carrying capacity, explaining why survival showed no sign of density-dependence. However, it is more likely that survival is not showing evidence of being down-regulated yet. It is therefore imperative to follow the population dynamics very closely for the next few surveys; which, we will be able to do thanks to the on-going monitoring.

The two stochastic population models allowed us to quantify the impact of the regime change that occurred in 2000 on the hihi population of Kapiti Island. The effect of *ad libitum* feeding on the hihi population was two-fold. First, the population went from having a probability of going extinct >0, when there was little-to-no supplemental food, to virtually no chance of dying out. Second, the carrying capacity became such that the abundance increased from 10 individuals in 2000 to almost 160 in 2009. While the predicted extinction probability under scenario 1 was very small, *c.* 2.5%, we did not include demographic stochasticity in either model, which may have resulted in predicting a lower extinction probability than it is in reality. The estimated probability of extinction may also be conservative because small populations are more vulnerable to stochastic events (Shaffer 1981). They also suffer more greatly from genetic diversity loss through drift, and inbreeding depression has been found in hihi populations (Brekke et al., 2010, 2011). Nonetheless, while the two models predicted population sizes that encompassed observed abundances, thus showing signs of being good models, the standard deviate tests showed that in both cases, they under-predicted abundance. This is particularly relevant for the model which predicted population size under little-to-no supplemental feeding, i.e., scenario 1. Indeed, the model appeared to be yielding conservative estimates of abundance, therefore the population may be able to stabilise higher than the *c.* 20 individuals predicted. While we cannot quantify by how much abundance was under-predicted, the true carrying capacity was likely to still be low and the potential population size small. As a result, removing supplemental feeding from Kapiti Island today may not be the right management choice to maximise future population viability.

Investigating other management scenarios, such as ones looking at the impact of reducing or increasing supplemental feeding by x% would be highly informative but data did not allow such models to be built. However, a new management regime has been put in place on Kapiti Island recently. In late 2010, managers reached the end of their *ad libitum* capacity and were forced to make a decision as to the future of management for the population. They came to the conclusion that capping the quantity of supplemental food to 75% of the 2009 amount was the best solution for both hihi and managers. As a result there may be a possibility for further model parameterisation, i.e., new scenarios, in the near future.

By clearly demonstrating the importance of supplemental feeding for the population of hihi on Kapiti, and indicating the importance of such management for the whole species, our findings highlighted an important and common issue of conservation translocation. *Ad libitum* feeding equates to increasing the amount of food provided indefinitely as the population increases, which leads to two problems. First, a management action such as supplemental food is costly in terms of time, people and money and feeding *ad libitum* requires an infinite supply of all three, which is highly unlikely on the long-term. The unsustainability of such management is clearly illustrated by the new management regime now in place for Kapiti Island. Second, the ultimate goal of translocation is to create new, self-sustaining populations, i.e., populations that survive and thrive without human intervention. By definition, managed populations are not self-sustaining. Therefore, whenever a species is considered for translocation, careful thoughts must be given to (1) how management can and will be sustained if the established population successfully breeds and increases in number, and (2) the possibility of an 'exit strategy' that leaves the translocated populations self-sustaining. For Kapiti Island, it may be that attending to the shortage in natural food sources by restoring the island's vegetation could be the way toward a self-sustaining hihi population. Indeed, supplemental feeding is necessary because there is currently not enough native vegetation on the island. While managers are considering all options to make hihi populations self-sustaining, including restoring more of the original habitat, it might take years for the vegetation to reach a level that could sustain a large hihi population. Until then, and as long as we aim to keep hihi population numbers as high as possible, supplemental feeding on Kapiti Island is the best and only option.

There are, in addition, consequences to intensively managing wild populations, especially with supplemental feeding. Supplemental feeding is known to alter behaviour such as migration and dispersal (Doligez et al., 2004; Finlayson and Moseby, 2004). In the case of the hihi, however, as natural food is sparse, the benefits of the habituation to feeders far outweigh the costs of it, as demonstrated by our results. The population on Kapiti Island is isolated and there is no dispersal at a large scale. At the island scale, because it is virtually predator-free, aggregating at feeders does not increase predation risks either. Moreover, some of the translocated populations of hihi are on the mainland and birds are able to disperse away from the area. In these cases, attracting hihi to feeders has the advantage of keeping them within the protected area, which is predator-free. However, one added risk is infectious disease, particularly those pathogens spreading via oral-faecal transmission. A recent emergence of salmonellosis in hihi may have been facilitated by high densities of birds at feeding stations (Ewen et al., 2007). Hygiene is of upmost importance to minimise the risks from infectious disease.

In conclusion, translocated populations are not static and management cannot be either. Finding management options that work is notoriously difficult and those that do are likely to be time-limited. Adaptive management is thus key for translocated populations but its efficiency is entirely dependent on the implementation of a targeted monitoring program. Therefore, as far as translocated populations are concerned, management cannot go without the monitoring of its effect.

CHAPTER 4

Modelling the dynamics of a translocated population under climate change

This chapter will be submitted for publication under the authorship of Alienor L. M. Chauvenet, Tim Coulson, John G. Ewen and Nathalie Pettorelli.

Co-author contributions: I was partly responsible for the design of the model and simulations; I coded the population model in R, performed the simulations and wrote this chapter. Tim Coulson helped design the population model as well as suggested different simulation to run. John G. Ewen provided advice on the life-history of hihi and Nathalie Pettorelli on the model building and simulations. All co-authors commented on the manuscript and helped with the writing.

ABSTRACT

Quantifying the impact of climate change on the viability of threatened species is paramount to efficient decision-making for conservation. Predictive population models can be built to investigate how changes in climatic parameters may affect species' population dynamics and thus long-term persistence. To date, published population models have often focused on a single aspect of climate change at a time, e.g. the increase in mean and variance of climatic variables or an increase in the frequency of extreme events, but have not investigated the potential combined impact of these aspects in threatened species viability. Here we built a stochastic, density-dependent, matrix population model for the hihi, a threatened bird endemic to New Zealand, to quantify the impact of different aspects of climate change on its dynamics. We found that predicted changes in mean and variance of temperature significantly reduced the population's carrying capacity and increased its probability of extinction, and that longer and more frequent hot spells further exacerbated these impacts. However, changes in rainfall or longer and more frequent droughts did not have a significant negative impact on hihi population dynamics. Our results demonstrate the importance of developing a holistic approach to quantifying the impact of climate change on threatened species' viability.

INTRODUCTION

One of the most pressing priorities in conservation science is to assess the impact of climate change on the future viability of threatened species and to increase the long-term efficiency of current conservation decisions. Climate has been shown to play a role in the dynamics of many species including ungulates (Coulson et al., 2001; Stenseth et al., 2004), rodents (Lima et al., 2002), and birds (Barbraud and Weimerskirch, 2003; Chauvenet et al. unpublished). Therefore changes to environmental conditions like those predicted under climate change are likely to affect the chance of persistence of these species. However, while there is a good understanding of how physical conditions are changing at the global and regional scale (IPCC, 2007, 2012), and where those changes are likely to have consequences on biodiversity as well as their directionality (Foden et al., 2008), too little has been done to quantify how predicted changes in climatic conditions will affect threatened species viability.

Most regions of the world are not just facing increases in the mean and variance of temperature and rainfall; they are also experiencing changes in the temporal autocorrelation of climatic conditions. In particular patterns of extreme weather are changing with longer and more frequent hot temperatures and less frequent cold days, and longer and more frequent droughts (IPCC 2007; 2012). However, published models looking at the impact of climate change often only investigate changes in mean and variance in climate variables (e.g. Sæther et al., 2000; Battin et al., 2007; Morris et al., 2008). So far, work investigating temporal autocorrelation in environmental conditions has mostly been theoretical (Pike et al., 2004) and results point to the fact that it has a significant impact on species' population dynamics (Mode et al., 1987; Caswell and Cohen, 1995; Johst and Wissel, 1997; Petchey et al., 1997; Morales, 1999; Petchey, 2000; Tuljapurkar et al., 2009). Moreover, what little that has been done to link environmental autocorrelation and species' risk of extinction has shown that increasing temporal correlation most often leads to increasing extinction risk (Johst and Wissel, 1997;

Inchausti and Halley, 2003; Wichmann et al., 2003; Pike et al., 2004; Jenouvrier et al., 2009). As these trends in extreme weather are expected to at least continue, and potentially increase in the future (Easterling et al., 2000; IPCC, 2012), it is paramount to take them into account to successfully quantify the impact of climate change on species and making informed conservation decisions. Yet, to date, no study has attempted to quantify the combined impacts of changes in mean and variance of weather variables and temporal autocorrelation in extreme climatic conditions on threatened species' long-term population persistence.

Predictive population models can be used to investigate and quantify how different aspects of climate change will affect a species' population dynamics and probability of extinction. There are several different kinds of population models. They vary in (i) their complexity, e.g., Ricker's equation versus an age-structured matrix population model (Ricker 1954; Caswell 2001), (ii) the amount of data required to parameterise them, e.g., time-series analysis versus an individual-based model (Grimm and Railsback 2005), and (iii) can be either deterministic or stochastic if demographic and/or environmental stochasticity are explicitly incorporated (Lande et al. 2003). Ideally population models should be complex enough to make informative predictions but not too complex that results are not verifiable.

Here, we present a stochastic, density-dependent matrix population model built to project the dynamics under climate change of a threatened population of hihi (or stitchbird, *Notiomystis cincta*) reintroduced to the island of Tiritiri Matangi (Tiri), New Zealand. Long-term demographic studies have shown that the species' vital rates are impacted by both rainfall and temperature and that this effect is age-specific (Low et al., 2007; Chauvenet et al. unpublished). The population on Tiri is considered one of the most successful hihi reintroduction as it has been steadily growing since its establishment (Ewen et al., 2011). Moreover, it is also a regular source of juvenile hihi for reintroduction elsewhere. However, climate change projections for New Zealand predicts that temperature will rise and rainfall will decrease in this part of the country (IPCC 2007) and that droughts and hot spells will last longer and be more frequent (IPCC 2012). Because the population is on an island and the birds are unable to successfully disperse to and from Tiri, it is important to understand and quantify how climate change can affect the future of this population. We hypothesise that:

H1: Predicted changes in the mean values of temperature and rainfall will decrease the population's carrying capacity and increase its probability of extinction as conditions depart from those experienced by the species in the past.

H2: An increase in the variance around the mean temperature and mean rainfall will increase the population's probability of extinction as the population experiences conditions that are more extreme than what they are used to.

H3: Temporal autocorrelation in weather parameters such that droughts and hot spells last longer and are more frequent will increase the population's probability of extinction as hihi endure longer periods of extreme conditions and those happen more often.

MATERIAL AND METHODS

Study species and its demography

The hihi is a small passerine endemic to the North Island of New Zealand. Hihi currently persist in five translocated populations and one remnant natural population (Taylor et al. 2005; Chauvenet et al. 2012). One of the best-studied and northernmost populations is located on Tiritiri Matangi Island (Tiri). Hihi were reintroduced to Tiri in 1995 and 1996 (Armstrong et al. 2002; Ewen and Armstrong 2007) and have since persisted under an intense management and monitoring regime that includes predator control, *ad* *libitum* supplemental feeding, nest box provision and detailed individual survival and breeding data collection (Ewen et al. 2011).

Demographic studies of the long-term monitoring dataset for the Tiri population showed that hihi survival is age-dependent such that fledglings have a lower survival rate than first-year adults, and both have lower survival rates than older birds (Chauvenet et al. unpublished). Age-dependent survival rates have also been found to depend on population density, mean temperature and total rainfall, and whether it is the breeding (φ; September to February) or non-breeding season (δ; March to August) (Chauvenet et al. unpublished). Hihi female breeding success, measured as the probability that an egg laid will become a fledgling (γ), has also been found to depend on female age, with females in their prime between 2 and 5 years old having a higher breeding success than first-year or senescent females. Moreover, γ has also been found to be a function of population density and mean temperature (Chauvenet et al., unpublished). Specifically, those three vital rates have been defined as:

$$\varphi = -0.22 - 1.041a_{12} + 0.578a_{29} + 0.264D_B + 0.181T_\mathrm{B} - 0.004R_\mathrm{B} - 0.016D_\mathrm{B}T_\mathrm{B} \quad (1)$$

$$\delta = 0.498 + 0.318a_1 + 0.0115a_{12} + 0.264a_{29} - 0.003R_\mathrm{NB} + 0.03a_{12}R_\mathrm{NB} + 0.004a_{29}R_\mathrm{NB} \quad (2)$$

$$\gamma = -0.91 + 0.582a_{26} - 0.088a_{69} - 0.185D_\mathrm{B} - 0.103T_\mathrm{B} \quad (3)$$

Equations 1-3 are on the logit scale; a_i represents the age-class for which survival is being modelled such that i can be fledgling $i = 1$, individuals between 1 and 2 years old $i = 12$, and between 2 and 9 years old $i = 29$; a_j represents the age-class for which overall breeding success is being modelled such that j can be females between 1 and 2 years old, between 2 and 6 years old $j = 26$, and between 6 and 9 years old $j = 69$. As individuals can only be in one age-category at any one time, the values of a_i and a_j are always 0 or 1. The average temperature during the breeding season is represented by T_B, the total amount of rainfall during the breeding season by R_B, total amount of rainfall during the non-breeding season by R_{NB}, and population density at the beginning of the breeding season by D_{B}.

Females most often lay 1 or 2 clutches during the breeding season (up to 4 clutches have been recorded but those events are extremely rare) and equation 3 represents the overall breeding success of females laying one clutch during the breeding season. Increasing the number of clutches laid per female in the model did not significantly change the results (not shown).

Model description

We developed a stochastic matrix model to project the hihi population into the future and investigate the impact of different aspects of climate change on its dynamics (Figure 4.1). The population was divided into 8 classes: fledgling (which is a five month period corresponding to the time juveniles enter the population as fledglings in March and become adults the next September), and then 8 year-long adult age classes, e.g., 1-2 yr. old, 2-3 yr.-old, etc. No bird was allowed to age past 9 years old as it is the oldest age ever recorded (low and Pärt 2009).

We used 'year' as time-step, and started the model at the beginning of the breeding season at time t_0, setting the initial abundance to 100 first-year individuals. The abundance N at each time-step (i.e. beginning of the breeding season at time t+1) is a function of the number of individuals in each class at time t, the total number of fledglings produced during the breeding season (F), and age- and season-dependent survival φ and δ between time t and t+1:

$$N_{t+1} = \sum_{i>1} \left(N_{t(i)} \times \varphi_{(i)} \times \delta_{(i)} \right) + F \times \delta_{(i=1)} \text{ (with } i = 1, 12, 29) \qquad (4)$$

where

$$F = \sum \left(\frac{N_{t(j)}}{2} \times Egg \times \gamma_{(j)} \right) \qquad \text{(with } j = 12{,}25, 69) \qquad (5)$$

and $N_{t(i)}$ is the number of individuals in age-class i at time t (beginning of the breeding season); $N_{t(j)}/2$ is the number of females in age-class j at time t (assuming equal sex-ratio); Egg is the number of eggs laid per female which, at each time-step, is sampled on a normal distribution of mean = 4.2 and sd = 1 corresponding to the average number of eggs laid when females lay only one clutch during the breeding season.

The values taken by the weather parameters $T_{\mathrm{B}}, R_{\mathrm{B}}$ and R_{NB} in equations 1-3 were dependent on the climate change scenario investigated in the simulations described below.

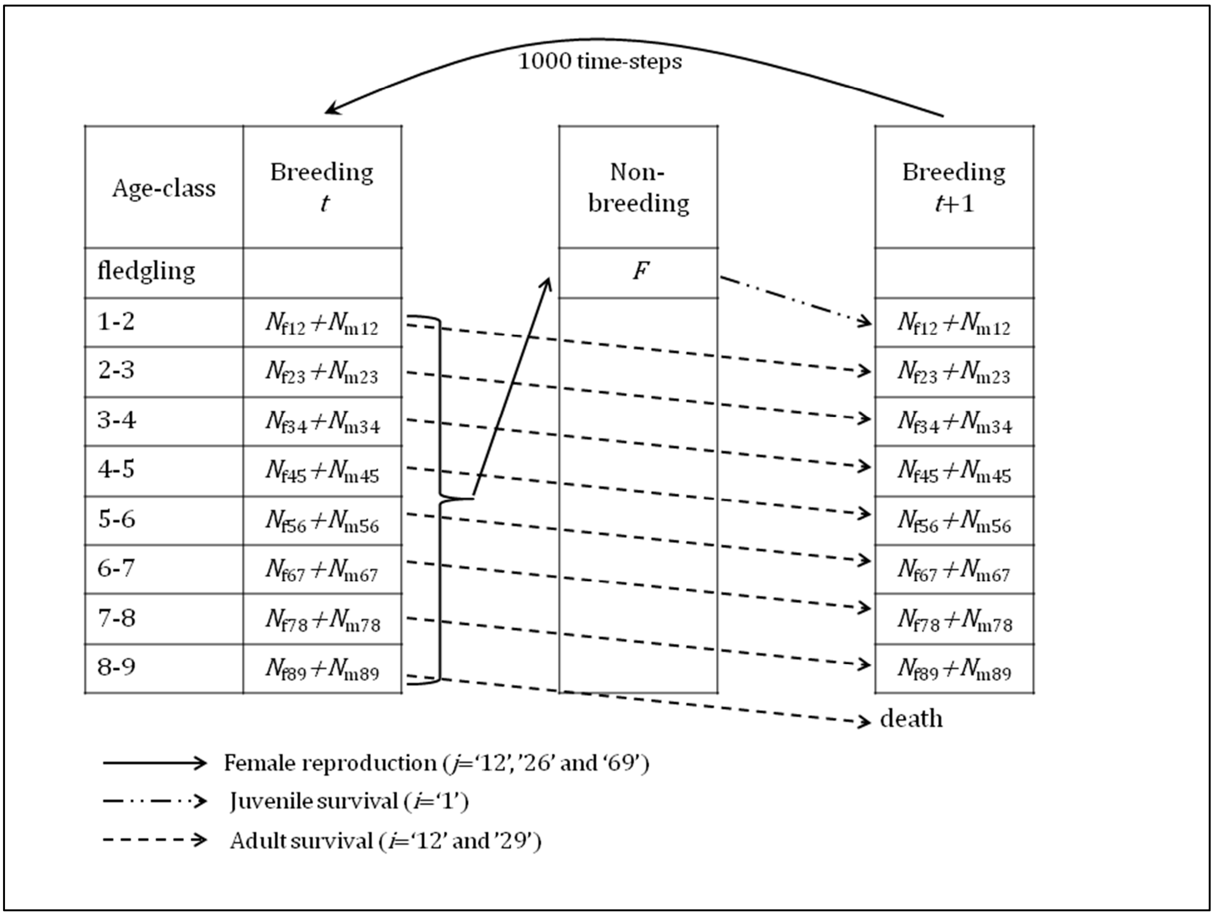

Figure 4.1. Graphical representation of the stochastic matrix population model used to project the hihi population under different aspects of climate change. 'N_f' and 'N_m' represent the number of females and males in the population in age-class i and j.

Table 4.1. Description of the baseline weather parameters. Shown are: the average mean temperature during the breeding seasons between 1995 and 2011 on Tiri and its standard deviation (SD), and the average total rainfall during the breeding and non-breeding seasons between 1995 and 2011 on Tiri and their respective standard deviations.

Parameter	Average	SD
Temperature	17°C	0.4
Rainfall (breeding)	393mm	84
Rainfall (non-breeding)	526mm	96

Simulations

To investigate the impact of future climate change on the hihi population, we ran a set of 15 simulations defined by the values of the weather parameters T_{B}, R_{B} and R_{NB}. One of these 15 simulations represented the “baseline” conditions, such that at each time-step values for T_{B}, R_{B} and R_{NB} were randomly sampled on the normal distribution of the average observed weather conditions (and their standard deviation) since the population was reintroduced (Table 4.1). The other 14 simulations were run to account for different aspects of climate change as suggested by global and regional projections from the IPCC (2007). We modelled a potential increase in mean temperature by 2°C and 4°C, a potential decrease in total rainfall by 10% during the breeding season and 7.5% during the non-breeding season and a potential increase in variance in the mean temperature total rainfall in both seasons, as single effects and combined together (see Table 4.2 for a detailed list of simulations; IPCC 2007, 2012).

We first performed those 15 simulations without temporal autocorrelation and then investigated the impact of five different patterns of autocorrelation in rainfall (droughts) and temperature (hot spells): longer lasting droughts, more frequent and longer lasting droughts, longer lasting hot spells, more frequent and longer lasting hot spells, co-varying droughts and hot spells. To model temporal autocorrelation, we used discrete first-order Markov chains models, i.e., the state of the system at time t was dependent on the state of the system at time $t + 1$ (Truscott and Gilligan, 2003). We thus defined different “climate states” which described the environmental conditions that could be experienced by the population at any time, e.g. “Drought” or “Non-Drought”, and set transition probabilities from one state to another. Because future temporal autocorrelation in temperature and rainfall in New Zealand has not been explicitly quantified, values for the transition probabilities were arbitrarily set to represent a significant departure from a system where there is no autocorrelation while making sure that the population did not only experiences droughts or hot spells.

Table 4.2. List of simulations run with and without temporal autocorrelation in weather parameters. The "Baseline" corresponds to the parameters described in Table 4.1. "Mean Temp" stands for average temperature, "Total Rain" for total rainfall and "SD" for standard deviation. There were 15 simulations run for each autocorrelation pattern (including baseline). Rainfall could be reduced by 7.5% or 10% depending on the season.

Simulation	Mean Temp +2˚C	Mean Temp +4˚C	TempSD x2	Total Rain -X%	RainSD x2
Baseline					
T1	X				
T2	X		X		
T3		X			
T4		X	X		
R1				X	
R2				X	X
TR1	X			X	
TR2	X		X	X	
TR3		X		X	
TR4		X	X	X	
TR5	X			X	X
TR6	X		X	X	X
TR7		X		X	X
TR8		X	X	X	X

First, consider temporal autocorrelation in rainfall for both seasons. At time t the system could be in either of two climate states: “Drought” or “Non-Drought”. If the year was in “Drought”, then the amount of rainfall experienced by the population at this time step in each season (R_{B} and R_{NB}) was equal to the smallest value out of 1000 values randomly sampled on normal distributions defined by means and standard deviations in rainfall for each season (means and s.d. were dependent on the simulation; Tables 4.1 and 4.2). If the year was in “Non-Drought” then R_{B} and R_{NB} were randomly sampled on the same normal distributions. We modelled two drought autocorrelation patterns: #1 when droughts lasted longer, achieved by increasing the chance of $t+1$ being in “Drought” if t was in “Drought” by 50%, but leaving an equal chance of being in “Drought” or “Non-Drought” at $t+1$ if t was in “Non-drought”; #2 when droughts were longer and more frequent, achieved by increasing the chance of $t+1$ being in “Drought” if t was either in “Drought” or in “Non-Drought” by 50% respectively (see Appendix 4A for transition probabilities matrices).

Second, consider temporal autocorrelation in temperature. At time t the system could be in either of two climate states: “Hot Spell” and “Average Temperature”. If the year was experiencing a “Hot Spell”, then temperature at this time-step (T_{B}) was equal to the highest value out of 1000 values randomly sampled on the normal distribution defined by mean and standard deviation in temperature (means and s.d. were dependent on the simulation; Tables 4.1 and 4.2). If the year was experiencing “Average Temperature” then T_{B} was randomly sampled on the same normal distribution. We modelled two temperature autocorrelation patterns: #1 when hot spells lasted longer, achieved by increasing the chance of $t+1$ being in “Hot Spell” if t was experiencing “Hot Spell” by 50%, but leaving an equal chance of experiencing “Hot Spell” or “Average Temperature” at $t+1$ if t was experiencing “Average Temperature”; #2 when hot spells lasted longer and were more frequent, achieved by increasing the chance of $t+1$ experiencing “Hot

Spell" if t was either experiencing "Hot Spell" or "Average Temperature" by 50% respectively (see Appendix 4B for transition probabilities matrices).

Finally, there also may be covariation between rainfall and temperature such that droughts and hot spells are more likely to occur together. Then the year could be in four climate states rather than two: "Drought and Hot Spell", "Drought and Average Temperature", "Non-Drought and Hot Spell", and "Non-Drought and Average Temperature". To model this drought-temperature autocorrelation, we defined transition probabilities between states such that if the year t was experiencing "Drought and Hot Spell", it was more likely that year $t+1$ was also experiencing "Drought and Hot Spell" than any other state. In addition if the year was in "Drought and Average Temperature", then the next year was more likely to remain in drought than not, and if the year was in "Non-Drought and Hot Spell", the next year was more likely to experience a hot spell than not. The complete list of transition probabilities is shown in Table 4.3.

In total, there were 15 simulations run without autocorrelation and 15 simulations run for each of the five autocorrelation patterns (drought #1, drought #2, temperature #1, temperature #2, and drought & temperature): $n = 15 \times 6 = 90$ simulations. Each simulation was repeated 1000 times. The total number of time-step was 1000 but we discarded the first 200 steps to measure the population's dynamics at an equilibrium state. To quantify the impact of climate change on hihi population dynamics and compare the results between simulations, we collected the mean population size and its standard deviation, the population age-structure in the form of the mean percentage of hihi in each age-class, and the probability of the population size dropping below two quasi-extinction thresholds of 10 and 20 individuals.

Table 4.3. Transition probability matrix for simulations where there is a drought and hot spell autocorrelation. Shown are the probabilities of transition from one state to another. Each row sums to 1. Years can be in drought, when rainfall is at minimum, or not in drought, when rainfall is average. Years can experience a hot spell, when temperature is at maximum, or not, when temperature is average.

To / **From**	Non-Drought/Average Temperature	Non-Drought/ Hot spell	Drought/ Average Temperature	Drought/ Hot Spell
Non-Drought/Average Temperature	0.7	0.1	0.1	0.1
Non-Drought/ Hot spell	0.15	0.35	0.15	0.35
Drought/ Average Temperature	0.15	0.15	0.35	0.35
Drought/ Hot Spell	0.1	0.1	0.1	0.7

RESULTS

The results of the “baseline” simulation without temporal autocorrelation corresponded to the dynamics of the population if environmental conditions were to remain the same in the future as they are currently. Our baseline provided a benchmark against which to compare results of simulations that included different aspects of climate change. Under current conditions, the average hihi population size, is predicted to be 215 (±65) and the probability of the population reaching either quasi-extinction threshold was 0 (Figure 4.2).

No autocorrelation

When there was no temporal autocorrelation in weather variables, all simulations involving an increase in mean temperature (2˚C, 4˚C, with and without an increase in temperature variance) showed a significant decrease in mean population size whereas simulations in which only rainfall was affected by climate change did not (Figure 4.2a). Moreover, regardless of the simulation, the probability of the population reaching below 10 was always null. Most simulations also yielded a probability of the population reaching below 20 of 0%. However, the six simulations in which the temperature standard deviation was doubled yielded a probability of the population reaching between 20 and 10 individuals significantly greater than 0 and up to 100% (Figure 4.2b). There seemed to be very little impact of climate change on the age-structure of the population (Figure 4.2c).

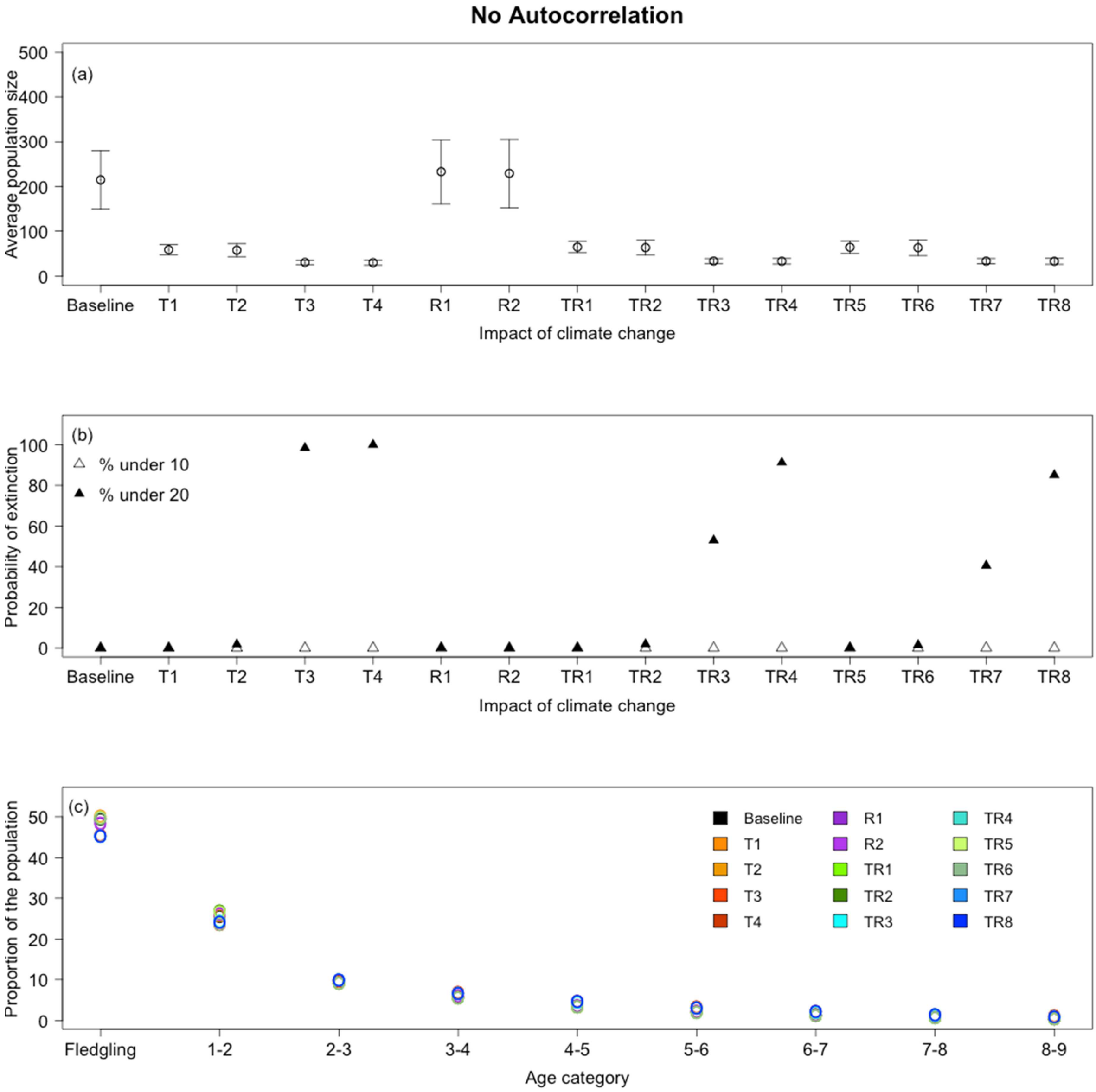

Figure 4.2. Impact of the different aspects of climate change (see Table 4.2) when there is no temporal autocorrelation in weather parameters on: (a) the average hihi population size, (b) the probability of the population being smaller than 20 and 10 individuals, and (c) the population's age-structure.

Drought autocorrelation

When the models included a temporal autocorrelation in drought (#1 and #2), the mean population size yielded by the "baseline" simulation was higher than with no autocorrelation (Figures 4.3a and Appendix 4C) by *c.* 80 individuals. However, all simulations that involved an increase in temperature showed a significant reduction in population carrying capacity compared to the baseline. The difference in mean population size between simulations where only mean temperature was increased and those where both mean temperature and its standard deviation were changed, was more apparent with the drought autocorrelation than without temporal autocorrelation (Figures 4.3a and Appendix 4C). Under both drought autocorrelation patterns there was a decreased chance of the population reaching below 20 individuals, but no change in the probabilities of the population reaching below 10 individuals (Figures 4.3b and Appendix 4C). Finally, simulations that included a decrease in total rainfall combined with an increase in rainfall standard deviation seemed to yield a slightly lower proportion of fledglings in the population, than those without, by *c.* 8% (Figures 4.3c and Appendix 4C).

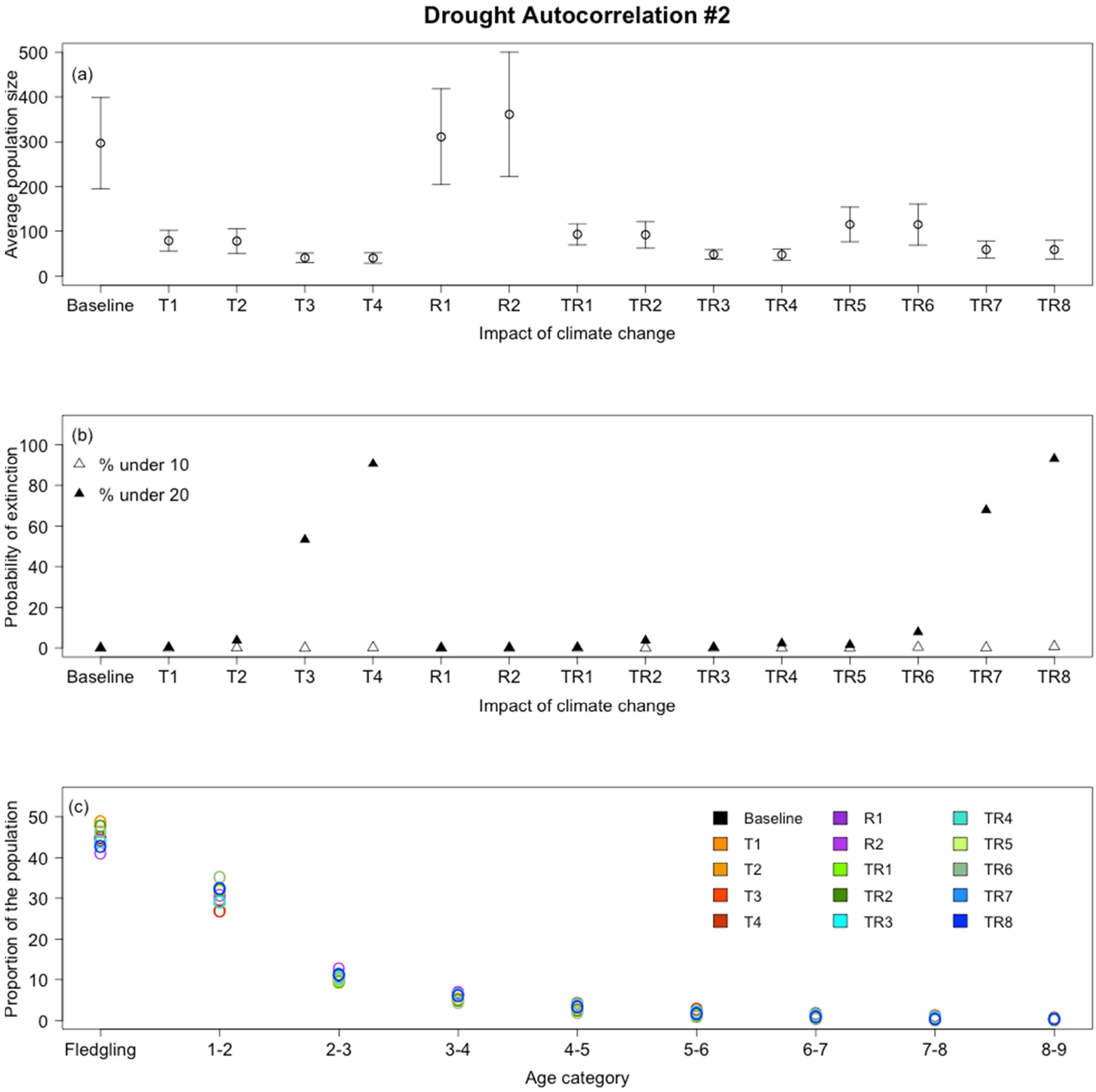

Figure 4.3. Impact of the different aspects of climate change (see Table 4.2) when there is temporal autocorrelation in rainfall such as droughts last longer and are more frequent on: (a) the average hihi population size, (b) the probability of the population being smaller than 20 and 10 individuals, and (c) the population's age-structure.

Temperature autocorrelation

When the models included temporal autocorrelation in temperature (#1 and #2), the “baseline” mean population size was smaller than when there was no autocorrelation, by *c.* 100 individuals. The same decreasing pattern was true for all simulations, including those without an increase in temperature (Figures 4.4a and Appendix 4D). Some simulations also showed probabilities of the population reaching below 10 individuals being greater than 0, in particular those where mean temperature was increased by 4˚C and temperature variance doubled (Figures 4.4b and Appendix 4D). The age-structure of the population seemed to be most affected when hot spells were longer and more frequent (#2) with a decrease in the proportion of fledglings and increase in the proportion of first-year individuals (Figures 4.4c and Appendix 4D).

Drought and Temperature autocorrelation

When there was covariation between droughts and hot spells, mean population size of the “baseline” simulation was higher than with only temperature autocorrelations but smaller than with drought autocorrelations or no temporal autocorrelation at all (Figure 4.5a). Probabilities of quasi-extinction showed that similarly to drought autocorrelation #1 and #2, the population never reached below 10 individuals. However, all simulations where temperature increased by 4˚C yielded probabilities of the population being less than 20 individuals >80% (Figure 4.5b). The age-structure of the population was similar to when there was only temperature autocorrelation (Figure 4.5c).

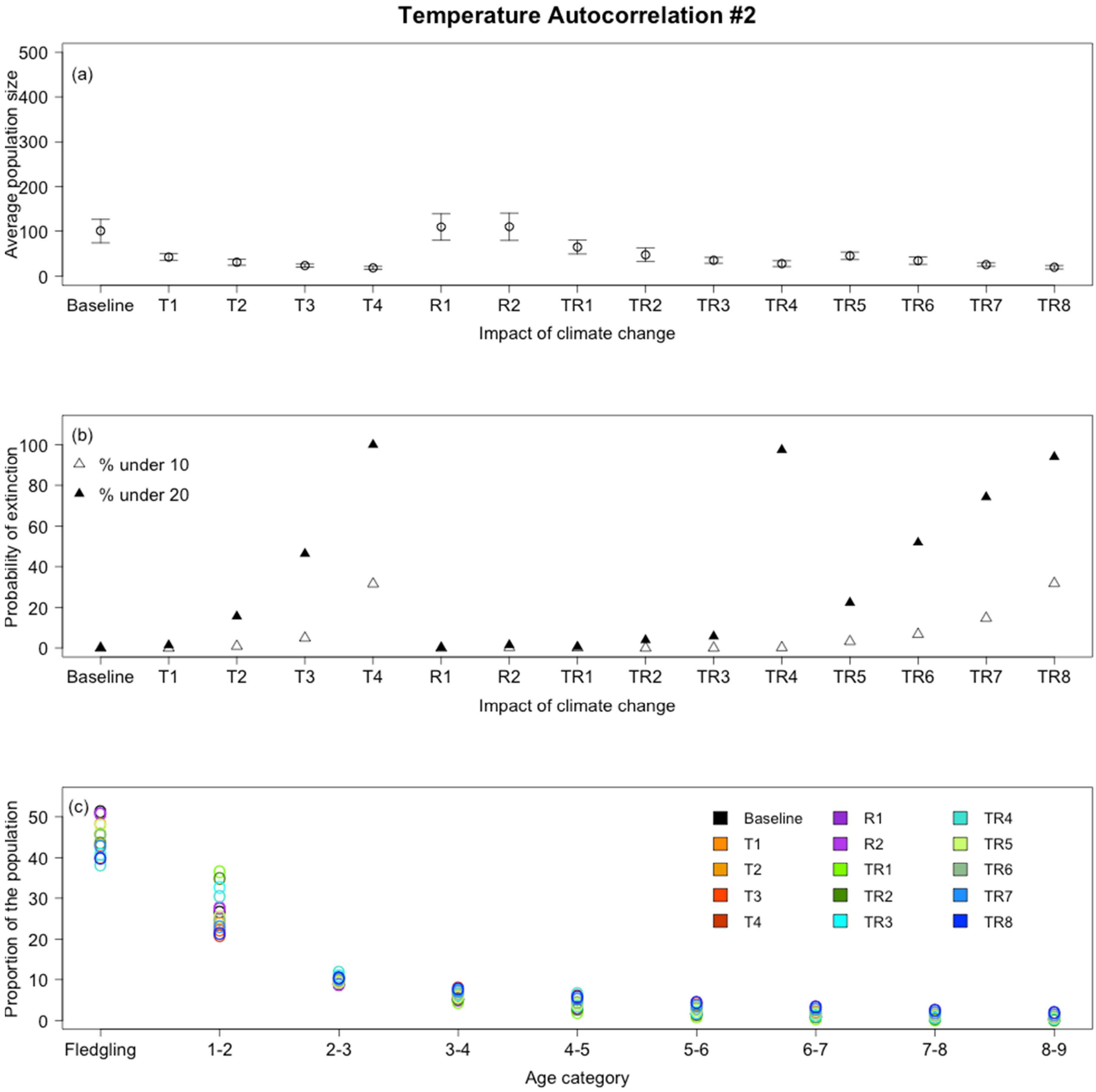

Figure 4.4. Impact of the different aspects of climate change (see Table 4.2) when there is temporal autocorrelation in temperature such as hot spells last longer and are more frequent on: (a) the average hihi population size, (b) the probability of the population being smaller than 20 and 10 individuals, and (c) the population's age-structure.

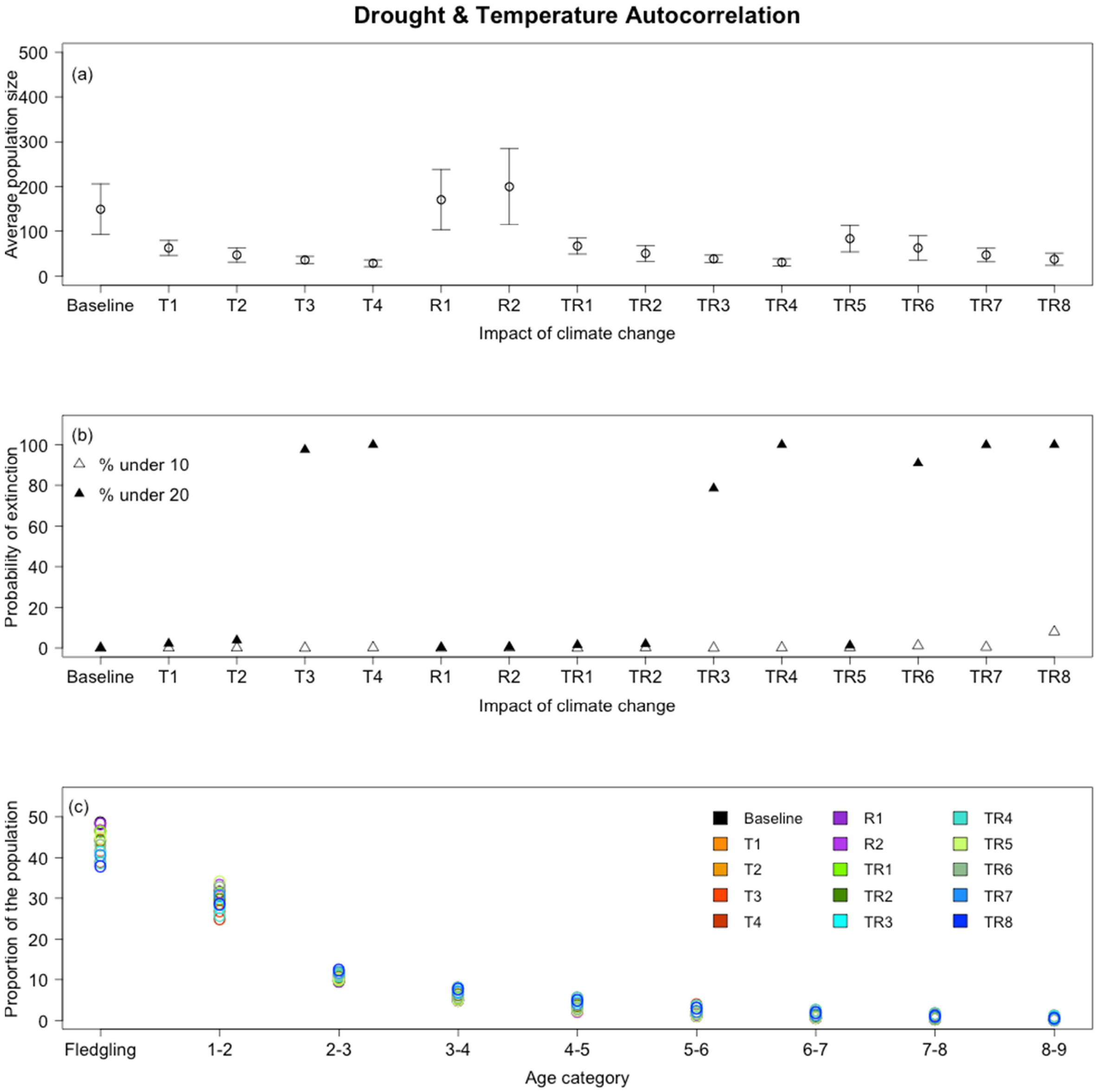

Figure 4.5. Impact of the different aspects of climate change (see Table 4.2) when there is temporal autocorrelation in rainfall and temperature such as hot spells and droughts are more likely to occur at the same time on: (a) the average hihi population size, (b) the probability of the population being smaller than 20 and 10 individuals, and (c) the population's age-structure.

Overall we found that changes in mean temperature and rainfall were not enough to increase the population's probability of extinction, they have to be coupled with increased variance and temporal autocorrelation (H1). An increase in temperature by 2°C or 4°C reduced the population's carrying capacity significantly whereas an increase in average amount of rainfall did not (H1). Moreover, increasing the variance around the mean temperature and mean rainfall increased the chance of the population being less than 20 individuals, particularly if both aspects were modelled together (H2). Finally, out of all the patterns of autocorrelation tested, temperature autocorrelations were the only ones that increased the chance of the population reaching 10 or fewer individuals (H3).

DISCUSSION

Climate change has been acknowledged as one of the worst threat to biodiversity and is predicted to remain so in the future. However, quantifying how climate change will affect species' long term persistence is complicated by the wide range of climatic parameters that can be studied and because each of these may have a different impact on species demography. The results of our simulations show that impacts most-often associated with climate change such as an increase in mean and variance of weather variables may be exacerbated by the fact that consecutive years are likely to share climatic characteristics with each other, i.e., temporal autocorrelation.

Little is known about the optimal climatic conditions for the hihi. The species is thought to have been widespread throughout the North Island before European colonisation of New Zealand, but absent from South Island, presumably because of the colder temperatures (Taylor et al. 2005). So far, when choosing sites to reintroduce hihi to, areas within the species former range have been prioritised (i.e. reintroduction) under the condition that they are free of non-native mammal predators (or have the potential to be). To date, no sites have been selected based on climatic conditions. A main assumption, linked to restricting release sites to be within the historic range of hihi, has been that the climate of North Island was suitable for the species in general. While this may be overall true at present, our results show that this assumption may not hold in the future. Indeed, two impacts of climate change that are amongst the most likely for New Zealand are the upward shift of the mean temperatures and the increase in the frequency and length of hot spells (IPCC 2007; 2012): we found that an increase in average temperature of just 2°C without temporal autocorrelation, and that temperature autocorrelation alone without other aspects of climate change, were able to half the population's carrying capacity.

Our findings illustrate two important points. First, predictive population models for threatened species should take into account the predicted increase in length and frequency of extreme weather. As demonstrated by our results, temporal autocorrelation alone may have a significant impact on population dynamics, and when coupled with other likely aspects of climate change may significantly increase the probability of extinction of a population. Second, the potential impact of climate change should always be taken into account when selecting species translocation sites for threatened species as it is a permanent solution. The hihi population on Tiri represents a large, on-going, and long-term conservation effort with resources being invested in both management and monitoring. As a result, the population is now hovering at carrying capacity and can be healthily harvested for further translocations. However, if, as predicted by our model, a small increase in temperature severely reduces the population's carrying capacity, the effort to raise population numbers to the current maximum may have been wasted. Moreover, the population may not be able to sustain future harvest as it is now.

There were several limitations to our study. First, we arbitrarily assigned transition probabilities between one climate state to another when we modelled drought, hot spells or a combination of both. Our choices may not reflect the exact future conditions that will be experienced by hihi on Tiri. Ideally, different combinations of transition probabilities could be tested, investigating the sensitivity of the population's carrying capacity, probability of extinction and age-structure to changes in those probabilities. However, we chose a small but informative set that was large enough to give a broad overview of the impact of temporal autocorrelation on hihi dynamics but not too large that results became difficult to interpret. Second, we modelled two aspects of temporal autocorrelation, length and frequency of extreme weather, but droughts and hot spells may also vary in intensity. While this could be explored in further analysis, the way we modelled droughts and hot spells, i.e., minimum possible rainfall and maximum possible temperature, insured that the most extreme conditions were represented and our results were not conservative. Finally, the different aspects of climate change investigated in each simulation were applied to the population from the first time-step but one could expect that changes in environmental conditions are gradual. For example the increase in temperature could be linear, with a small change in mean temperature every decade (IPCC 2007, 2012). Alternatively, as reflected by some mitigation scenarios (IPCC 2007), changes in climate variables may be fast-paced at the beginning, but slow down later as climate change is successfully mitigated.

Overall we showed that some aspects of climate change may have a more detrimental effect on species' viability when combined, that when acting separately. Moreover, we demonstrated that taking into account changes in the length and frequency of extreme events, as well as changes in mean and variance of weather variables, when quantifying the impact of climate change on species persistence is very important. Simplifying environmental change to one impact may indeed lead to a poor understanding of how a system will react to future environmental conditions and run the risk of conservation decisions being less than optimal. Because conservation resources are limited, and conservationists are regularly faced with choices about where to direct their effort

(Chauvenet et al., 2010), we must strive for the best understanding of the effect of climate change has on species as possible. The holistic approach to quantifying the impact of climate change on threatened species' viability we propose, will guarantee that the best possible knowledge is available for conservation decision-making.

CHAPTER 5

MaxEnt as a tool for selecting suitable translocation sites under climate change

This chapter will be submitted for publication under the authorship of Alienor L. M. Chauvenet, John G. Ewen, and Nathalie Pettorelli.

Co-author contributions: I was responsible for the habitat suitability modelling and the writing of this chapter. John G. Ewen and Nathalie Pettorelli provided advice on the design of the modelling. Nathalie Pettorelli suggested the use of GLM to compare its performance to MaxEnt's. Both co-authors provided editorial comments on the chapter.

ABSTRACT

Solutions to help species adapt to the impact of climate change are urgently needed and translocations have been proposed as one such tool. However, the poor planning and previous lack of scientific rigour of translocation attempts have yielded low success rates for large investments, mostly because of unsuitable release sites. Yet, choices regarding release strategy are mostly made *ad hoc*, based on expert knowledge, and habitat suitability models (SDM) have seldom been used to identify translocation sites. Moreover, to date, long-term environmental changes in selected sites have never been explicitly accounted for. Here we investigated the distribution of current and future suitable habitat for a New Zealand endemic bird, the hihi, identifying where they could be translocated next to survive climate change. We first contrasted the performance of two SDM (MaxEnt, a presence-only algorithm, and GLM, a presence-absence method) and found MaxEnt to perform best when presence records contain man-made populations. Then, we found that, as expected from global change predictions, hihi suitable habitat will likely shift poleward in the coming decades. This may result in two translocated populations and the remnant natural population being in unsuitable conditions in the future, and the north part of South Island becoming suitable for hihi even though it was not part of their historical range. Our results Illustrated how translocating populations without first assessing how climate change will impact the area can potentially lead to mistakes and to the waste of limited conservation funding. s

INTRODUCTION

The Ecological Niche Theory states that, for every species on Earth, a set of environmental conditions (i.e. its niche) within which it can achieve positive population growth rate, can be isolated (Hutchinson, 1957; Chase, 2011). Those environmental conditions are both of biotic (e.g., food or competitors) and abiotic (e.g., climate or elevation) nature. The species "realised niche", which can be described as the area where it lives as opposed to where it could live if not for other biotic or historical constraints, is supposed to be a good representation of habitat in which the species can remain extant if conditions stay the same (Chase 2011). However, climate change is predicted to have a severe disruptive effect on the spatial distribution of environmental conditions on the global scale. Average, minimum and maximum temperatures and precipitations are expected to change, as well as vegetation phenology and the frequency and intensity of extreme events (Foden et al., 2008). As a result, the set of environmental conditions in which a species has been thriving in the past, may shift away from the species' distribution.

For some species, climate change might trigger the emergence of a significantly different set of environmental conditions in most of its distribution range, creating a disparity between the new conditions experienced by the species and its realised niche. These species will therefore either have to adapt to new conditions or shift their range to follow suitable ones (Davis and Shaw, 2001; Pettorelli, 2012). There is already evidence of species having shifted their distribution in response to climate change. For example, Parmesan et al. (1999) report poleward shifts of several European butterfly species' ranges; Hickling et al. (2006) show that a large selection of vertebrate and invertebrate species in Britain has been moving northward and uphill. However, not all species that will need to shift their range will be able to do so. First, they may not be mobile enough, or too slow moving to follow rapidly shifting suitable environmental conditions (Devictor et al., 2008; Schloss et al., 2012). Alternatively, they may also be faced with a physical barrier to their dispersal such as having to cross an ocean, a mountain or a city. Those species can be helped using translocation (Seddon, 2010). Translocations are defined as “any movement of living organisms from one area to another” (IUCN 1987) and are commonly-used for species conservation and ecosystem restoration purposes (Seddon 2010). There are two main types of translocation: reintroduction, when species are moved in parts of their historical range, and assisted colonisation (also known as benign introduction; IUCN 1998), when they are moved into an area where they were never recorded before.

Conservation translocation is expensive (Caldecott and Kavanagh, 1983; Moran et al., 2005) and failure not only wastes precious and limited conservation funding, it also often results in the death of individuals from a threatened species. Therefore, one of the most important steps when performing translocation is to select suitable sites for the new population (Osborne and Seddon, 2012). Reviews of past translocation outcomes found that translocation success is generally low and that poor habitat quality prominently features as one of the main reasons (Griffith et al., 1989; Osborne and Seddon 2012). This shows the difficulty of choosing appropriate translocation areas, even when not thinking about future suitability. Conditions within the selected habitat not only need to be suitable at the time of the translocation, they also need to remain so in the future, as the impact of climate change intensifies. Habitat suitability models, also called Species Distribution Models (SDM), can help assess the suitability of potential translocation sites using data on the current distribution of species (Osborne and Seddon, 2012; Chauvenet et al., in press). There are several different SDM algorithms that are freely available, and each has advantages and drawbacks (see Table 5.1 for a review).

Here we used a presence-absence model, Generalised Linear Modelling, and a presence-only model, MaxEnt, to model the distribution of current and future suitable habitat for the hihi (*Notiomystis cincta*), a small passerine bird endemic to New Zealand. The hihi is classified as Vulnerable on the IUCN Red List and is currently found in 5 translocated populations and 1 remnant natural population (Figure 5.1). Its distribution is much more restricted, and its numbers much lower, compared to its historical presence throughout North Island, NZ (Taylor et al, 2005). There is an on-going recovery program aiming at re-establishing hihi by creating new populations through translocations. It is known that hihi survival rates and reproduction success, which directly impact long-term persistence, are partially dependent on climate (Low and Pärt 2009; Chauvenet et al. unpublished). Therefore, they are a good candidate for habitat suitability modelling which assumes a direct link between environmental conditions and species persistence. The IPCC (2007) predicts that, depending on the scenario and the region, the average temperature of New Zealand could increase between 1.1 and 6.4°C by 2100, with an increase of 2-4°C being most likely. In addition, average amount of rainfall could change by up to 10%, with an increase in drought length and frequency in the North, and an increase in extreme rainfall in the Centre and South of the country. Therefore, in order to perform the most cost-efficient translocations of hihi, it is essential to identify potential translocation sites that will remain suitable in the future. By using habitat suitability modelling to identify these sites, we perform a key step for the future management of hihi. We hypothesised that:

H1: Hihi habitat suitability will be strongly linked to the average temperature during the breeding season and total precipitation during the non-breeding season as both have been found to significantly influence hihi dynamics (Chauvenet et al. unpublished).

H2: MaxEnt will perform better (higher AUC) than GLM as it is a machine-learning algorithm that has been shown to outperform other habitat suitability models, when there are less than 30 presence records (Wisz et al., 2008).

H3: The predicted increase in average temperature and decrease in rainfall in New Zealand will shift suitable habitat for hihi poleward by shrinking its extent in the northern part of the country and expanding it in the southern part, including on South Island (IPCC 2007).

MATERIAL AND METHODS

Distribution data

The exact current distribution of the hihi is known as the species occupies a restricted number of small islands and fenced territories (Figure 5.1). Therefore, to map hihi distribution, we overlaid a map of North Island, NZ, with one of the environmental layers later used in GLM and MaxEnt, and described below. Those layers are divided into grid cells, which we used to record the latitude and longitude of the centre of every pixel covering known suitable range of the hihi. We defined suitable range as every location in which hihi currently persists or was recorded to have bred and survived for at least a couple of years since the recovery program started in the 1980's. This included three translocation sites where hihi have been translocated but the populations eventually went extinct: Mokoia Island, Hen Island and Cuvier Island. They were still included as part of the suitable range because these failures were assumed not to be linked to weather conditions. Indeed, several hypotheses unrelated to climate have been put forward to explain the population's decline on Mokoia: not enough supplemental food, nest mites (*Ornithonyssus bursa*), aspergillosis (*Aspergillus fumigatus*) or the high density of predatory morepork (*Ninox novaeseelandiae*) (Armstrong et al., 2002; Armstrong et al., 2007; 2010). Similarly, both Cuvier and Hen Islands had kiore, or pacific rats (*Rattus exulans*), when hihi were reintroduced which was likely to have been a strong contributing factor to the fate of the small translocated populations (Rasch et al., 1996).

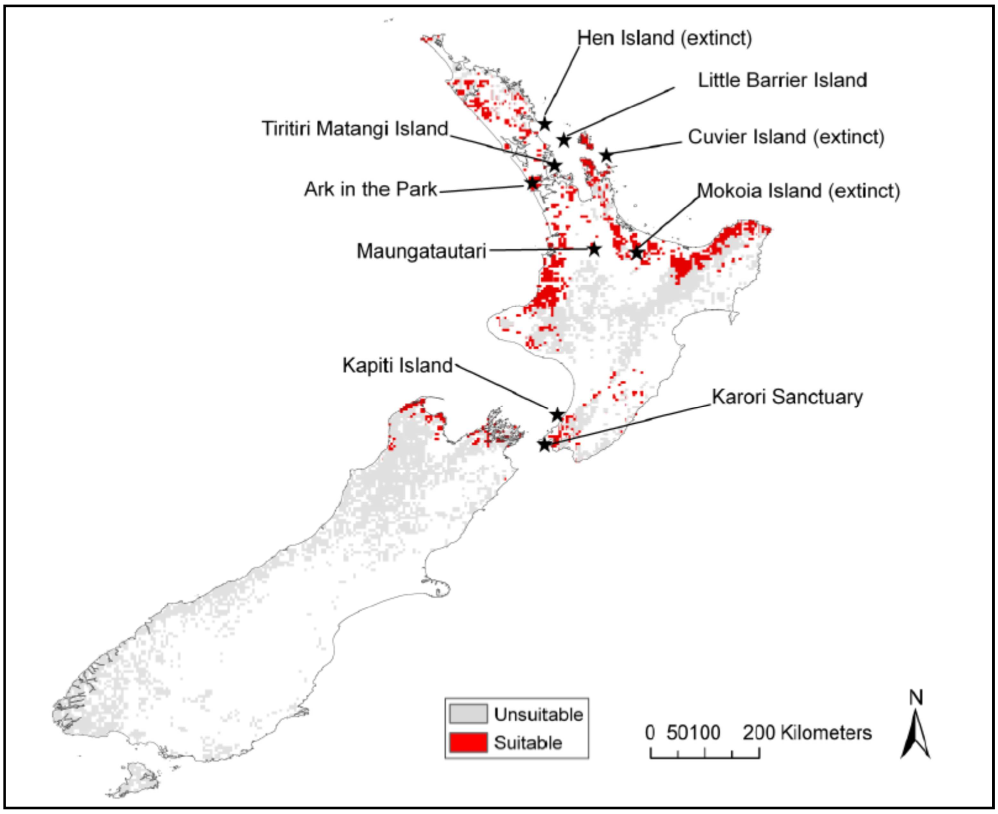

Figure 5.1. Map of current suitable habitat for the hihi obtained using MaxEnt. Every coloured pixel corresponds to a patch of native forest and red pixels show habitat that is suitable for the hihi. For both SDM, the threshold for unsuitable/suitable habitat was determined using the sensitivity-specificity sum maximisation approach (Liu et al., 2005).

Table 5.1. Review of the pros and cons of the most commonly-used SDM algorithms for modelling species distribution. "PA" stands for presence-absence and "PO" for presence-only data requirement.

Name	Data	Brief Description	Pros	Cons	Reference
BIOCLIM	PO	It assesses the suitability of a location by comparing the values of environmental variables at any location to a percentile distribution of the values at known locations of occurrence.	• Easy to understand and to teach • Can be run from R (package 'dismo')	• Outperformed by more recent algorithms • Not very good in the context of climate change	Elith et al. (2006) Hijmans and Graham (2006) Hijmans and Elith (2011)
DOMAIN	PO	It calculates the Gower distance between environmental variables at any location and those at any of the known locations of occurrence.	• Extensively used for species distribution modelling • Can be run from R (package 'dismo')	• Outperformed by more recent algorithms • Performed poorly in the context of climate change	Carpenter et al. (1993) Elith et al. (2006) Hijmans and Graham (2006) Hijmans and Elith (2011)
Generalized Linear Models	PA	GLM is a generalization of basic least squares regression. It fits models using	• Very flexible: multiple linear,	• Requires absence data	Guisan et al. (2002)

(GLM)		maximum likelihood (ML) and by allowing the magnitude of the variance of each measurement to be a function of its predicted value	logistic or Poisson regression models can be run • Run in R		Hijmans and Elith (2011)
Generalized Additive Models (GAM)	PA	Classified as a "regression" method but akin to "machine learning" methods. Similar to GLM but, in GAMs, the linear predictor is the sum of smoothing functions.	• Can fit more complex functions than GLM • Run in R (package 'mgcv')	• Requires absence data • Complexity	Wood, (2006) Hijmans and Elith (2011)
MaxEnt	PO	It is a machine learning algorithm that relies on the principle of maximum entropy to identify habitat with the highest probability of presence of species.	• Designed for making predictions • Most widely used SDM at present. • Can be run as a standalone Java program or in R (package 'dismo')	• Not always as flexible as GLM or GAM: cannot use a formula notation	Phillips et al. (2006, 2009) Hijmans and Elith (2011)
Environmental Niche Factor Analysis (ENFA)	PO	It compares the distribution of the presence records of species in the "ecogeographical variables" space compared to all other locations in the study area.	• Similar to GLM but without needing absence data • Run with the standalone BIOMAPPER software • Good when data quality is poor	• Outperformed by GLM when the presence-absence data is good, i.e., absence records are not unknown or unreliable	Hirzel et al. (2001)

Genetic Algorithm for Rule-Set Prediction (GARP)	PO	It contains several distinct algorithms in an iterative, artificial-intelligence-based approach which are used to produce “rules” Those rules are used to define if portions of the species’ distribution are within its niche or not.	• A superset of other modelling approaches, it should have a greater predictive ability than any of them	• The underlying model used in GARP is not accessible and hard to interpret	Stockwell and Peters (1999) Peterson (2001)

Environmental data

To test our hypotheses (H1-3), we downloaded GIS layers containing data on several environmental variables that were recorded between 1950 and 2000 (referred to as the "current" conditions), and for which predictions exist for 2050 and 2100 (referred to as "future" conditions), from the WorldClim database (version 1.4; www.worldclim.org; Hijmans et al., 2005). We chose to work at a 2.5 arcminute resolution, which is the second smallest grid size available from WorldClim. The smallest resolution, 30 arcsecond, was not used because assumptions made during the downscaling process for future conditions may yield uncertain results (Ramirez-Villegas and Jarvis 2010).

Environmental layers downloaded were: total monthly precipitation and average monthly temperature (i.e., one layer per month for each variable), as well as the 19 "BioClim" variables (version 1.4; www.worldclim.org; Hijmans et al., 2005) which are climate variables derived from the minimum, maximum and average temperature, and total precipitation (Appendix 5A). Because the average temperature during the breeding season and total precipitation during the non-breeding season have been found to partially drive hihi dynamics (Chauvenet et al. unpublished), we averaged the mean monthly temperature across September, October, November, December, January and February to create a "breeding temperature" layer. Similarly, we summed the total monthly precipitations across March, April, May, June, July and August to create a "non-breeding precipitation" layer. We used the two new created layers rather than individual monthly layers of mean temperature and total precipitation in the analyses below.

As far as future conditions were concerned, we downloaded layers of predicted climate for three emission scenarios (B2, A1B, and A2) and two climate models (HADCM3 from the Hadley Centre for Climate Modelling and CSIRO from the Commonwealth Scientific and Industrial Research Organisation). Those scenarios represent three different potential futures for the Earth; A1B is often referred to as a "middle of the road" scenario where population growth gradually declines after 2050 and the world relies both on fossil and non-fossil fuels equally; B2 corresponds to a world with a slow and continuous population growth but more ecologically friendly, and A2 refers to a world with a continuously fast increasing population, regionally-driven economic development and decline in the environment (IPCC 2007). Two different Global Climate Models (or GCMs) were used as it is known that different models may yield different results and those two models are amongst the most commonly used in the literature (see, e.g., Loarie et al., 2008; Evangelista et al., 2011; Synes and Osborne, 2011; Luedeling and Neufeldt, 2012). Moreover there was no Regional Climate Model (RCM) for New Zealand readily available.

Habitat Suitability Modelling

Because the extent of the range where hihi is present was entirely known, although our record dataset did not contain absence locations, we could easily create an absence record by identifying areas where the species has not been reintroduced. Moreover, the certainty regarding the truthfulness of presence and absence records was very high, i.e., we knew absences were true absences rather than the result of not seeing the species at the time of survey. This yielded the unique opportunity to use and contrast two commonly-used habitat suitability modelling methods: Generalised Linear Modelling (or GLM), which is a presence-absence model, and MaxEnt, which is a presence-only model (H3; see Table 5.1 for a description). Both models and subsequent testing were performed in R (2.15.0; R Core Development Team 2011) using the ‘dismo’ package (Hijmans et al., 2012).

GLM: presence-absence

We first constructed an absence record for the hihi by randomly selecting data points throughout North Island, as it is where hihi were historically found. We chose 5000 points, which corresponds to approximately half of the total pixels in North Island but also tested the sensitivity of GLM results to different sample sizes and found it didn't impact our results (Appendix 5B). Then, we ran GLM models with a binomial error structure and a logit link (and 5000 absence data points) to find the best combination of climate variables to predict hihi habitat suitability in New Zealand. This involved first selecting the variables that were not correlated with each other within the 21 predictor variables dataset (i.e., breeding temperature, non-breeding precipitation and the 19 BioClim variables). We then used all the uncorrelated variables in GLM models, alone and as additive combination. Moreover, because relationships between habitat suitability and predictor variables may not be linear, we also investigated whether each variable was significant as a second degree polynomial. The best model was selected using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). Because of the random nature of the artificial absence record, we performed the model selection step 500 times which meant repeating the procedure of selecting 5000 absence data points, fitting GLM models and selecting the best model with AIC 500 times.

Using the best model, we predicted the current distribution of suitable habitat for the hihi, and then the future distribution of its suitable habitat for the 3 scenarios, the 2 GCMs and 2 time frames, i.e., $3 \times 2 \times 2 = 12$ simulations. When using SDM in a conservation context, it is sometimes best to distinguish suitable from unsuitable habitat, rather than present probability of species presence because the former is easier to interpret and use to make decisions. This required setting a threshold below which habitat is not suitable and vice-versa. Arbitrary thresholds, e.g., 0.5 (Stockwell and Peterson, 2002) or 0.3 (Robertson et al., 2001), are often used in ecology but they are subjective and can be biased (Liu et al., 2005). Instead, we used the "maximum of the sum of the sensitivity and specificity" threshold approach which maximised the agreement between observed and predicted distributions (Liu et al., 2005; Hijmans and Elith 2011).

The fit of the GLM model to the data was assessed using the area under the ROC curve (AUC). An AUC of 1 indicates that the predictor variables perfectly explain the species distribution while a value of 0.5 indicates that model predictions are not better than random, thus the higher the AUC value the better. To calculate AUC, we used k-fold partitioning (Hijmans and Elith 2011): the presence data was partitioned into 5 groups, and this action repeated 5 times. Each time, 1 group was used for model testing and the other 4 for model fitting and we averaged the AUC across the 5 simulations.

MaxEnt: presence-only

We used MaxEnt 3.3.3 (Phillips et al., 2006; Phillips and Dudık 2008). All 21 variable predictor variables (i.e., breeding temperature, non-breeding precipitation and the 19 BioClim variables) as one of the purposes of this machine-learning algorithm is to identify variables that are good predictors of species' habitat suitability. When running MaxEnt, we modified two of its parameters: the default prevalence and the percentage of the dataset set aside for testing. The default prevalence parameter, or tau τ, in MaxEnt is τ=0.5 which amounts to saying that if a survey is conducted in the known suitable range of the species, the chance of sighting is 50%. However, from previous studies (Armstrong et al., 2002, 2007; Chauvenet et al., 2012) we know that the sighting probability of hihi is very high *c.* 80%. As a result we set τ=0.8 to reflect the fact that if we were doing surveys in hihi range, we would have a large chance of encountering the birds. We chose to put 20% of the data aside for testing purposes (a similar method to k-fold partitioning).

We first ran the MaxEnt algorithm with only the layer containing the current climatic conditions to map the current suitable habitat for hihi. We then ran MaxEnt with layers for the 3 scenarios, the 2 GCMs and 2 time frames, i.e., 3x2x2=12 simulations. Similarly to GLM, we also separated suitable from unsuitable habitat using the "maximum of the sum of the sensitivity and specificity" as a threshold and the fit of the MaxEnt model to the data was assessed using the AUC.

Finally, suitable hihi habitat is not only dependent on climatic conditions, but also on the right habitat type and natural food supply. Indeed hihi will be unlikely to survive, or at least have a much reduced chance of survival, in urban areas or in patches of exotic vegetation. We therefore clipped the suitable habitat predicted by GLM and MaxEnt to a layer of the distribution of native forest from the New Zealand Land Cover Database (http://www.mfe.govt.nz/issues/land/land-cover-dbase/index.html). We chose not to include that layer into the models themselves because it may have masked the effect of climatic variables. Moreover, all current locations are located inside native forest patch so there would have been no variation to model.

RESULTS

The presence record for the hihi contained 27 point locations distributed into 9 populations (Figure 5.1).

We expected hihi suitable habitat distribution to be better predicted by the breeding season and total precipitation during the non-breeding season (H1) but found that it was not true for GLM or MaxEnt. Moreover the best predictors of hihi habitat suitability among the BioClim set were almost all temperature-based variables rather than related to rainfall. For the GLM model, there were 8 predictor variables that were uncorrelated: breeding temperature, non-breeding precipitation, BioClim2 (mean diurnal temperature range), BiolClim3 (isothermality), BioClim4 (temperature seasonality), BioClim8 (maximum temperature of the wettest quarter) BioClim9 (maximum temperature of the driest quarter) and BioClim15 (precipitation seasonality). The best model according to AIC contained all except BioClim8, BioClim15 and non-breeding precipitation (Table 5.2, Appendix 5B). Moreover, all included variables were second degree polynomials (Table 5.2). In MaxEnt, the variables with the largest contribution in predicting hihi suitable habitat were: BioClim9 (50.3%), BioClim2 (24.3%), BiolClim6 (9.9%; mean temperature of the coldest month), BiolClim15 (5.8 %), BioClim5 (5.1%; max temperature of warmest month). The rest of the predictor variables contributed a marginal percentage or no percentage to the habitat suitability models.

The average AUC for the GLM method was 0.51 (s.d. 0.22), while it was 0.891 (s.d. 0.027) for the MaxEnt method. Therefore, as expected, MaxEnt significantly outperformed GLM (H2). Because of the poor performance of GLM, we concluded that MaxEnt yielded the most trustworthy results and only further describe its results. We found that, at present, there are many small patches of native vegetation that MaxEnt indicated as suitable for hihi (in red on Figure 5.1). Specifically, 31.4% of the total native vegetation of North Island, or 17% of the total native vegetation of New Zealand, was classified as suitable under current conditions. Current suitable habitat tended to be distributed alongside the coasts of the North, West and South sides of the Island. The East coast and the centre of North Island were both predicted as unsuitable (grey pixels in Figure 5.1).

Table 5.2. Estimates of Generalised Linear Model (GLM) used to predict the suitability of hihi. '*' indicates a significant result, and '^{2}' indicates a second degree polynomial.

Variable	Estimate	SE	Z value	P value
Intercept	-2287.00	908.10	-2.519	0.011775*
Breeding temp	-7.62	3.02	-2.522	0.011664*
Breeding temp^2	0.02	0.01	2.505	0.012261*
BioClim2	-6.98	1.67	-4.177	2.95E-05*
BioClim2^2	0.04	0.01	3.862	0.000113*
BioClim3	89.07	38.93	2.288	0.022146*
BioClim3^2	-0.96	0.42	-2.28	0.022587*
BioClim4	0.17	0.08	2.313	0.020719*
BioClim4^2	0.00	0.00	-2.12	0.034047*
BioClim9	10.25	3.33	3.077	0.002093*
BioClim9^2	-0.03	0.01	-3.076	0.002101*

When projecting the suitable range of hihi in the future, we combined the results of both GCM as they yielded similar results for all scenarios (Table 5.3). Indeed, they agreed on more than 73%, and up to 90%, of where the most suitable habitat for the hihi will be in 2050 and 2100, thus showing a high level of consistency. Moreover, by only selecting pixels identified as suitable by both GCM, we increased the level of confidence of the projections. We expected that hihi suitable range will shift southward as a response to climate change and found this pattern to be true (H3; Figure 5.2). The Northern part of New Zealand, which was highly suitable in current conditions, may become almost entirely unsuitable in the next few decades. However, the South-West and South-East of North Island, as well as the Northern part of South Island showed a larger extent of suitable hihi habitat in 2050 and in 2100 than under current conditions. As a result, out of all the current hihi populations, two of the translocated ones (Tiritiri Matangi Island and Ark in the Park) and the remnant population on LBI may be faced with unsuitable conditions in the future (Figure 5.2). Interestingly, scenario A1B, which is one of the better outcomes for the Earth, was the only scenario that resulted in an overall increase of suitable pixels for the hihi in 2050 and 2100 (Table 5.3). Both B2 and A2 resulted in a percentage of suitable pixels smaller than the one under current conditions (17%), but yielded different suitable habitat distribution from each other (Figure 5.2).

Table 5.3. Comparison of MaxEnt results using the CSIRO and HADCM3 GCMs. "Shared suitable pixels" were pixels predicted as suitable for the hihi by the two GCMs. Numbers in bold indicate where the percentage of suitable habitat in the future was greater than in the current conditions.

Time	Scenario	Number of suitable pixels for CSIRO (% of total available)	Number of suitable pixels for HADCM3(% of total available)	Number of shared suitable pixels (% of total available)
2050	B2	966 (**19.3**)	627 (12.5)	545 (10.9)
	A1B	1210 (**24.1**)	1233 (**24.6**)	890 (**17.7**)
	A2	1019 (**20.3**)	1114 (**22.2**)	801 (15.9)
2100	B2	1228 (**24.9**)	704 (14)	593 (11.8)
	A1B	1697 (**33.8**)	1774 (**35.28**)	1240 (**24.7**)
	A2	1450 (**29.9**)	905 (**18**)	787 (15.7)

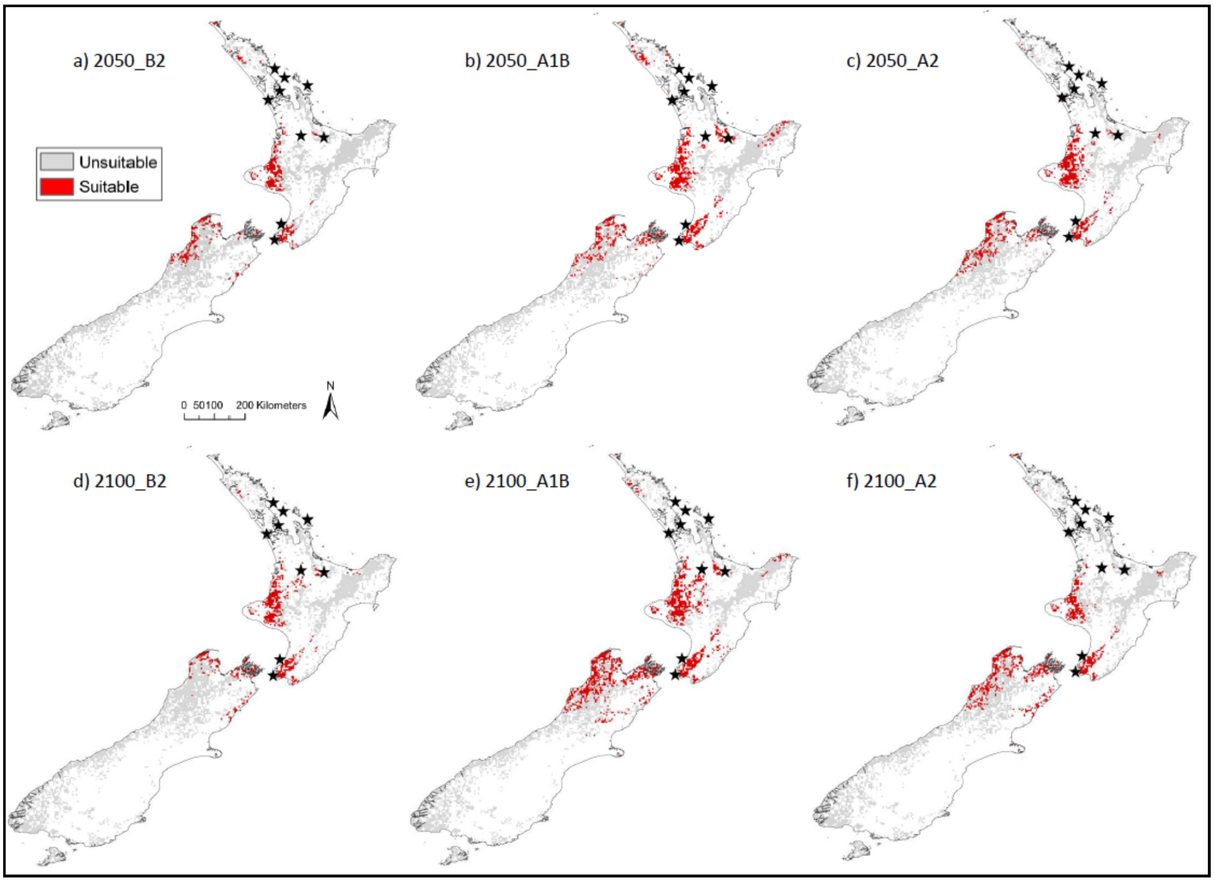

Figure 5.2. Map of future suitable habitat for the hihi in 2050 and 2100 obtained using MaxEnt. Shown are the pixels selected as suitable by both HADCM3 and CSIRO, for 3 different scenarios: B2 (a, d), A1 (b, e), A2 (c, f), and for 2 timeframes: 2050 (a-c) and 2100 (d-f). Every coloured pixel corresponds to a patch of native forest and red pixels show habitat that is suitable for the hihi. For both SDM, the threshold for unsuitable/suitable habitat was determined using the sensitivity-specificity sum maximisation approach (Liu et al., 2005).

DISCUSSION

It is clear that climate change will have a strong impact on the distribution of suitable climatic conditions, and thus habitat for the hihi. It is expected, and has already been observed, that climate change will cause species' optimal habitat to move poleward as global temperature rises (Parmesan and Yohe, 2003; Root et al., 2003; Hickling et al., 2006). Indeed, we found that the most suitable climatic conditions for the hihi are expected to shift southward by at least a couple hundreds of kilometres in the next few decades. Not only that, but range that was not part of hihi distribution historically, i.e., South Island, will boast highly hospitable climate for the species in the near future.

By using two very different habitat suitability models, we were able to investigate which method gave was the most efficient, and best results, for the hihi. Not surprisingly, the presence-only software MaxEnt performed best, as it was designed to model our kind of data. By adding absence data to our dataset to use in GLM, we essentially marked a lot of potentially suitable habitat as unsuitable. Because hihi distribution is almost entirely man-made, and the species is not able to naturally disperse towards that potentially suitable habitat, this may explain why GLM did not perform well. Nevertheless, testing both methods enabled us to identify a SDM that can be efficiently used for future management of hihi.

The fact that precipitation seemed to have little impact on hihi habitat suitability was unexpected. This could be explained by the limited variation in the amount of yearly precipitation between the locations of the current hihi populations. Indeed, there is relatively little variability in rainfall across North Island, particularly where hihi have been translocated. Moreover, because it was using presence-only data, and our sample size was small and spatially-biased, MaxEnt was likely not very good at predicting suitability in areas where climate was beyond observed conditions. Therefore, although our results seemed to indicate that hihi habitat suitability was mostly driven by temperature and that precipitation only had a small impact, they should be treated with caution.

One of our aims was to assess the future suitability of the current hihi locations. As every population is either on an island or isolated, hihi will not be able to disperse naturally if conditions become unsuitable where they live now. It was apparent that the translocation sites that are northernmost (Tiritiri Matangi Island and Ark in the Park) might not remain within the best climatic conditions for hihi as climate changes. However, one of the management actions for translocated hihi populations is *ad libitum* supplemental feeding. As it is a parameter that could not be taken into account in MaxEnt, there was no telling how it affects the overall suitability of translocation sites. It may potentially compensate for the expected climate harshness these populations will face. However, the remnant population on LBI is not currently supplemental fed and is also predicted to be in a less than suitable climate by 2050. This was a worrying result as the population on LBI is also the largest one and a constant source of individuals for future translocations.

One of the most interesting, and potentially controversial, findings of this analysis was the fact that a large part of the future suitable habitat for hihi is in an area of New Zealand where the species was not found historically. Therefore, our results suggested that assisted colonisation, rather than reintroduction, may be in the future for the species. Assisted colonisation, which has been defined as "translocation of a species to favourable habitat beyond their native range to protect them from human-induced threats, such as climate change," (Ricciardi and Simberloff, 2009a; Seddon, 2010) is still a fairly contentious idea because it is first and foremost an introduction. The risks associated with introducing species are high and the impact of introduced species can range from benign (which is what we aim for with assisted colonisation) to invasive, and invasive species can have devastating consequences economically and ecologically. However, if translocated there, it is very unlikely that the hihi will become invasive on

South Island. Indeed the species is a small cavity-nester, which, until all introduced predators have been eradicated, can only be translocated into fenced territories. Indeed, evidence from the last 30 years of recovery program shows that hihi were not capable of surviving dispersal beyond predator-free areas. They may thus be an excellent candidate for assisted colonisation.

There are several limitations to our study, however. First, habitat suitability modelling have been criticised in the past for simplifying too much the relationship between environment and species distribution (Davis, Jenkinson, et al., 1998; Davis, Lawton, et al., 1998; Pearson and Dawson, 2003). Indeed, the principle behind SDM is that an exhaustive list of simple environmental characteristics, often only abiotic ones are included, will determine whether a species is able to survive in a given location (Elith and Leathwick, 2009). In reality, species are part of communities and inter-specific relationships will play a major role is their persistence. This may be particularly true when investigating the impact of climate change as species are likely to move into novel environment and thus encounter new species assemblage (Davis, Jenkinson, et al., 1998; Davis, Lawton, et al., 1998; Pearson and Dawson, 2003).

Second, our results, like in any habitat suitability modelling exercise, are entirely dependent on selecting appropriate predictor variables. If the list of predictors we used in MaxEnt or GLM did not contain the key variable to determine hihi habitat suitability because we are yet to discover it, then predictions achieved here are useless. The high value of AUC achieved in MaxEnt, however, indicated that the predictor variables used were a good fit for the species. The key to performing the best possible habitat suitability models may be to include predictor variables that make sense biologically. Nevertheless, it is best not to be too restrictive in that choice. We tried to only use the average temperature during the breeding season and the total precipitation during the non-breeding season as predictor variables in MaxEnt because they are specifically known to influence hihi dynamics, but this yielded an AUC of 0.75 (results not shown).

Third, to predict the future suitability of hihi habitat, we arbitrarily selected two GCMs and three hypothetical climate change scenarios. Although not a lot, there were some discrepancies between the predictions of CSIRO and HADCM3 models for the same scenarios, showing that if we had only chosen one model, we may not have seen the uncertainty in suitability predictions. Moreover, if we had chosen other GCMs, it is likely we would have obtained slightly different results. In addition, we investigated three scenarios, with distinct storylines (IPCC 2007) and made predictions on habitat suitability if either one becomes true. In reality, there is a large amount of uncertainty in climate predictions, and future climate will depend on the mitigation strategies that are put in place today and in the future. Therefore, the fine-scale predictions of future suitable habitat for the hihi might not be correct if none of the investigated scenarios become true. However, we are confident that the consistent pattern of suitable habitat shifting southward will hold whatever the impact of climate change.

Finally, another inherent assumption made when using habitat suitability models is that the current species range is a good indicator of suitable habitat. However, this may not be true (Osborn and Seddon 2012). Similarly, as attested by the poor performance of GLM, current absence from habitat may not signify unsuitability of non-occupied range. Indeed, the reason why hihi are not more widespread on North Island is because they were extirpated several decades ago and have been unable to recolonise because of their vulnerability to predators and the sparse native vegetation. As a result, the habitat in which hihi can thrive may actually be more varied and much larger than predicted. Nevertheless, our results were achieved with the best available data.

Overall, our findings demonstrated that species distribution models are an easy to use, and useful, tool to identify habitat suitable for species translocation. Surprisingly, while some examples of SDM being used to identify potential translocation sites can be found in the published literature, there is no evidence yet of SDM used for selecting release habitat under global environmental change. By not explicitly taking into account the potential impact of climate change on the spatial distribution of environmental conditions, managers run the risk of investing money, time, and effort into the translocation of a species where it has no chance of long-term persistence. This is not only a waste of conservation resources, which are known to be in limited supply, but it begs the question of the ethics of human intervention when it is not planned using the best available method and lead to the direct death of the individuals of a threatened species.

We recommend that Species Distribution Models be systematically used to select translocation sites for threatened species. They should not only be parameterised with data on current climate but should also investigate the impact of projected climate change on the distribution of suitable habitat. SDM will minimise the chance of failure of translocation attempts on the short and long-term, but will also maximise their cost-efficiency. Otherwise, uninformed conservation translocation will continue to be performed, the overall success of translocation attempts will remain low and the efficiency and reputation of this potential adaptation toll remain low.

CHAPTER 6

Overall Discussion

INTRODUCTION

The world's biodiversity is facing an unprecedented level of threat. Humans are thought to be responsible for a 100- to 1000-fold increase in species loss compared to natural extinction rates (Pimm et al., 1995). The most well-know direct threats to species are the "evil quartet" of over-exploitation, introduced species, habitat loss, degradation and fragmentation, and trophic cascade co-extinctions (Diamond, 1984). In addition to those, climate change is widely accepted as the worst indirect threat to biodiversity. Climate change has a global impact and is predicted to affect the average and variance of temperatures and precipitations, increase the frequency and strength of extreme natural events and change vegetation phenology (Foden et al., 2008).

Conservationists have therefore been looking at solutions to help mitigate the impact of global environmental change on species. One potential tool is translocation. Defined as "any movement of living organisms from one area to another" (IUCN 1987), there are two major types of translocations: reintroductions and introductions. Reintroductions aim to move individuals of a species into areas where it was found historically but has since been extirpated. Introductions aim to move individuals of a species into areas that were not part of its historical range. Translocation has been used as a species conservation tool for decades e.g., the earliest reintroduction record dates back to 1907 (Kleiman, 1989; Seddon et al., 2007). Nevertheless it wasn't until 1980s that the lack of scientific rigour when designing and monitoring translocations became a concern in the light of the overall poor success rate of projects. Yet, 30 years later, there is still no systematic use of quantitative tools when planning and implementing translocations (Seddon et al., 2007).

Translocations have recently started being considered as tools to help species adapt to climate change under the name assisted colonisations. While the concept of assisted colonisation has been heavily debated in the literature, little effort has been made to improve translocation success more generally. Considering that translocations, of any kind, are costly endeavours (Caldecott and Kavanagh 1983; Moran, Cullen, and Hughey 2005) and that failure means not only losing the investment made in terms of time and money but also the death of individuals from a threatened species, improving their success should be a priority.

With this thesis, I aimed to (1) understand how translocated species will respond to climate change and if their population viability will be comprised and (2) develop a quantitative framework to improve the success rates of conservation translocation under global environmental change.

I used the hihi (stitchbird; *Notiomystis cincta*) as a study species. It is a small cavity-nesting passerine bird (Castro et al., 2003) native to the North Island of New Zealand, and classified as vulnerable on the IUCN Red List (Birdlife International 2007). Following European colonisation of New Zealand, hihi were driven to quasi-extinction by introduced mammal predators (mainly rats *Rattus* sp.), habitat loss and diseases (Rasch et al., 1996). Hihi eventually became restricted to one remnant population on Little Barrier Island (LBI or Hauturu; www.hihiconservation.com). They have been the subject of several successful and unsuccessful translocations in the past few decades and, today, persist in six wild populations (LBI and five translocated ones). In every translocated population, hihi are being monitored individually. The hihi recovery program is, therefore, the source of a multi-population monitoring dataset that is coordinated by the national Hihi Recovery Group. Complementary multi-site information helps put data into context and offers a resource that is perfect to model the dynamics of translocated populations. The hihi thus presented an ideal case study to answer my thesis aims for two reasons. First, I was able to study two translocated populations that were established on islands more than a decade ago and have been intensively monitored ever since. Second hihi are highly vulnerable to the impact of climate change because (1) they are a rare and highly specialised New Zealand endemic, and (2) current populations survive on small islands or island-like areas, which makes them isolated and almost incapable of naturally shifting their range in response to climate change.

KEY FINDINGS

In this thesis, I have showed that biological, environmental (Chapter 2) and management (Chapter 3) factors significantly impact the dynamics of translocated populations. Those factors may also interact with each other in complex ways, rendering predictions of future dynamics difficult. I have showed that climate is a key driver of translocated populations' dynamics and climate change is likely to affect their long-term viability (Chapter 4). I demonstrated that not taking climate change into account when selecting translocation sites could lead to populations being moved into areas that will not remain suitable in the future, thus compromising the survival of threatened individuals and wasting limited conservation funding (Chapter 5). I also developed a general framework to plan and implement translocations under climate change as a set of quantitative questions accompanied by the methods that can be used to answer them (Chapter 1): simple analytical tools such as population dynamics modelling and habitat suitability modelling are key to maximising the success of translocations as an adaptation tool to climate change.

This thesis presents results that are novel and significant advances in the field of translocation science and reintroduction biology. First, studies that look at the potential impact of interactions between intrinsic and extrinsic factors on population dynamics are rare for threatened species and non-existent for translocated ones. I thus present the first study of this kind for a translocated population, identifying a complex link between climate, species' vital rates and long-term population dynamics. Second, I also develop the first predictive population model that quantifies both the impact of increases in mean and variance in temperature and rainfall on species' persistence, and the impact of temporal correlation in those variables that causes extreme weather like droughts and hot spells to change in length and frequency, on threatened species' viability. Those two approaches are particularly relevant for populations that are isolated and unable to naturally disperse, because they will inevitably be faced with new environmental conditions as climate changes. This will be the case for many translocated populations as it is not uncommon to translocate into areas from which individuals cannot disperse as it is easier to control threats such as predators (Armstrong and McLean, 1996; Prendergast et al., 1999). Finally, I also present the first quantitative guidelines for planning and implementing translocations under climate change, i.e., assisted colonisation, which address the known issues limiting translocation success. Their use could guarantee that translocation projects across the globe are performed while taking into account climate change, something that is not yet common, with decisions being quantitative, hence justifiable and transparent.

Each chapter of this thesis lists and discusses its own set of limitations regarding methodologies or assumptions made. However, the overarching approach used to reach the stated aims has two major limitations. The first one is that all studies were conducted using a single species of small passerine bird, which is endemic to New Zealand and have only been translocated to areas where they used to be found in the past. This may have several consequences on the ability to draw general conclusions for translocated populations. First, findings regarding the impact of different factors on hihi dynamics may not be comparable with results that would be obtained using another translocated population such as from a different species or taxa, from New Zealand or elsewhere. It is fair to expect that the intrinsic differences between two species, even closely related ones, will impact their response to environmental change. However, the general conclusions regarding the importance of climate as a driver of population dynamics, and the complexity of its impact due to possible interactions with other factors, will hold for many species, in particular those that are isolated and unable to disperse to escape climate change, like the hihi. Second, because all hihi populations have so far been reintroduced, rather than introduced, there may be unknown biases in certain aspects of the species' dynamics. This may be due to the fact that current reintroduced populations are experiencing very similar conditions to those the species has evolved experiencing. As a result, conclusions drawn from the study of the dynamics of reintroduced populations may not be informative regarding the dynamics of introduced ones. To my knowledge, there is no published study that compares the dynamics of introduced and reintroduced populations of the same species and this bias has not been evaluated. The second one is that the two populations of hihi for which population dynamics is studied in depth are not natural ones, but were reintroduced in the early 1990s. As a result, it is possible that the conclusions reached when studying them may not reflect conclusions that would be reached if the population studied were natural ones. This could have significant implications for the future management of the species as results from the predictive population model and habitat suitability model could be invalid and unfit for management decision-making. At present little is known of the ecology of hihi when they were still extensively present on North Island. One way to make sure the results presented here are not biased due to populations being man-made would be to initiate a long-term monitoring study of the last remnant hihi population on LBI. While those birds are already monitored to an extent, the terrain and vegetation of LBI have thus far prevented in-depth study like those on Tiri or Kapiti. Therefore, the studies conducted for this thesis were done using the best available data.

FUTURE RESEARCH DIRECTION

What next for the hihi?

Research and conservation go hand in hand when it comes to recovery efforts for the hihi. As a result, there have been extensive research of the species' behaviour ecology (e.g. Castro et al., 1996; Armstrong et al., 1999; Ewen et al., 1999; Low, 2005; Ewen and Armstrong, 2007), population dynamics (e.g. Armstrong and Perrott, 2000; Armstrong et al., 2002; Low et al., 2007; Low and Pärt, 2009) and population genetics (e.g. Brekke et al., 2009, 2010, 2011; Wang et al., 2010). Along with a growing understanding of these aspects, conservation decisions for single populations and the species as a whole have improved, potentially getting closer to an unknown optimal. Nevertheless, the success of each translocated population of hihi is not equal. Only two of the extant hihi populations were studied for this thesis, and both can be considered a success, albeit a costly one in terms of management. However, some of the translocated hihi populations are not doing as well as those on Tiri and Kapiti, even though they are exposed to the same management. While results in this thesis are hinting at a potential climatic component to the struggle of theses populations, studying the dynamics of less successful hihi populations could greatly improve future decision-making and overall success rate for the species.

Moreover, at present, research involving hihi's behaviour ecology, population dynamics or population genetics, is somewhat performed on its own, each isolated from the other disciplines. To maximise the success of hihi translocations, we should move towards a more integrative and interdisciplinary approach. For example, by coupling the extensive knowledge of hihi genetics and demography in predictive population models, we could gain an even more accurate understanding of the chance of long-term persistence of the species (Robert et al., 2007). Indeed, inbreeding depression has been linked to decline and extinction of wild and captive populations (Frankham, 1995; Madsen et al., 1999; Brook et al., 2002). The hihi population on Kapiti Island was found to have lost most of its genetic variation (Brekke et al., 2011) and may benefit from a better integration of genetics and demography when planning future management. This is especially true in the face of climate change as extreme weather events are going to be more frequent and last longer, which may lead to more frequent and greater drops in population size. The stochastic population model presented in Chapter 3 could be modified to quantify the impact of these potential bottlenecks on the population’s long-term persistence.

In addition, models that are more complex than those that have been built to date could include hihi behaviour to further understand the dynamics of the populations. An example of such models is an Individual-Based Model (or IBM; Grimm and Railsback, 2005), which allows incorporating heterogeneity in behaviour, survival and/or reproduction for each individuals of the population. For example, hihi are highly promiscuous (Castro et al., 1996) and extra-pair copulation is a common behaviour. However there seems to be individual variation in males and females strategies due to sex-specific benefits to producing extra-pair offspring. The impact of this behaviour on long-term persistence could be quantified with an IBM.

The population on Tiritiri Matangi Island is regularly harvested for juveniles to supplement already established populations and sometimes as a source for creating new ones. So far, only very simple harvesting models have been created to quantify how many individuals can be removed from the population based on a fixed target e.g., maintain population growth rate, keep the population above a certain number of adults or breeding pairs (Armstrong and Ewen, in press). The stochastic matrix population model that is presented in Chapter 4 could be modified such that the impact of climate change on the size of harvesting quotas or their optimal frequency could be quantified.

Finally, all translocated populations are intensely managed which means a large monetary investment in overall management (predator control, supplemental feeding, nest boxes) and monitoring (individual survival and breeding). However, they each experience distinct environmental conditions and are expected to face different levels of habitat suitability in the future, thus have unequal probabilities of extinction. Because conservation funding is a finite resource, for the hihi and in general, one question that could be asked is: is the current resource allocation optimal or should money be prioritised toward populations more likely to survive on the long-term. Evidence from the results presented in this thesis, suggest that on the long-term the answer may be yes. Optimisation techniques such as Stochastic Dynamic Programming could be used to answer that question (Chauvenet et al., 2010) and optimise the investment into hihi conservation.

What next for translocations?

The fields of translocation science and reintroduction biology are in constant development and there are many areas where future research could bring exciting and novel results. In this section I do not present an exhaustive list of those but rather discuss three topics that I personally think should be further explored.

There are a number of factors that are likely to influence the success of translocated populations but are yet to be fully investigated. First, we have little no to idea how individual heterogeneity in the release cohort influences immediate post-release survival and breeding success of new populations. Individual heterogeneity can manifest itself through discrete behaviours seen in the population, which impact individuals' vital rates (Vindenes et al., 2008). Because translocated populations often start out small, the fate of single individuals has a greater impact on the ultimate fate of the whole population that if the population was large. Individual heterogeneity could thus have a direct impact of the initial success of a translocation attempt and, as a consequence, the long-term chance of persistence of the population.

Moreover, individual heterogeneity may also influence the ability of the translocated population to withstand stochastic events. Fox (2005) found that species' extinction risk is reduced by heterogeneity in demographic rates. It would be interesting to quantify the trade-off between the amount and distribution of individual heterogeneity in a translocated population and its chance of persistence, especially as it is often a small population thrust into an environment that may be entirely novel. For example, the more heterogeneous a population, the more likely it is that a genotype or phenotype advantageous in the face of catastrophic events will be present, reducing the change of a population going extinct but leaving very few individuals alive. However, if all individuals share the same trait that allows surviving a stochastic event, then it may be more advantageous to have little heterogeneity because almost all the population will survive. On the other hand, if all individuals share a trait that makes the population vulnerable to stochastic events, the lack of heterogeneity will result in total extinction.

Finally, no tool currently exists for managers to decide on the optimal management regime for a population that has been translocated. Some studies have looked at a single, or sometimes a couple, of management actions and their optimal implementation over time but results are limited (Lubow, 1996; Haight et al., 2000; Tenhumberg et al., 2004; Rout et al., 2007). Today, the best practice is to use adaptive management: a management action is initially chosen using the best available knowledge and expert views, it is implemented over a few years and results are monitored and analysed, based on those results the next management action is decided, then monitored and so on and so forth until the population reaches the desired state. This can be a risky strategy as populations that have just been translocated could be very sensitive to management and the wrong decision at the wrong time could have devastating consequences. A model that predicts the optimal management path from the onset would be ideal: an optimisation model could be built to predict what management is best for a population over time using Stochastic Dynamic Programming. The optimal time-dependent management would be based on the initial state of the translocated population, the long-term objective for that population, the different management actions available, how the population respond to each of these actions.

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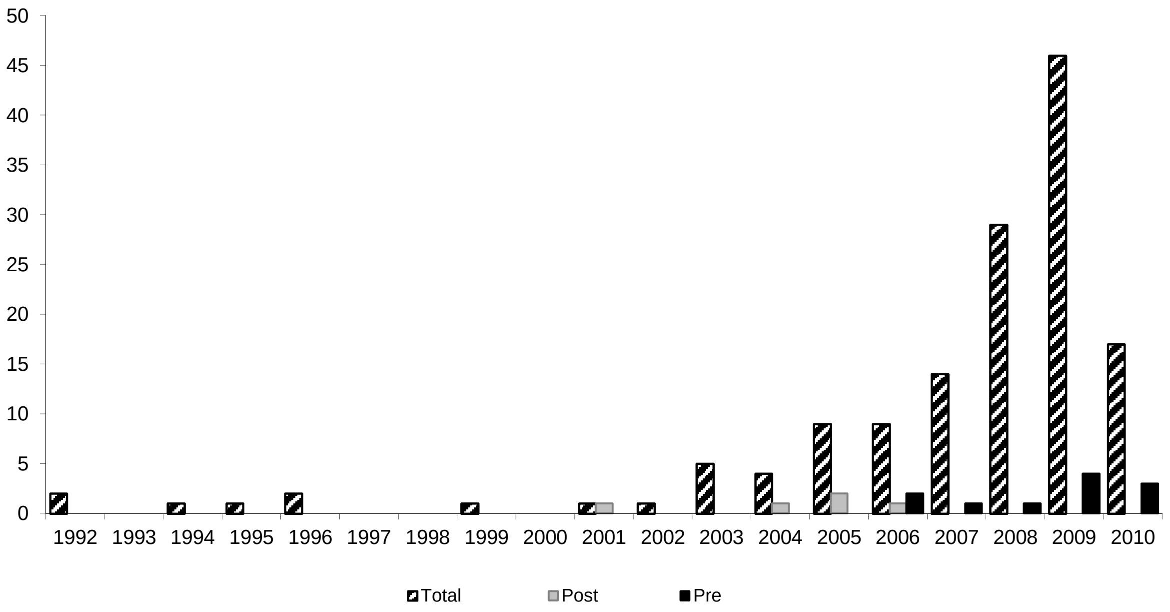
Appendices

Appendix 1A. Number of published articles found in ISI web of knowledge that combine conservation translocation and any mention of climate change. 'Total' is a count of the total number of articles mentioning both climate change and conservation translocation in general; 'Pre' is a count of articles that mention climate change in the planning of a conservation translocation; 'Post' is a count of articles that mention climate change as an explanation for the outcome of a translocation project.



APPENDIX 1B. Articles found in ISI web of knowledge that mentions climate change and an actual translocation project. A tick in the 'Pre' column signals articles that show climate change as taken into account at the planning stage. A tick in the 'Post' column indicates papers in which climate change is mentioned as an explanation for a translocation project outcome.

Pre	Post	Authors	Species	Information
	√	Moss (2001)	capercaillie (*Tetrao urogallus*)	Reports the impact of climate change on the reintroduced capercaillie.
	√	Epps et al. (2004)	bighorn sheep (*Ovis canadensis*)	Reports that climate change can explain population decline and range shift in reintroduced and native populations of bighorn sheep.
	√	Cooney et al. (2005)	greenback cutthroat trout (*Oncorhynchus clarki stomias*)	Climate change is considered after translocations of greenback cutthroat turtle, two scenarios (increase of 2°C and 4°C) are modelled against probabilities of translocation success.
	√	Nolet et al (2005)	beaver (*Castor fiber*)	Explains low success of one beaver translocation by a change in food quality due to climate change.
√		Chan and Packer (2006)	Karner Blue butterfly (*Lycaeides melissa samuelis*)	Assesses potential reintroduction sites for Karner blue butterflies in light of climate change.
√		Martínez-Meyer et al. (2007)	Mexican wolf (*Canis lupus baileyi*) and Californian condor (*Gymnogyps californianus*)	Uses ecological niche modelling to identify future reintroduction sites while taking climate change into account.
√	√	Saltz et al. (2006)	Asiatic wild ass (*Equus hemionus*)	Investigates future impact of climate change on a reintroduced Asiatic

			wild ass population.
√	McLachlan et al. (2007)	Florida torreya (*Torreya taxifolia*)	Reports on the planning of assisted migration of Florida torreya
√	Hellmann et al. (2008)	butterflies (*Erynnis propertius* and *Papilio zelicaon*)	Translocation experiment of two butterfly species to test the effect of climate variation on their survival.
√	Carroll et al. (2009)	butterflies (*Aporia crataegi* and *Polyommatus semiargus*)	Uses climate change modelling to examine the potential for reintroduction of the two butterfly species in Britain.
√	Marsico and Hellmann (2009)	*Lomatium utriculatum, Lomatium nudicaule*, and *Lomatium dissectum*	Translocation experiment of seeds of three species of *Lomatium* to test for poleward limit and migration under climate change.
√	Valle-Díaz et al. (2009)	*Ceiba aesculifolia*	Studies altitudinal gradient in survival of *Ceiba aesculifolia,* and concludes that assisted migration could take place in higher altitudes
√	Willis et al. (2009)	butterflies *(Melanargia galathea* and *Thymelicus sylvestris)*	Uses climatic-envelope model to look for suitable introduction site outside current range before introducing both species in found suitable habitat.
√	Beever et al. (2010)	American pikas (*Ochotona princeps*)	Examines effect of climate on pikas and uses findings to find possible introduction sites.
√	Mitchell et al. (2010)	tuatara (Rhynchocephalia)	Reports an impact of climate change on temperature-dependent sex-ratio and considers translocation to colder habitat to remove the male bias in the population.

√	Morueta-Holme et al. (2010)	Iberian desman (*Galemys pyrenaicus*)	Models the impact of climate change on the desman distribution and shows suitable habitat for assisted range shift.

APPENDIX 2A. Justification of the use of Overall Breeding Success (OBS) in reproduction analysis.

The rationale behind using OBS instead of another measure of reproduction is best illustrated with an example. Consider Female A which laid 10 eggs and produced 5 fledglings, Female B which laid 5 eggs and produced 5 fledglings, and Female C which laid 3 eggs and produced 3 fledglings. Based solely on the number of eggs laid, Female A was the most successful. If looking at the number of fledglings produced, both Female A and B were equally successful but C less so. Instead, if calculating OBS, Female A only fledged 50% of her eggs while Female B and C both fledged 100% of the eggs they produced. Female A thus spent the most energy but only fledged as much as Female B. OBS highlighted that Female B and C were better at raising young during the breeding season because they maximised the number of fledglings for their egg laying effort.

APPENDIX 3A. . Results of POPAN analysis. The parameter pent is always sex*time.

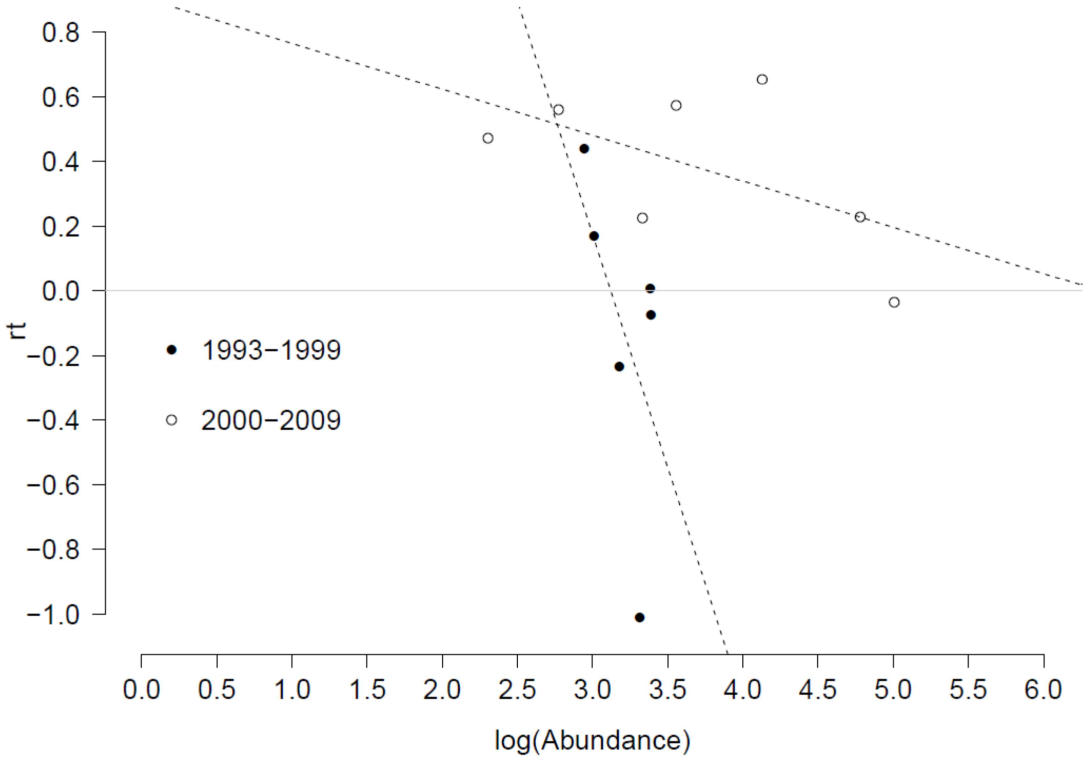
Model	K	AICc	ΔAICc	weight	Deviance
φ(time) p(time)	70	1610.849	0	1	347.3121
φ(sex * time) p(time)	87	1620.758	9.90845	0	317.7912
φ(time) p(sex * time)	88	1643.137	32.28762	0	335.8998
φ(sex * time) p(sex * time)	105	1662.622	51.77246	0	311.5193

APPENDIX 3B. Standard deviate test results. We tested whether the mean of the standard deviates was different from 0 with a t-test and whether the variance of the standard deviates was different from 1 with a chi-squared test for both scenarios.

Scenario	Mean	Variance
1	-0.246*	0.82
2	-0.479*	0.28*

*p<0.05

APPENDIX 3C. Plot of intrinsic population growth rate, rt, against log(abundance) for the two management periods. The dashed lines represent linear models of rt as a function of log(Abundance).



APPENDIX 3D. Results of tests for statistically significant density-dependence for the Kapiti population during the two management regimes. The test is based on a parametric bootstrapping likelihood ratio test and was developed by Dennis & Taper (1994).

Parameters	1993-1999	2000-2009
a_1	0.8921	0.5797
b_1	-0.034	-0.0033
σ^2	0.02962	0.02275
p	0.4422	0.032*

*significant result indicates density-dependence

APPENDIX 4A. Transition probability matrices for the drought autocorrelation pattern #1 and #2

Drought autocorrelation #1

	Non-Drought	Drought
Non-Drought	0.5	0.5
Drought	0.3	0.7

Drought autocorrelation #2

	Non-Drought	Drought
Non-Drought	0.3	0.7
Drought	0.3	0.7

APPENDIX 4B. Transition probability matrices for the temperature autocorrelation pattern #1 and #2

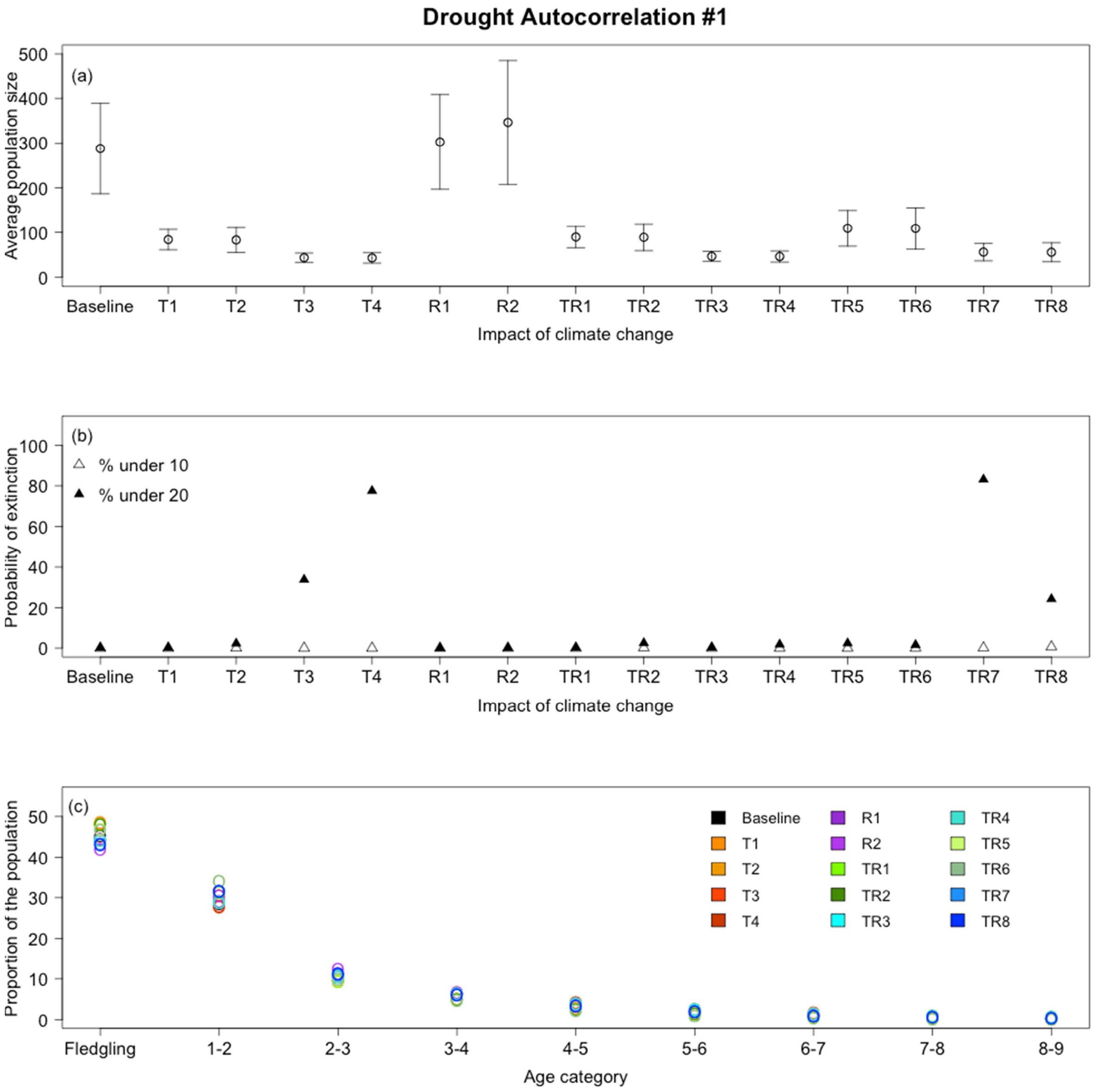
Temperature autocorrelation #1

	Average Temperature	Hot Spell
Average Temperature	0.5	0.5
Hot Spell	0.3	0.7

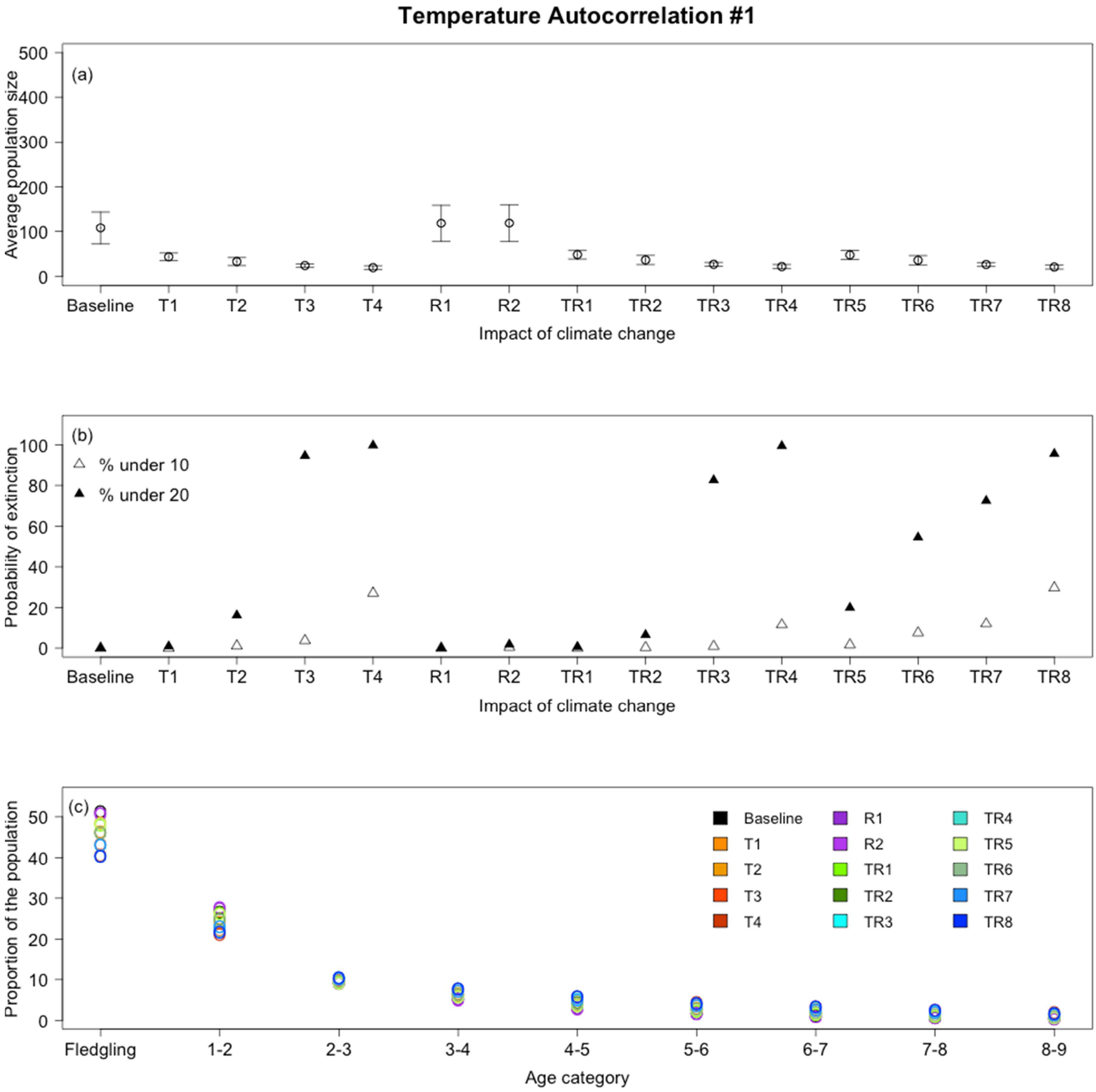
Temperature autocorrelation #2

	Average Temperature	Hot Spell
Average Temperature	0.3	0.7
Hot Spell	0.3	0.7

APPENDIX 4C. Impact of the different aspects of climate change (see Table 4.2) when there is temporal autocorrelation in rainfall such as droughts last longer on: (a) the average hihi population size, (b) the probability of the population being smaller than 20 and 10 individuals, and (c) the population's age-structure.



APPENDIX 4D. Impact of the different aspects of climate change (see Table 4.2) when there is temporal autocorrelation in temperature such as hot spells last longer on: (a) the average hihi population size, (b) the probability of the population being smaller than 20 and 10 individuals, and (c) the population's age-structure.



Appendix 5A. Description of the BioClim Variables as found on http://www.worldclim.org/bioclim.

BioClim variable	Description
1	Annual Mean Temperature
2	Mean Diurnal Range (max temp - min temp))
3	Isothermality (BioClim2/BioClim7) (* 100)
4	Temperature Seasonality (standard deviation *100)
5	Max Temperature of Warmest Month
6	Min Temperature of Coldest Month
7	Temperature Annual Range (BioClim5-BioClim6)
8	Mean Temperature of Wettest Quarter
9	Mean Temperature of Driest Quarter
10	Mean Temperature of Warmest Quarter
11	Mean Temperature of Coldest Quarter
12	Annual Precipitation
13	Precipitation of Wettest Month
14	Precipitation of Driest Month
15	Precipitation Seasonality (Coefficient of Variation)
16	Precipitation of Wettest Quarter
17	Precipitation of Driest Quarter
18	Precipitation of Warmest Quarter
19	Precipitation of Coldest Quarter

APPENDIX 5B. Sensitivity of GLM results to variation in the number of absence data points. For each absence sample size, the GLM was run 500 times. Shown is the mean AUC per 500 runs, as well as the percentage of simulations for which (1) the best model was the one further used in the analysis (model 1), (2) the best model contained the same variables as model 1 plus BioClim8 and BioClim8^{2,} (3) the best model contained the same variables as model 1 plus BioClim15 and BioClim15$^{2.}$ Non-breeding precipitation was never in the best model.

Sample size	AUC (SD)	Percentage of simulations where best model is model 1 (%)	Percentage of simulations where best model is model 1 + BioClim8 (%)	Percentage of simulations where best model is model 1 + BioClim15 (%)
500	0.50 (0.22)	49	5	46
2000	0.51 (0.22)	57	5	38
5000	0.51 (0.22)	72	10	18
9429	0.51 (0.22)	71	10	19