Dispersal: the effects of phenotype and habitat selection in reintroduced populations

A thesis presented in partial fulfilment of the requirements
for the degree of

Doctor of Philosophy
in
Conservation Biology

at Massey University,
Manawatū, New Zealand.

Kate Mackinnon Richardson

2015

Abstract

Dispersal is a complex behaviour, recognised as the primary mechanism by which gene flow occurs. In the field of reintroduction biology, dispersal can influence reintroduction success both positively and negatively, yet the mechanisms underpinning dispersal in reintroduced populations are not well understood.

Extensive literature is now available on the proximate forces driving natal dispersal, and in this thesis I draw on this field to inform our understanding of dispersal processes in reintroduced populations. It is widely accepted that both internal state (phenotype) and the external environment have multi-causal effects on natal dispersal patterns across three recognised phases of movement (departure, exploration, settlement), but the relationship to post-release dispersal is less well understood. I use reintroduced populations of an endangered passerine, the hihi (stitchbird, *Notiomystis cincta*), to answer specific research questions regarding the proximate factors driving both post-release and natal dispersal in this species.

I first examine phenotypic variation in behavioural traits (personality) in my study species, in particular the effects of early natal nutrition on the expression of personality, and the influences on subsequent survival and dispersal. I find complex relationships between natal nutrition and personality that are sex-specific, and that “bold” individuals have higher survival probabilities. I find evidence for a relationship between personality and natal dispersal patterns in one study population, but not in another.

I then examine the influence of internal state (personality, early natal nutrition and degree of inbreeding) on post-release dispersal of newly translocated hihi at two sites, and find that all of these factors affect dispersal behaviour in the initial post-release and exploration phases.

I then examine the role of the external environment on both natal and post-release dispersal using species distribution models. There is a strong social effect in habitat selection of natal dispersers, but no detectable social effect in habitat selection of post-release dispersers, and evidence for use of physical characteristics of the environment in habitat selection at both stages.

Finally, I discuss the wider implications of dispersal to reintroduction biology. I advocate for careful consideration of proposed release sites, and an integrated landscape approach within reintroduction planning.

This thesis is dedicated to the female hihi of
Alberts 9 and MPD 1 – free (unbanded) spirits
until the end.

Table of Contents

Acknowledgements

Where to start? The list of people who have contributed in some way to the completion of this thesis is long, and I will start by offering up an apology to those that I will inevitably miss.

To my supervisors, Doug Armstrong, John Ewen and Isabel Castro, for your unending and unwavering support, and for always being on hand to answer questions and offer advice – I couldn't have done it without you, and I can't think of a better team of supervisors I could have worked with. Doug: thank you for your constant support, patience, ability to gently pull me back on track without me noticing, and your willingness to always readily assist during my Palmy visits regardless of your other commitments. The chocolate, muffins, and occasional loans of lunch have been appreciated also! John: for the enormous amount of time and energy you have contributed to not only to my thesis but to Maungatautari hihi in general, and for always being available and accessible despite being the furthest away! Isabel: for introducing me to the world of hihi in the first place (8 years ago now!).

To the Maungatautari whānau: a long list indeed. Chris Smuts-Kennedy first introduced me to the site, and oversaw the monitoring and banding of hihi in the first year after release. To the MEIT staff and volunteers who helped in the field, assisted with logistics and/or generally made my project possible – a heartfelt thank you to you all, in particular Paul Quinn and Rod Millar for going above and beyond to help the hihi project run more efficiently, and to Chris Smuts-Kennedy, Gemma Green, Ally Tairi, Mark Lammas, Craig Laxon and Lance Tauroa. To the MEIT pest team (aka the mouse boys) – James Matthews, Piers Griffiths-Jones, Ben Pattinson-Yorke, Will Telford, Johnny Broughton, Neil Omundsen, Paul Quinn – thanks for allowing me to convert you to team hihi, for the rides/drop-offs, tips about short-cuts, and for the (accurate) band combinations and hihi sightings (James, I still don't believe you saw one on Oreipunga Road). Bryan Jenkins deserves special acknowledgement for a beautifully built cage for the personality tests. John Polstra provided ATV training to myself and volunteers, and Tony Rolley 4WD training.

Paul and Leanne: a heartfelt thank you for opening your home to the hihi team, and for starting the venerable tradition that became Friday dessert nights.

Lydia Doerr: a special acknowledgement for being there from almost the beginning, and for continuing on the good work after I left. I couldn’t have asked for a more dedicated or skilled hihi field assistant, and I am grateful for your friendship and assistance throughout to share the ups and downs (literally!) of hihi work on the maunga.

Numerous volunteers assisted in the field throughout the course of this project. I would like to especially acknowledge Rob Pickles for assistance with radio tracking in 2011, Scott Freeman for assisting with territory mapping and mistnetting in 2011/12, and the Tiritiri Matangi translocation team in 2011, in particular Neil Fitzgerald for patiently teaching me to attach hihi transmitters. Thanks also to Landcare Research Hamilton for donation of 7 transmitters. Out in the Styx provided accommodation when all else failed – a big thank you to Lance and Mary Hodgson.

To the Maungatautari landowners who gave access across their land to the site: Albert and Elwyn Andree-Wiltens, Bill and Sue Garland, John and Penny Scott, Gary and Adele Saywell, Tao and Carol Tauroa, Sharon Brown, Leon and Kate Ramsay, Bruce and Bev Dean. Ngāti Korokī Kahukura, Ngāti Hauā, and Raukawa iwi, and the MEIT Biodiversity Management Committee for permission to carry out research on the maunga.

To the hihi research team: Leila Walker assisted with personality tests in 2011 and field work at Maungatautari, and willingly shared her data from the natal nutrition experiments. Patricia Brekke for genotyping of all Maungatautari-bred hihi, provision of pedigree-based inbreeding coefficients for analysis, and allowing me to drag her up Albert’s gully (sorry!). Kevin Parker has been involved throughout – from discussions of early ideas about dispersal, translocations and personality, to assisting in the design of the personality tests and managing the 2011 translocation – thank you for being ever willing to listen and respond to my many questions, provide sound advice, and for only suggesting I live in a tent once (you’re almost forgiven!). Leila Walker, Patricia Brekke and Troy Makan all provided useful feedback on draft chapters.

On Tiritiri Matangi: Dave Jenkins and Daryl Stephens for always making trips to the island as easy and enjoyable as possible, and for helping facilitate field work on the island. Ngātiwai, Ngāti Manuhiri, Ngāti Rehua and Ngāti Paoa for permission to conduct field work on Tiritiri Matangi. Supporters of Tiritiri Matangi (SOTM): thank you for your support, enthusiasm, and involvement with field work (special mention to Morag Fordham, Alison and Roger Bray, Yuki, John Stewart and Kay Milton who all made the trip down to Maungatautari to assist with field work at various times). Thanks to John Ewen for use of the Tiritiri Matangi data, and all those involved in collecting it over the years.

At Massey University: to the Ecology Group, and in particular those I’ve shared office space with along the way – Liz Parlato, Emma Williams, Nic Gorman, Kyle Morrison, Julia Panfylova, and Faline Drummond. Paul Barrett for organising and sending gear my way.

Thanks to Brent Beaven at DOC for granting me leave to finally complete this thesis, and the DOC Rakiura team for covering my workload in my absence.

A special thank you to the Hihi Recovery Group for supporting my research, and particular acknowledgement to NZ Safety Ltd, the sponsor of the group, for covering the cost of transmitters in 2011. I would also like to acknowledge funding from the Zoological Society of London, JS Watson Trust, and the Massey University Doctoral Scholarship. The opportunity to attend AniMove at the Max Planck Institute in 2013 allowed me to develop spatial analysis skills and contributed to the analysis carried out in Chapter 4.

To my family, for your patience and support throughout the journey, particularly to my mum and dad for becoming passionate hihi supporters, and especially for the logistical support in the early days of field work.

And finally, to the Maungatautari hihi – may you live long and prosper.

CHAPTER 1

Introduction

Dispersal[1] is the primary mechanism by which gene flow occurs, both within and between populations. In the past decade and a half, the study of dispersal has developed considerably, and it has become recognised as an extremely complex behaviour influenced by a wide range of both genetic and environmental factors (Clobert *et al.*, 2012). Dispersal occurs across three primary phases: departure, exploration/transience, and settlement (Ronce, 2007; Clobert *et al.*, 2009), and studies into the causal factors of dispersal behaviour increasingly recognise the importance of distinguishing these phases (Matthysen, 2012).

Understanding dispersal behaviour can be crucial to the conservation of many species, and in particular to **reintroduction**[2] biology, where dispersal can influence reintroduction success and composition of founder populations through both immediate **post-release dispersal**[3], and through **natal dispersal**[4] of juveniles, as well as seasonal movements of adults or dispersal to new breeding sites. To date, the majority of the literature on the topic of dispersal has focused on the mechanisms driving natal

---

[1] Dispersal = movement leading to spatial gene flow, that does not require, but is typically followed by, reproduction (Clobert *et al.*, 2012).
[2] Reintroduction = the intentional movement and release of an organism inside its indigenous range from which it has disappeared (IUCN/SSC, 2013) .
[3] Post-release dispersal = movements of individuals from the release site after translocation.
[4] Natal dispersal = movement from the natal site (birth or hatch site) to the first breeding site.

dispersal, with fewer studies focused on post-release dispersal, despite the importance of the latter to reintroduction.

In this chapter, I first review current thinking in the dispersal literature, and summarise research to date relating each aspect to the field of reintroduction biology. I then present a case study of these issues in an endangered New Zealand passerine (hihi/stitchbird, *Notiomystis cincta*) that has been the subject of multiple reintroduction attempts. Finally, I present an outline of the questions presented in this thesis, which examine the proximate causes of variation in natal and post-release dispersal in reintroduced populations, and the effects of these on reintroduction success.

Dispersal literature: from early studies to recent advances

Early studies focused on apparent sex-biases in dispersal (with male-biased dispersal most common in mammals, and female-biased dispersal most common in birds), the role this played in inbreeding avoidance, and the relationship to mating strategy (Greenwood, 1980). It is now widely accepted that the influences of variation in **dispersal decisions**[5] are multi-causal, and that these vary across the three stages of dispersal (Figure 1.1). Variation in dispersal behaviour occurs, and has consequences, at the individual, population, metapopulation, and species level. Four potential evolutionary forces have been identified that ultimately shape these differences: avoidance of inbreeding and competition with kin, increasing parental fitness by distributing offspring across varying environmental conditions, escape from unfavourable conditions, and the potential costs of dispersal (Matthysen, 2012). At the proximate level, the factors influencing dispersal have been placed into two categories:

---

[5] Dispersal decision = where an organism changes movement status with relation to dispersal stages; does not necessarily imply a conscious decision (Clobert *et al*. 2012).

those relating to the internal state of the individual, and those relating to the external environment.

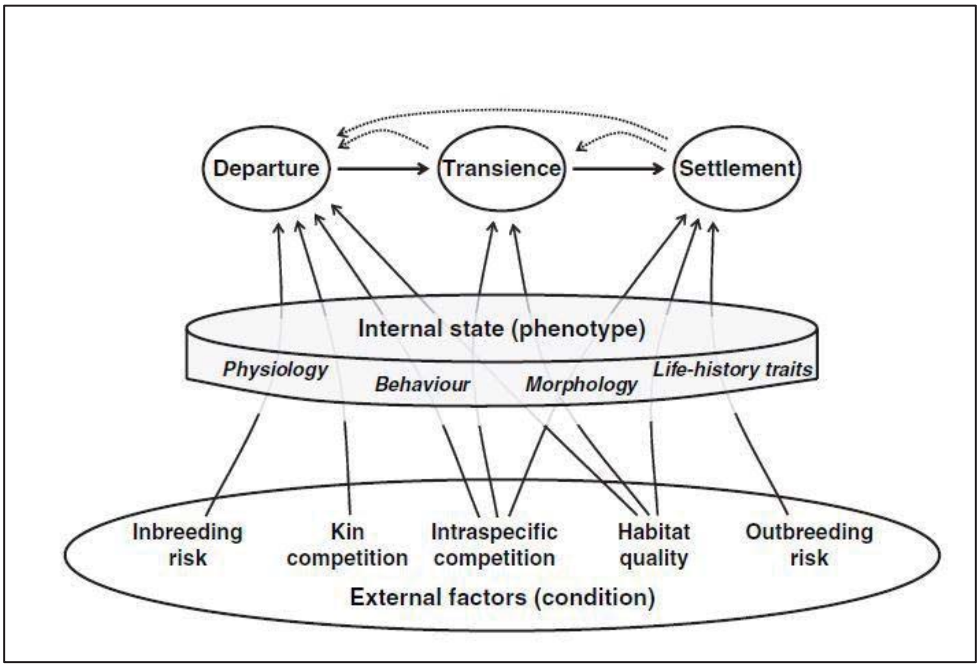


Figure 1.1 Conceptual framework to explain individual variation in dispersal, modified from Clobert *et al.* (2009).

Internal state

Internal state can refer to a variety of phenotypic traits, many of which have been associated with dispersal propensity, including morphology (O'Riain *et al.*, 1996; Massot and Clobert, 2000; Balbontín *et al.*, 2009), physiology (Belthoff and Dufty, 1998), behavioural traits (Dingemanse *et al.*, 2003; Duckworth and Badyaev, 2007; Cote *et al.*, 2010b; Quinn *et al.*, 2011), and condition (O'Riain *et al.*, 1996). Variation in these traits can be genetic (G), environmental (E), an interaction between the two (G x E) (Cote *et al.*, 2010a; Cote and Clobert, 2012), and can be mediated by epigenetic or maternal effects (Massot and Clobert, 2000; Duckworth, 2009). **Dispersal syndromes**[6]

---

[6] Dispersal syndrome = covariation of multiple traits (whether behavioural or life-history traits) associated with dispersal, equivalent to a multivariate dispersal phenotype (Clobert *et al.* 2012).

(Ronce and Clobert, 2012) are defined as patterns of covariation between phenotypic traits associated with dispersal. Dispersal behaviour has now been demonstrated to covary with numerous phenotypic traits (as above), but syndromes are described as multi-dimensional, highly idiosyncratic, highly variable both within and between species, and scale-dependent (Ronce and Clobert, 2012) - i.e. there is no clearly identifiable or consistent link between specific phenotypic traits and dispersal, despite widely occurring covariation across many traits.

Ronce and Clobert (2012) identified three possible explanations for the occurrence of dispersal syndromes: 1) that the dispersal event itself affects the expression of other phenotypic traits (this can only be the case for traits measured after the dispersal event), 2) variation in the environment jointly affects the expression of dispersal and other phenotypic traits, and 3) genetic correlations between dispersal and other phenotypic traits, caused either by linkage disequilibrium (between genes affecting dispersal and genes affecting other phenotypic traits) or pleiotropic effects of the genes affecting dispersal. Consequences of these forms of covariation may include demographic effects on patterns of invasion, range expansion and extinctions, and genetic effects on gene flow and adaptation to changing environments (Ronce and Clobert, 2012).

External environment

External factors influencing dispersal can be related to physical characteristics of **habitat**[7] (Cruz-Angón *et al.*, 2008), and biotic cues (including conspecifics, competitors, predators and parasites) (Serrano *et al.*, 2003; Ward, 2005; Tschirren *et al.*,

---

[7] Habitat = while definitions of this concept vary, throughout this thesis we use the definition used by Osborne and Seddon (2012): “a species-specific complex of interacting physical and biotic components, including other species”.

2007; Forsman *et al.*, 2008; Parejo *et al.*, 2008; Forsman *et al.*, 2009; Parejo and Aviles, 2011), all of which can influence dispersal decisions across multiple phases. Positive or negative density-dependent effects on dispersal can occur, and can be sex-specific or condition-dependent (Eikenaar *et al.*, 2007; Martin *et al.*, 2008; Richardson *et al.*, 2010). The presence of parents or kin can influence dispersal decisions, potentially as a form of avoidance of either inbreeding or kin competition (Daniels and Walters, 2000; but see Eikenaar *et al.*, 2008). External factors at both the natal site and in the surrounding environment can influence decisions across the different dispersal phases.

Increasingly recognised are the interactions between internal state and the external environment, in that dispersal decisions, and particularly dispersal syndromes, are often context-dependent. Dispersal decisions relating to the external environment will be reliant on the individual's ability to obtain and process public information (Doligez *et al.*, 2003; Danchin *et al.*, 2004), and this cognitive ability can be influenced by internal state (Kurvers *et al.*, 2010; Cote and Clobert, 2012). Social effects can also be context-dependent, with heterogeneity in the degree of conspecific attraction vs repulsion between individuals in some populations (Cote and Clobert, 2007) that can have differential effects on fitness (Cote *et al.*, 2008).

Relevance of the dispersal literature to reintroduction biology

Post-release dispersal - effects of internal state

The relationship between internal state and post-release dispersal has rarely been investigated, despite the potential importance of these factors to influence reintroduction success and founder population composition, with most published studies of post-release dispersal being descriptive, or limited to only effects of sex and age (e.g.

Moehrenschlager and Macdonald, 2003; Tweed *et al.*, 2003; Spinola *et al.*, 2008) or release strategy (e.g. Calvete and Estrada, 2004; Bradley *et al.*, 2012). The few studies to date that have focused on internal state show some promise. Bremner-Harrison *et al.* (2004) investigated the link between personality type (see Chapter 2) and post-release survival in swift foxes (*Vulpes velox*), finding bolder individuals had lower post-release survival in the first six months after release, whereas Sinn *et al.* (2014) found bolder Tasmanian devils (*Sarcophilus harrissii*) had higher survival up to eight months after release. Hardouin *et al.* (2015) investigated the role of inbreeding in post-release dispersal of North African houbara bustard (*Chlamydotis undulata undulata*), and found a sex-specific effect of inbreeding coefficient, with more inbred males dispersing further than less inbred males, and no effect detected in females. More inbred individuals appear less able to cope with effects of environmental stress (Crnokrak and Roff, 1999; Keller and Waller, 2002), hence the degree of inbreeding should be considered as another factor that can influence internal state.

Post-release dispersal – effects of the external environment

Reintroduction biology can gain from a greater understanding of the effects of the external environment on post-release dispersal patterns, with potential to also draw from the field of habitat selection (e.g. Stamps and Swaisgood, 2007; Mayor *et al.*, 2009). Many studies acknowledge the importance of selecting appropriate **release areas**[8] in terms of habitat, and incorporate research into habitat selection into **conservation translocation**[9] (hereafter "translocation") programmes. This is generally done via either

---

[8] Release area = habitat where translocated animals are hoped to remain in order to found a population, c.f. release site = a smaller location within the release area where animals are released (Le Gouar *et al.*, 2012).

[9] Conservation translocation = the deliberate movement of organisms from one site for release in another, intended to yield a measurable conservation benefit at the levels of a population, species or ecosystem (IUCN/SSC, 2013).

a priori or *post hoc* assessments of habitat selection for the target species. *A priori* studies generally use information from remnant populations to make inferences about habitat preference, and to therefore predict suitable release areas for reintroduction (Pearce *et al.*, 1994; Pearce and Lindenmayer, 1998; Wilson and Paton, 2004). One potential drawback is the assumption that relict ranges reflect true habitat preference, whereas in some cases they may simply reflect last refuges (Beauchamp and Worthy, 1988; Osborne and Seddon, 2012). Pearce and Lindenmayer (1998) acknowledged this and used bioclimatic modelling to infer former range limits of helmeted honeyeater (*Lichenostomus melanops cassidix*), and predicted potential release areas within this range.

Post-release monitoring of translocated individuals can provide information about habitat preferences, that can in turn predict future release areas (Niemuth, 2003; Bleyhl *et al.*, 2015), but this does assume that habitat selection of translocated individuals is an outcome of **informed dispersal**[10]. Long-term datasets from successfully reintroduced populations can be especially useful to determine true habitat preferences (Fustec *et al.*, 2001; Hirzel *et al.*, 2002; White *et al.*, 2003).

The vast majority of studies examining habitat selection in translocated animals have focused on physical characteristics of the environment (e.g. Pearce *et al.*, 1994; Pearce and Lindenmayer, 1998; Ostro *et al.*, 2000; Fustec *et al.*, 2001; Niemuth, 2003; Wilson and Paton, 2004; Rittenhouse *et al.*, 2008). Very few have taken into account biotic factors. Exceptions include studies looking at interactions between translocated animals and humans (Frair *et al.*, 2007; Bleyhl *et al.*, 2015), predators (Frair *et al.*, 2007), and

---

[10] Informed dispersal = where dispersal decisions[4] are affected by information or cues (Clobert *et al.* 2012).

resource availability (White *et al.*, 2003). Mihoub *et al.* (2011) outlined why the success of reintroductions to heterogeneous habitats is dependent on habitat selection strategies, and suggested that the chance of persistence is lower if strategies are random or based on conspecific presence/avoidance, but higher if based on intrinsic quality or conspecific reproductive success. Strong conspecific attraction can lead to an ecological trap if the original habitat selected is low quality (Grether *et al.*, 2014), but this is rarely examined and is of particularly relevance to **reinforcements**[11] where conspecifics are already present.

Case study: dispersal behaviour in a reintroduced passerine

In New Zealand, reintroductions of endangered passerines to the mainland have become increasingly common, both as part of ongoing conservation programmes and as part of community restoration projects. Many of these occur to release areas where invasive predators have either been eradicated or are controlled to extremely low levels, but are often adjacent to areas where no predator control is undertaken, or where habitat is fragmented. Dispersers can therefore have high mortality, or simply become geographically isolated and lost to the population. Dispersal therefore presents a major challenge both for the conservation of these species, and to the wider success of mainland restoration projects. The hihi is one such species for which dispersal has become an issue of concern (Ewen *et al.*, 2013b). Reduced to one island population by the 1880s, reintroduction attempts began in the 1980s to other predator-free offshore islands. However, these were initially unsuccessful, and this was hypothesised to be due to the lack of mature forest on such islands (Taylor *et al.*, 2005). In the mid-2000s, the Hihi Recovery Group (Taylor *et al.*, 2005; Ewen *et al.*, 2013a) began to look towards

---

[11] Reinforcement = the intentional movement and release of an organism into an existing population of conspecifics (IUCN/SSC, 2013).

mainland release areas where mature forest remained. After the initial two reintroduction attempts, concerns arose that dispersal may undermine their success (Richardson, 2009; Ewen *et al.*, 2013b), and understanding dispersal behaviour in hihi has become a research priority for the recovery programme.

Thesis outline

Chapters 2, 3 and 5 investigate the role of internal state in natal and post-release dispersal patterns. Chapter 4 investigates the role the external environment plays in natal and post-release dispersal, with a focus on habitat selection and conspecific effects. Chapter 6 discusses issues for consideration in reintroduction and restoration planning more generally. Chapter 7 presents a synthesis of the themes of this thesis and future directions. Each chapter and its aims are described below.

Chapter 2: Personality in hihi: the role of the early environment and influence on life history traits

This chapter develops a methodology for assessing personality traits in hihi, and uses this to assess the role of the early environment in the development of personality traits, and their influence on subsequent life history traits including natal dispersal. Questions asked are:

- Does the early natal nutritional environment influence the expression of personality traits?
- Does personality influence later life history traits, including survival and natal dispersal patterns?

Chapter 3: Multiple influences in post-release dispersal of a reintroduced passerine.

This chapter examines the role of internal state in individual variation in post-release dispersal behaviour. I use radio tracking data from two reintroductions of hihi to the mainland (Ark in the Park in 2007, and Maungatautari Ecological Island in 2011) to ask the following questions:

- Is post-release dispersal driven by a) sex-specific differences, b) personality, c) inbreeding, d) the early natal nutritional environment, and/or e) condition?
- Do the effects of internal state vary across the three recognised stages of post-release dispersal (initial departure from release site, exploration, settlement)?
- What is the relationship between movements in the initial and exploration phases, and later settlement decisions?

Chapter 4: Habitat selection in a reintroduced population

Chapter 4 examines the role of the external environment in dispersal decisions at the settlement stage. I examine habitat selection in hihi dispersal at a site where multiple releases occurred during the study period, Maungatautari Ecological Island. This reserve provides a large area of mature forest for dispersers to explore, while dispersal outside of the release area is constrained by farmland surrounding the site. Questions asked are:

- Can physical characteristics of preferred habitat be identified in hihi?
- How do conspecifics influence habitat selection of both natal and post-release dispersers?

Chapter 5: Natal dispersal patterns in an establishing reintroduced population

Chapter 5 examines natal dispersal patterns in an establishing population of hihi at Maungatautari Ecological Island. I use natal dispersal data from juveniles bred within the release area in the first three years after release to examine the following:

- How do natal dispersal distances vary between individuals in the initial years post-release, and how do these differ between the sexes?
- What are the effects of personality, early natal condition and inbreeding on natal dispersal distances?

Chapter 6: Considering dispersal in reintroduction and restoration planning

Chapter 6 examines the wider implications of dispersal to reintroduction biology, and discusses a range of management options for dealing with this issue. This chapter advocates for careful consideration of proposed release areas, and advocates for an integrated landscape approach within reintroduction planning.

Chapter 7: Synthesis and future directions

This chapter draws together the major themes of this thesis, summarises main findings, and provides direction for future research in this area.

While not directly related to my PhD thesis, during the course of field work detailed information was collected regarding the population establishment of hihi at Maungatautari Ecological Island. In Appendix A (2010/11 and 2011/12) and B (2012/13) I present the season reports written for the Hihi Recovery Group, and in Appendix C estimates of population growth rate (λ) for the population between 2010/11 and 2012/13.

Comment on statistical analyses in this thesis

Throughout this thesis, I make use of Bayesian methods in the statistical analyses. A detailed discussion of the relative merits of Bayesian vs frequentist methods in model selection is beyond the scope of this thesis (see Hooten and Hobbs, 2014; Barker and Link, 2015; Dorazio, 2015 for reviews of this topic). There is currently no consensus among statisticians on the topic of model selection, and both **DIC**[12] and **AIC**[13] yield similar results for ranking models. However, DIC is not ideal for all classes of models, and in particular has been criticised for the potential to poorly evaluate model complexity (pD), its use with mixture models, and its lack of direct connection with predictive ability (Hooten and Hobbs, 2014).

However, Bayesian methods, in contrast to frequentist methods, use probability models to describe uncertainty about parameters, and distinguish between quantities that are known and unknown – both for parameters, and for missing values (Barker and Link, 2015; Dorazio, 2015). It is for the latter reason that I use Bayesian methods in this thesis, as they offer a means of accounting for missing values in datasets. A number of covariates in the chapters to follow contain missing values, such as for haematological parameters where no blood could be collected from some individuals, or for some personality measures where, e.g., technical failures occurred during filming or other issues arose.

---

[12] Deviance Information Criterion; a within-sample quasi-Bayesian score for prediction (Hooten and Hobbs, 2014).

[13] Akaike's Information Criterion; a within-sample non-Bayesian score for prediction (Hooten and Hobbs, 2014).

CHAPTER 2

Personality in hihi: the role of the early environment and influence on life history traits

---

This chapter is intended for submission as a manuscript, with a focus on the effect of the natal nutritional environment on personality. Co-authors and their respective contributions are as follows:

Leila Walker (University of Cambridge & Zoological Society of London) - design and completion of natal nutrition experiments, comments on manuscript.

Doug Armstrong (Massey University), primary supervisor – assistance with analysis for survival and natal dispersal data, comments on manuscript.

Kevin Parker (Massey University) – assistance with study design, in particular design of personality test, comments on manuscript.

John Ewen (Zoological Society of London), co-supervisor – assistance with study design in particular design of personality test, provision of survival and natal dispersal data, facilitation of collaboration, comments on manuscript.

Abstract

Studies of animal personality have traditionally considered personality to be a relatively rigid trait determined by the genetic makeup of the individual, with some phenotypic plasticity. The role of ontogeny has received relatively little attention, yet recent work indicates the early environment may play a stronger role in the development of personality than previously thought. We investigated the effect of experimental nutrient supplementation in the nest on personality traits in a wild-living passerine, the hihi (*Notiomystis cincta*). We first developed an appropriate method for testing personality in our study species, by modifying traditional cage-test designs to enable testing of 99 juvenile hihi *in-situ*, and measurement of five personality scores: activity, acclimation time, exploration, boldness and escape latency. We investigated the effect of experimental nestling nutritional supplementation on personality traits as juveniles, and correlates with life history traits (survival and natal dispersal). We found strong evidence that the early environment influences the development, or expression, of personality traits, and demonstrated that these effects are sex-specific. Juveniles of both sexes that received carotenoid supplementation in the nest were bolder than those that did not, and females receiving carotenoid supplementation had slower escape times. Juveniles of both sexes receiving protein supplementation in the nest had lower activity scores, and males receiving protein supplementation had longer acclimation times, and females higher exploratory scores. Bold individuals had higher survival probabilities, but we did not find strong evidence that personality influenced natal dispersal. Our results are significant as they a) demonstrate a successful test of personality that can be carried out quickly *in-situ*, and b) provide strong evidence showing the importance of early natal nutrition in the development and expression of personality traits.

Introduction

The study of what has been termed "personality", or "behavioural syndromes", has become increasingly popular in the literature over the past decade. Burtt and Giltz (1973) first identified the behavioural differences between individuals as "personality", and described it as the difference between what an individual is physiologically able to do, and what it will do. Some authors define personality traits as behavioural differences that are stable over time and across contexts or situations (Carere and Maestripieri, 2013), while others state that syndromes do not have to be stable over a lifetime to qualify as personality traits (Sih and Bell, 2008; Sih, 2013). Regardless, a variety of studies have shown correlations between these phenotypic traits and other factors, with correlations between personality and anti-predator behaviour (Quinn and Cresswell, 2005; Jones and Godin, 2010), ability to cope with social stress (Verbeek *et al.*, 1999), learning ability (Exnerova *et al.*, 2010), social information use (Kurvers *et al.*, 2010), song behaviour (Garamszegi *et al.*, 2008; Naguib *et al.*, 2010), extra-pair paternity rates (van Oers *et al.*, 2008) and post-release mortality (Bremner-Harrison *et al.*, 2004).

Personality – nature vs nurture?

Personality has been viewed (and indeed defined) as a relatively rigid trait determined by the genetic makeup of the individual, with some phenotypic plasticity (reviewed in van Oers and Naguib, 2013). In comparison, the ontogeny of personality has received relatively little attention (Stamps and Groothuis, 2010; Groothuis and Maestripieri, 2013). Given the critical importance of the early environment to a wide range of life-history parameters (Lindström, 1999; Metcalfe and Monaghan, 2001; Blount *et al.*, 2003; Kasumovic, 2013), the potential importance to the expression of personality traits should not be overlooked. A number of studies have now reported a link between personality traits and the early environment (Dingemanse, 2004; Carere *et al.*, 2005), and some have demonstrated the influence of early natal nutrition (via experimental supplementation of either protein or micronutrients) in the expression of personality traits in zebra finches (*Taeniopygia guttata*) (Krause *et al.*, 2009; Noguera *et al.*, 2015) and waterfowl (*Anas* sp.) (Rowe *et al.*, 2015). However, while nutrition clearly plays some role in the expression of personality phenotypes, precisely which aspect of the diet underlies this effect remains unclear.

Personality and life history traits

Personality can influence fitness, with different optima under different environmental conditions (Carere and Maestripieri, 2013), hence there are important implications for our understanding of population ecology (Sih *et al.*, 2012). Under a theoretical model suggested by Wolf *et al.* (2007), different personality types are predicted to adopt different life history strategies, with "faster" individuals predicted to exhibit early maturity, faster reproduction, and shorter lifetimes. Blas *et al.* (2007) found that the success of different personalities varied as a function of population density and predictability of food resources, suggesting the relationship to be context-dependent. In great tits (*Parus major*), the relationship between survival and personality was sex-specific and dependent on food availability, with “slow” males having higher survival in years of lower food availability than years of higher food availability, whereas females were affected in the opposite way (Dingemanse, 2004; van Oers and Naguib, 2013). The role of personality in metapopulation dynamics and spatial ecology has also become increasingly recognised, with the emergence of personality-dependent dispersal (Cote *et al.*, 2010a). Both exploration and aggressiveness have been positively associated with dispersal, with more exploratory and aggressive individuals (those at the "fast" or "proactive" end of the personality spectrum, Groothuis and Carere, 2005; Cockrem, 2007) typically displaying greater dispersal propensity (Dingemanse *et al.*, 2003; Quinn *et al.*, 2011).

Testing personality in the wild

Appropriate tests of personality will vary between species, with tests of specific traits meaningful to the life history of one species potentially being less appropriate for other species (van Oers and Naguib, 2013). Any study of personality in a species first requires validation of testing methodology to ensure it is meaningful. Most early research on personality has been carried out under captive, controlled conditions, but this is problematic for the majority of species for logistical or ethical reasons. Hence a need has arisen to develop methodologies for testing personality in the wild that ensure standardised conditions but minimise stress to the animal (e.g. Kluen *et al.*, 2012).

This study

Here, we examine personality traits in an endangered New Zealand passerine, the hihi (*Notiomystis cincta*), the role of the early environment (via experimental manipulation of nestling diet) in the expression of these traits, and the relationship with key life history traits in both established and recently reintroduced populations. First, we develop and trial a simple cage test appropriate to our study species. We then examine the effects of sex and age, and aim to answer the following questions:

- What is the effect of early nutritional supplementation on personality traits in juvenile hihi? (this chapter)
- How do personality traits influence survival in an established population? (this

chapter)

- How do personality traits influence natal dispersal movements in an established population? (this chapter)
- How do personality traits influence post-release dispersal movements in a reintroduced population? (Chapter 3)

Methods

Study species

The hihi is an endangered New Zealand passerine (Vulnerable on the IUCN Red List; IUCN, 2013) that has been subject to multiple reintroduction attempts (Ewen et al., 2013). Reduced to a sole island population by the 1880s (Hauturu/Little Barrier Island), hihi now persist at additional reintroduction sites including two islands (Tiritiri Matangi and Kapiti), and three mainland reserves (Karori Wildlife Sanctuary, Maungatautari Ecological Island and Bushy Park). All populations are reliant on management, including maintenance of an environment free from mammalian predators (all populations), as well as provision of supplementary food (all reintroduced populations; Chauvenet et al., 2012) and artificial nest boxes (all reintroduced populations except Maungatautari and Kapiti).

Study site

Tiritiri Matangi Island (36°36’S, 174°53’E) is a 220 ha Scientific Reserve in the Hauraki Gulf, north east of Auckland, New Zealand. Hihi were reintroduced to Tiritiri Matangi in 1995 and the island now supports approximately 100 breeding pairs. The population is intensively managed through the provision of supplementary food (sugar water) and nest boxes (Taylor *et al.*, 2005), and control of infestations of the bloodsucking mite *Ornithonyssus bursa* (Ewen *et al.*, 2009). Breeding activity is intensively monitored, and all nestling hihi are colour banded in the nest at 21 days of age. Island-wide resighting surveys are carried out in September and February each year (pre- and post-breeding), hence a comprehensive survival and breeding database exists for this population.

Personality testing

We personality tested 99 juvenile hihi (57 males and 42 females) on Tiritiri Matangi Island between 25 February and 23 March 2011. These were all captured in mist nets at different locations across the island. 38 of these birds were subsequently recaptured and translocated to another site in April 2011 (Chapter 3), and the other 61 remained on Tiritiri Matangi Island, with 35 of these known to survive to their first breeding season, starting in September 2011. The majority of the birds tested were from first clutches (80), with a smaller number from second clutches (17) or clutch unknown (2).

Traditional assays of personality generally involve a period of captivity (e.g. Verbeek *et al.*, 1994; Herborn *et al.*, 2010). However, this is not always possible or preferable when working with wild populations, and particularly with endangered species. We developed a method refined from these traditional assays, that took 10-15 minutes per bird and enabled us to measure five different personality scores.

We tested birds in a specifically designed cage (Figure 2.1, 150 x 50 x 50 cm) similar to that used in captive tests, with a removable divider across the middle modified from that used by Herborn *et al.* (2010). Each end of the cage had three perches (two low and one high), and vegetation (a mix of natural fern fronds and some artificial vegetation) was placed around the side and back edges of the cage. The cage was made from plywood with the exception of the front side which was covered with wire mesh; this enabled observation from one side, as well as enabling the observer (KMR) to approach without being seen from the side or back. Each end had a small hole that could be opened to allow the bird to escape, and the front side had two doors that both opened wide.

The cage was set up daily in proximity of the mist net site (within 50-100 m). Once caught, birds were promptly removed from the mist net and transferred into a black bird bag, weighed and then removed from the bag by hand. The bird was then released into the cage via the escape hole, and the observer would move out of sight. After 5 minutes, the observer would approach the cage from the back, and remove the central divider. After another 5 minutes, the escape hole on the opposite side to the bird was opened. If the bird remained after 5 minutes, the front doors would be left open until the bird left.

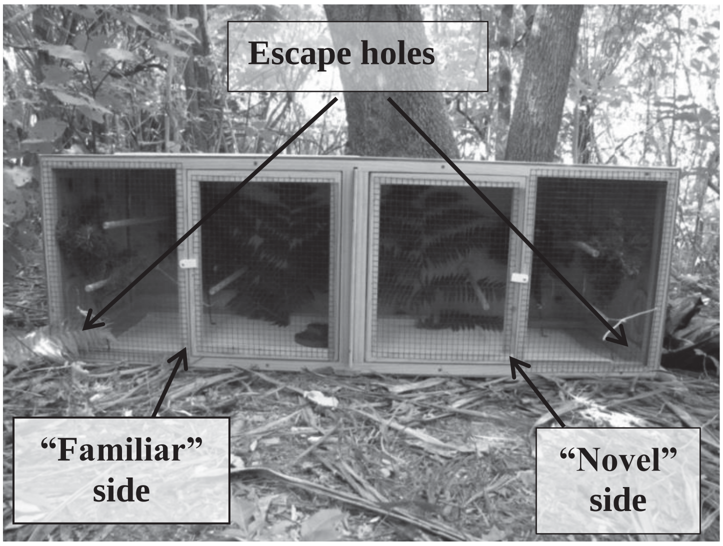


Figure 2.1 Cage set-up for personality tests. All birds were placed in the cage via the escape hole on the left-hand side of the photo. After five minutes the central divider was removed, and after another five minutes the escape hole on the opposite side to the bird was opened.

All tests were filmed using a Canon SX20 camera on a tripod set up ~2-3 m in front of the cage. Footage was subsequently viewed using Windows Media Player. This footage was used to calculate the following personality scores:

- Activity score: the number of movements (hops or flights) made by the bird in the first five minutes in the cage.
- Boldness: the latency (seconds) of the bird to move to the "novel" side of the cage after removal of the divider.
- Exploratory score: the number of movements made on the "novel" side of the cage minus the number of movements made on the “familiar” side (as per Herborn *et al.*, 2010).
- Latency to escape: the latency (seconds) for the bird to escape the cage in the third five minute period.
- Acclimation time: the time between release into the cage and the first body shake. We noted while viewing film footage that almost all birds underwent an initial very high movement phase (presumably an attempt to escape), but after a varying period of time would settle onto one of the perches, shake and ruffle their body feathers, and then sit still and survey the surroundings briefly before resuming movement. There was considerable variation among individuals in the time taken for this to occur, hence we measured this, and termed it "acclimation time".

In contrast to Kluen *et al.*’s (2012) findings with blue tits (*Cyanistes caeruleus*), we did not find that 10 minutes was sufficient for the bird to "settle down" in the cage. We ran initial trials on nine individuals, using the same method as described above but with up to 15 minute intervals instead of five, and found that after 30-45 minutes, all except one of the birds still exhibited high levels of movement. Hence, for ethical reasons, we further refined the method to reduce the time in captivity to no more than 15 minutes per bird.

Ethical note

All aspects of this work were carried out under a High Impact Research Permit from the New Zealand Department of Conservation (AK-30463-FAU) and with approval from the Massey University Animal Ethics Committee (11/02). Approved methods were assessed and refined in the field to minimise or eliminate any potential adverse effects to individual animals, as noted above.

Natal nutrition experiment

All 80 first clutch individuals were subject to experimental supplementary feeding in the nest. Second clutch nestlings did not receive any supplementary feeding in the nest. The experimental design is described in detail in Walker *et al.* (2013a). In brief, all individuals were assigned to one of four treatment groups (both within- and between-nests, either N+C+, N-C+, N+C- or N-C-), with N+ nestlings fed a high protein dietary supplement (Wombaroo™ Lorikeet and Honeyeater Food, Wombaroo Food Products, Glen Osmond, SA, Australia), and N- nestlings fed a control supplement (sugar water). C+ nestlings received this supplement enhanced with carotenoids (lutein and zeaxanthin in the form of OroGLO® liquid; Kemin Industries, Des Moines, IA, USA), and C- without. Carotenoids are important biomolecules that can only be obtained through dietary means, and have previously been linked to a range of health benefits in hihi (Ewen *et al.*, 2006; Ewen *et al.*, 2008; Thorogood *et al.*, 2008; Ewen *et al.*, 2009) as well as in other species including humans (e.g. Johnson, 2002). In the Walker *et al.* (2013a) study, a sex-specific effect of the high protein diet was found on nestling growth parameters, and an interactive effect between the high protein diet and carotenoid supplement on survival to fledging, but no effects were detected on survival from fledging to recruitment. Additional effects were found on plumage characteristics, with carotenoid supplementation linked to elevated yellow saturation in male breeding plumage, and protein supplementation reducing white luminance of male ear tufts (Walker *et al.*, 2013b).

Data analysis

A preliminary inspection of the data did not indicate any correlation between the five personality scores measured, and this was supported by a principal components analysis (max r_s=0.4, for activity score and boldness, $p<0.05$; Appendix 2.1). We square-root transformed data for activity and acclimation time to improve normality, and as boldness and escape latency both displayed a distinctly bimodal distribution we rescored these to 1 (did not move to novel side/shy, or did not escape) or 0 (did move to novel side/bold, or did escape). To test for relationships between the personality scores and sex, age, and nestling dietary treatments, we used either linear mixed models (activity score, acclimation time, exploratory score), or generalised linear mixed models with a binomial error distribution and logit link (boldness, escape latency), in packages nlme and lme4 in R v. 3.01 (R Development Core Team, 2013) (functions lme and glmer respectively). In each model we included age (number of days since hatch date), sex, protein supplement (N+ or N-) and carotenoid supplement (C+ or C-) as fixed effects, and also included interactions between sex and N, sex and C, and C and N. We included the mother of the individual as a random effect. All explanatory variables and interactions were fitted to full maximal models, and reduced by sequentially removing components using the drop1 function (using $p < 0.05$ as selection criterion). We removed terms until AIC was minimised and the minimal adequate model was found. Model normality and homogeneity of variance assumptions were confirmed based on visual examination of residual plots.

We were able to examine the relationship between the five personality scores we measured in these juveniles, and their subsequent survival over three breeding seasons (2011/12, 2012/13 and 2013/14), for the individuals that remained on the island. We used survival data for 59 of the 61 individuals (the two of unknown clutch number were omitted from this analysis). We first modelled the effect of time (t), sex (s) and clutch on both survival probability (ϕ) and resighting (p) probability, using the standard live recaptures only model. This determined that the best model for our data was ϕ(t) p(s). We then coded this as a likelihood-based CJS model in WinBUGS 1.4 (Lunn *et al.*, 2000), with a fixed time effect on ϕ and an effect of sex on p. We first ran a constant model and then included each of the personality covariates one at a time. We used standardised z-scores for acclimation time, activity score and exploratory score, and the bimodal scores as above for boldness and escape latency. For each personality variable we also tested for an interaction with sex and clutch. Where missing values were present, we imputed them by sampling from either a normal, Bernoulli or Poisson distribution as appropriate (Nakagawa and Freckleton, 2008). For all models there was a burn in of 10,000 samples, and we then introduced another 100,000 samples after convergence was reached. Alternative models were compared using DIC (Deviance Information Criteria) values (Spiegelhalter *et al.*, 2002).

For the natal dispersal analysis, we first calculated natal dispersal distances (NDD, distance from natal nest box to first breeding nest box) for the 26 individuals we had natal dispersal data for – i.e. birds that had been personality tested, remained on the island, and first bred in the 2011/12, 2012/13, or 2013/14 breeding season. Individuals from nest boxes at either end of the island are able to disperse further than those from nest boxes in the middle of the island, hence we calculated the distance of each individual's natal nest box to the geographic mean of the island (*dcent*), as a previous analysis of natal dispersal patterns in this population had also accounted for (Richardson *et al.*, 2010). We analysed the data in WinBUGS by fitting general linear models (with normal error terms) to examine the effect of each of our personality scores on natal dispersal distance (in contrast to dispersal patterns at other study sites in this thesis which show a typical left-skewed dispersal kernel, Tiritiri Matangi dispersal distances fit a normal distribution). We began by running a constant model, and then introduced sex (*s*) and *dcent* as explanatory variables. In contrast to our previous analyses, we did not find that adding either *s* or *dcent* improved the model, so we did not include these variables in subsequent models. We then introduced each of the personality covariates one at a time as with the survival analysis, again testing for interactions between these covariates and sex or clutch. Again, there was a burn in of at least 10,000 samples for each model, and we introduced another 100,000 samples after convergence was reached. Alternative models were compared using DIC values.

Results

Effects of sex and age

There were significant effects of sex, age, and nestling dietary treatments on the measured personality scores (Table 2.1, Figures 2.2a-g). Both activity score and boldness were influenced by sex, with females showing significantly higher activity scores (p=0.04; Figure 2.2a) and being more bold (p=0.02, Figure 2.2b) than males. Age had an effect on boldness, with older juveniles being less bold (p=0.07, Figure 2.2c).

Effects of natal nutritional environment

Nestling dietary treatments also significantly affected personality (Table 2.1). Juveniles that received the carotenoid supplement in the nest tended to be more bold than those that did not (p=0.08, Figure 2.2d), and females receiving the supplement were less likely to escape (p=0.04, Figure 2.2e).

Females that had received the protein supplement tended to have higher exploratory scores than those that had not (p=0.06, Figure 2.2f). Males that received the protein supplement tended to have longer acclimation times (p=0.08, Figure 2.2g) than males that did not.

Survival analysis

The best models all included boldness as a covariate, with the model including an interaction between boldness and clutch having the strongest support (Table 2.2). Less bold individuals (those that did not move to the novel side of cage during personality testing) had lower survival probabilities (Figure 2.3). This difference was strongest for second clutch birds. None of the other personality scores significantly affected survival.

Natal dispersal analysis

There was little support for any effect of personality on natal dispersal distances (Table 2.3), although there was a weak tendency for natal dispersal distance to be higher for individuals with a longer acclimation time (Figure 2.4; ΔDIC=0.5 c.f. constant model).

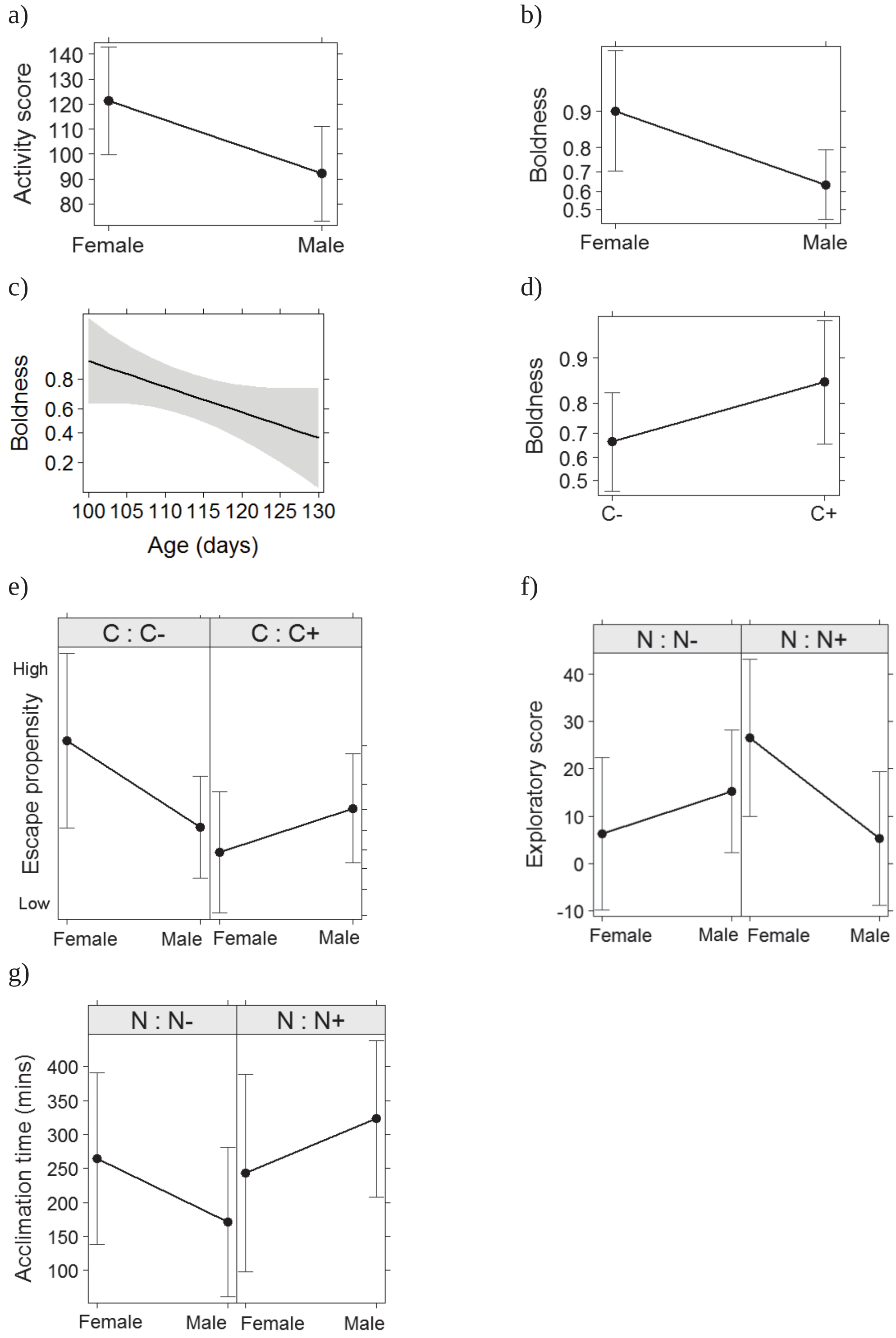


Figure 2.2 Significant interactions from linear mixed models and generalised linear mixed models testing for relationship between personality scores and sex, age, and nestling nutrient treatments, showing interactions between a) activity score and sex; b) boldness and sex, c) boldness and age, d) boldness and carotenoid supplementation in the nest; e) escape latency, sex, and carotenoid supplementation in the nest; f) exploratory score, sex and protein supplementation in the nest; and g) acclimation time, sex, and protein supplementation in the nest.

Table 2.1 Summary of covariate effects on personality traits measured in hihi on Tiritiri Matangi Island, and effects of personality traits on survival and natal dispersal. C=carotenoid supplementation in nest, N=protein supplementation in nest, *=interaction term. ✔=strong effect, ✓=weak/marginal effect.

	Covariate effects							Effect on life history traits	
Personality trait	Age	Sex	C	N	Sex*C	Sex*N	C*N	Survival	Natal dispersal
Activity score	✓	✔		✓					
Acclimation time		✓	✓	✓		✔			✓
Exploratory score		✓		✓		✔			
Boldness	✓	✔	✓					✔	
Escape latency		✓	✔		✔				

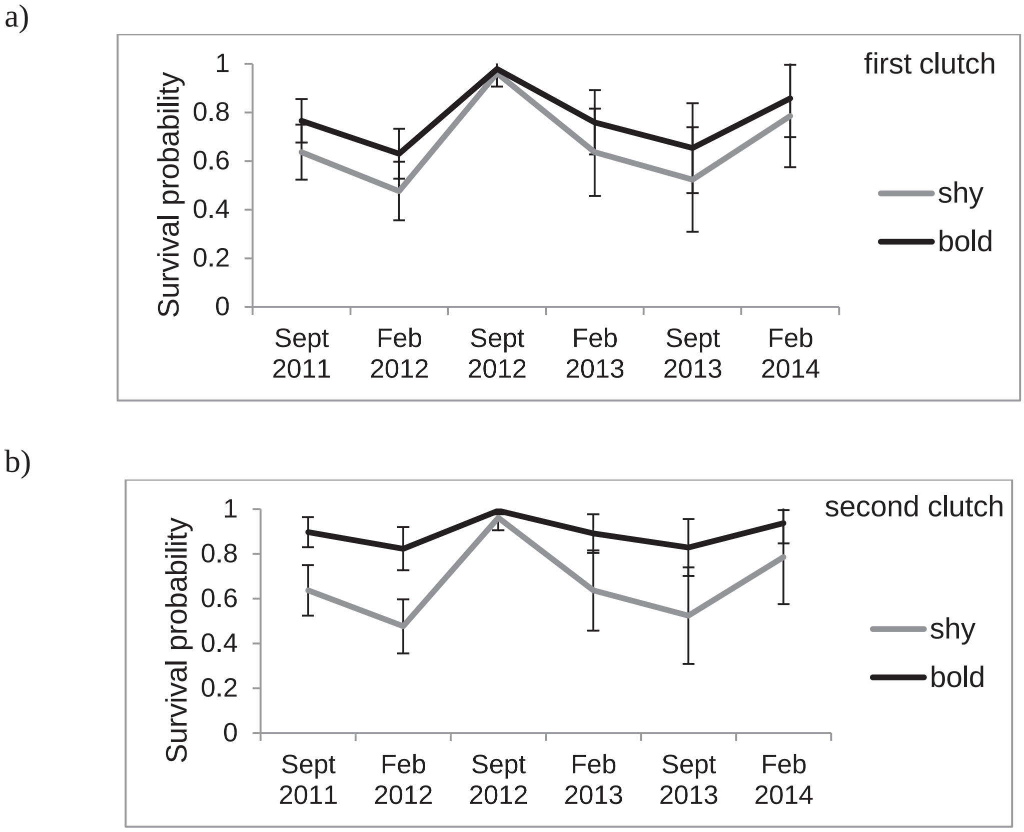


Figure 2.3 Survival probabilities from CJS model *boldness*clutch* for a) first clutch and b) second clutch birds from September 2011 to February 2014. Error bars denote 2.5% and 97.5% credible intervals.

Table 2.2 Results of likelihood-based CJS model with fixed time effect on ϕ and an effect of sex on p. Personality variables added one at time to assess effect on survival of juveniles from February 2011 to February 2014. Best model is in bold.

	pD[a]	**DIC**[b]	**ΔDIC**[c]
Boldness * clutch	**8**	**300.75**	**0**
Boldness	7	302.16	1.41
Boldness * sex	8	303.76	3.01
Constant	6	304.65	3.9
Escape latency * clutch	8	305.32	4.57
Escape latency	7	305.37	4.62
Activity	7	305.49	4.74
Activity * sex	8	306.39	5.64
Exploration	7	306.57	5.82
Acclimation	7	306.61	5.86
Activity * clutch	8	306.94	6.19
Acclimation * clutch	8	307.09	6.34
Exploration * sex	7	307.29	6.54
Escape latency * sex	8	307.32	6.57
Acclimation * sex	8	307.62	6.87
Exploration * clutch	8	308.60	7.85

Table 2.3 Results of linear models assessing effect of personality variables on natal dispersal distances. Best model is in bold.

	pD[a]	**DIC**[b]	**ΔDIC**[c]
Constant	**1.98**	**358.82**	**0**
Acclimation time	3.07	359.32	**0.5**
Sex	3.00	359.92	1.1
Boldness	3.01	360.51	1.69
Exploratory score	3.01	360.51	1.69
Activity score	3.01	360.61	1.79
Escape latency	3.00	360.79	1.97
Dcent	2.99	360.83	2.01
Exploratory score * sex	4.02	361.14	2.32
Acclimation time * sex	4.05	361.20	2.38
Escape latency * sex	4.03	361.86	3.04
Boldness * sex	4.05	361.93	3.11
Activity score * sex	4.03	361.97	3.15

[a] pD = Effective number of parameters (mean of posterior deviance minus mean of posterior distribution.

[b] DIC = Deviance information criterion, where lower DIC means higher predictive value.

[c] ΔDIC = Difference in DIC from that of best model.

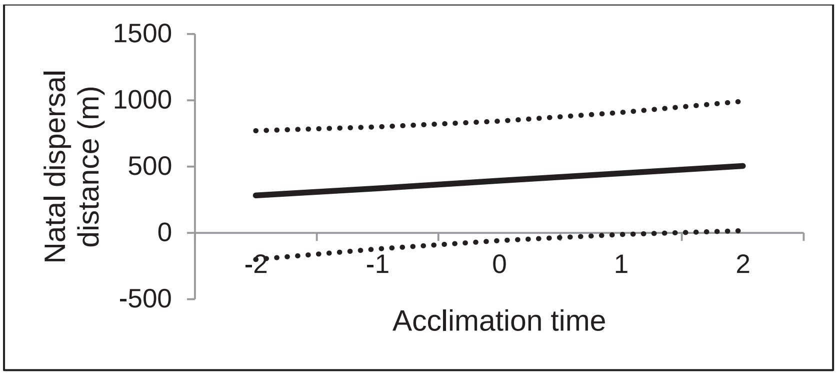


Figure 2.4 Relationship between acclimation time and natal dispersal distance as predicted from the generalised linear model including acclimation time as a fixed effect (Table 2.3). Dotted line denotes 2.5% and 97.5% credible limits.

Discussion

Our results suggest strong, and highly complex, interactions between early nutrition, phenotypic expression, and subsequent effects on life history parameters. We show sex-specific effects of both protein and carotenoid supplementation of nestlings on later expression on four personality traits (acclimation time, exploratory score, boldness and escape latency), and later life effects of boldness on survival probability.

Testing personality in the wild

We further refined traditional methods to devise a quick, simple test of personality in a wild species. Unlike Kluen *et al.* (2012), our test was carried out *in-situ*, due to logistical and ethical constraints in bringing our species into captivity. Our method enabled the test to be carried out in controlled, comparable conditions with multiple individuals, while minimising the possibility of adverse effects to individual birds. We demonstrated five measurable personality traits.

Personality in juvenile hihi

We demonstrated variation in a range of personality traits in juvenile hihi. Differences between male and female hihi were apparent, with females having significantly higher activity scores, and being bolder than males. Other studies have found differential effects of personality between the sexes on life history traits (Dingemanse and Réale, 2005), but it seems to be less common to demonstrate clear and consistent differences in personality traits between males and females. Sex-specific differences in the repeatability of scores has been demonstrated in zebra finches (males showing more consistency than females, (Schuett and Dall, 2009)) and field crickets (boldness being more repeatable in females than males, (Hedrick and Kortet, 2012)), suggesting that sex-specific differences in personality may be species- and context-specific. In hihi, a sexually dimorphic species with a complex breeding system (Castro *et al.*, 1996; Ewen *et al.*, 1999), it is perhaps not unexpected to find differences between male and female scores of personality for boldness and activity scores.

Age at the time of testing did not affect any of the scores, with the exception of boldness. Hihi that were older at the time of testing were less bold. It is not possible to determine if this represents temporal change in this trait, or demonstrates real differences in boldness between juveniles hatched earlier in the season.

Effect of early environment on personality

In support of recent suggestions that ontogeny, and in particular early nutrition, play a strong role in the development (or expression) of personality traits (Stamps and Groothuis, 2010; Groothuis and Maestripieri, 2013; Noguera *et al.*, 2015), we found strong evidence that nutrient supplementation in the nest influenced at least four of our measured personality traits.

In contrast to Krause *et al.* (2009) we found protein supplementation to increase exploratory scores, but only for females. In addition, we also found a sex-specific effect of acclimation time in males. Walker *et al.* (2013a) found a sex-specific effect of protein supplementation on survival and growth rates in our study population, with supplementation increasing nestling growth parameters and increasing female (but decreasing male) survival to fledging. The sex-specific effect of protein on survival to fledging was suggested to be a function of the better ability of female physiology to cope with increased protein supply (Walker *et al.*, 2013a), but we suggest an alternative explanation could also be considered, that protein supplementation had a sex-specific effect on the expression of behavioural or other phenotypic traits, which may have resulted in differential survival in nestling hihi.

Carotenoid supplementation has been previously linked to health benefits in a range of species, and has in this study been demonstrated to influence personality, with hihi that received a carotenoid supplement as nestlings being bolder as juveniles, and in females, having slower escape times. Noguera *et al.* (2015) also found micronutrient supplementation (including carotenoids) to increase boldness in male (but not female) zebra finches. We found that bolder individuals had higher survival probabilities up to three years later, and while no direct effect was found between carotenoid supplementation and survival to recruitment (Walker *et al.*, 2013a), it appears that carotenoids are able to influence survival indirectly by changing behaviour.

In our study population, both carotenoid and protein supplementation of nestlings also influenced plumage characteristics in later life, which in turn have been linked to reproductive success (Walker *et al.*, 2014). The link between melanin production and personality traits appears well established across species (Roulin, 2004; Mateos-Gonzalez and Senar, 2012; Fargallo *et al.*, 2014; Pascual and Senar, 2014; Saino *et al.*, 2014), mediated by pleiotropic effects of the melanocortin 1 receptor (Ducrest *et al.*, 2008), and there is evidence linking carotenoid-based pigmentation signals to dominance (Pryke *et al.*, 2002; Pryke and Andersson, 2003) or personality traits in some (Senar and Escobar, 2002; Grunst *et al.*, 2014; Backström *et al.*, 2015), but not all (e.g. Johnson and Fuller, 2014) species. Our results raise the possibility that plumage could act as a signal of personality type in hihi, and that this can be manipulated by the early natal nutritional environment.

Personality and life history traits –effects on survival and natal dispersal

As in other studies (Smith and Blumstein, 2007; Biro and Stamps, 2008), we found a relationship between personality traits of juveniles and their subsequent survival up to three breeding seasons later, with bold individuals having higher survival probabilities. This relationship was strongest for second clutch birds. These results support the findings of Smith and Blumstein (2007), who in a meta-analysis of personality studies showed a positive correlation between exploratory tendency and survival. It is not clear why the effect was stronger in the second clutch birds, but it is possible that the food supplementation experiment the first clutch birds were subjected to influenced results for this group and partially masked the relationship.

In contrast to studies with the great tit (Dingemanse *et al.*, 2003; Quinn *et al.*, 2011), we did not find any strong relationship between personality and natal dispersal patterns, although our sample size for this aspect of the study was relatively smaller. We found a weak indication that individuals with longer acclimation times had greater dispersal distances. Previous work (Richardson *et al.*, 2010) showed that density and sex ratio were strong determinants of natal dispersal patterns in this population, and it is possible that these factors may have overridden, masked or interacted with any possible effect of personality. Alternatively, our measure of dispersal (NDD) was relatively simple, and the effect of personality on dispersal behaviour may be more complex, influencing dispersal movements at the initial departure, transience, or settlement phase and requiring multiple measures of behaviour across these stages to be detected (van Overveld *et al.*, 2014).

Conclusions

Our study demonstrated a successful method to robustly assess personality traits in a wild-living passerine. We measured a range of personality traits comparable to those used in more traditional assays of personality, and, similarly to other studies, found correlates between one of these personality traits, boldness, and survival up to three breeding seasons later. Most critically, we demonstrated the sex-specific effect of experimental nutrient supplementations in the nest on the expression of personality traits in later life, showing that both protein and carotenoid supplementation in the nest influence expressions of personality traits that can have effects persisting to later life.

Appendix 2.1 Output of correlation tests and principal components analysis

Results of Spearman rank-order test of correlation

	Acclimation	Activity	Boldness	Escape_latency	Exploratory
Acclimation	1.00	-0.03	0.02	0.16	-0.18
Activity	-0.03	1.00	-0.44	-0.23	-0.02
Boldness	0.02	-0.44	1.00	0.38	-0.20
Escape_latency	0.16	-0.23	0.38	1.00	-0.26
Exploratory	-0.18	-0.02	-0.20	-0.26	1.00

Output from Principal Components Analysis

Component loadings

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Acclimation	0.22	0.52	0.80	-0.15	-0.15
Activity	-0.51	0.35	-0.28	-0.54	-0.49
Boldness	0.64	0.01	-0.27	0.18	-0.70
Escape_latency	0.53	0.06	-0.24	-0.71	0.40
Exploratory	-0.04	-0.78	0.39	-0.39	-0.30

Importance of components:

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Standard deviation	1.32	1.08	0.95	0.88	0.65
Proportion of Variance	0.35	0.23	0.18	0.15	0.09
Cumulative Proportion	0.35	0.58	0.76	0.91	1.00

CHAPTER 3

Multiple influences in post-release dispersal of a reintroduced passerine

---

This chapter is intended for submission as a manuscript (sans Appendix 3.4). Co-authors and their respective contributions are as follows:

John Ewen (Zoological Society of London), co-supervisor – assistance with study design, facilitation of collaboration within research group, comments on manuscript.

Leila Walker (University of Cambridge & Zoological Society of London) – design and completion of natal nutrition experiments, comments on manuscript.

Patricia Brekke (Zoological Society of London) – provision of pedigree-based inbreeding coefficients, comments on manuscript.

Kevin Parker (Massey University) – assistance with study design, translocation management, comments on manuscript.

Isabel Castro (Massey University), co-supervisor – assistance with study design, comments on manuscript.

Doug Armstrong (Massey University), primary supervisor – assistance with study design, data analysis, comments on manuscript.

Abstract

Post-release dispersal is widely known to influence reintroduction success, yet few studies have examined the factors driving this critical behaviour. Comprehensive research into natal dispersal patterns implicates a wide range of factors, but it is not known if these same influences drive variation in post-release dispersal. We use radio-tracking data from translocations of a reintroduced passerine to two release areas to investigate the role of an individual's a) sex, b) personality traits, c) degree of inbreeding, d) early natal nutritional environment, and e) condition on post-release dispersal from initial release to exploration and settlement. We demonstrated considerable within-species variation in dispersal at both release areas, with females showing greater dispersal tendencies but faster settlement patterns. We found effects of personality, with individuals that distress-called during handling exhibiting greater dispersal at both the initial and exploratory phases. More inbred individuals exhibited reduced exploration in the first four weeks, as did individuals that had received a protein supplemented diet in experimental manipulations of nestling diet. Condition at time of release did not have any detectable effect. Our study is the first detailed investigation of the intrinsic factors driving variation in post-release dispersal. As with studies of natal dispersal, we found effects of multiple factors, with personality, early natal condition and genetic quality converging to shape spatial behaviour of individuals immediately after translocation.

Introduction

Reintroduction success can be influenced by several factors, one of which is post-release dispersal (henceforth “PRD”) from the intended release area (Le Gouar *et al.*, 2012). PRD can lower establishment probabilities for reintroduced populations if dispersing individuals become lost to the population, either by increased mortality or geographic isolation (Chapter 6/Richardson *et al.*, 2015b). Individuals that do not disperse out of the release area, or have limited dispersal, will become the effective founders of the reintroduced population (Anthony and Blumstein, 2000); hence understanding why individuals vary in dispersal behaviour is of critical importance to the conservation management of reintroduced populations and can assist in the development of release strategies and site selection.

The drivers of intraspecific variation in PRD are not well understood, but our limited knowledge can perhaps be informed by the comprehensive research into natal dispersal (the movement of juveniles from their natal site to first breeding territory) (Clobert *et al.*, 2012). It is recognised that natal dispersal occurs over multiple phases – from the initial departure from the natal site, to the exploratory phase that follows, and eventual settlement (Clobert *et al.*, 2009). We consider PRD within a similar framework (sensu Moehrenschlager and Macdonald, 2003; Bradley *et al.*, 2012), from the initial movements of the animal immediately upon its release into a new environment, to subsequent exploration of the area and settlement. There may be critical differences between natal dispersal and PRD given the differing forces driving them: PRD is clearly a more "forced" dispersal, and individuals may already be settled in a home range or be territorial at the source site. In addition, PRD typically occurs after the individual has experienced a series of stressful events during translocation (i.e., capture, handling, transfer), followed by release in a novel and unfamiliar environment (Dickens *et al.*, 2010; Parker *et al.*, 2012b). Natal dispersal, in contrast, allows the individual time to gain information about its environment prior to dispersal, although to some extent this dispersal behaviour may also be forced by interactions with parents, siblings or unrelated conspecifics (Matthysen, 2012). Beyond this initial phase, we expect that the proximate forces driving individual variation in exploration behaviour may show similarities between the two types of dispersal.

The factors influencing natal dispersal can vary across the three phases (del Mar Delgado *et al.*, 2010; van Overveld *et al.*, 2014), and are typically placed into two broad categories: those related to internal state of the individual, and those related to the external environment (Matthysen, 2012). Here, we focus on internal state, which can relate to phenotypic traits, such as personality (Dingemanse *et al.*, 2003; Duckworth and Badyaev, 2007; Cote *et al.*, 2010a), stress response (Belthoff and Dufty, 1998), and morphology (O'Riain *et al.*, 1996; Massot and Clobert, 2000; Balbontín *et al.*, 2009). Internal state can be influenced by genotype (Hardouin *et al.*, 2015) or condition (del Mar Delgado *et al.*, 2010). Phenotypic traits linked to dispersal (“dispersal syndromes”; Ronce and Clobert, 2012) are increasingly recognised to be driven by heritable factors, but with potential for mediation by a range of environmental factors, in particular the early natal environment (Chapter 2; Duckworth, 2009; Krause *et al.*, 2009; Noguera *et al.*, 2015).

There are very few studies examining the role of internal state in translocation success, and even fewer with specific reference to PRD (although there is a greater awareness of the role of the external environment; Pearce and Lindenmayer, 1998; White *et al.*, 2003;

Frair *et al.*, 2007). Personality has been found to influence post-release survival in translocated animals, with “bolder” (sometimes referred to as "fast" or "proactive"; Groothuis and Carere, 2005; Cockrem, 2007) individuals showing higher post-release mortality in swift foxes (*Vulpes velox*; Bremner-Harrison *et al.*, 2004), but lower mortality in translocated Tasmanian devils (*Sarcophilus harrissii*; Sinn *et al.*, 2014). The relationship with PRD was not investigated in either study. In North African houbara bustards *(Chlamydotis undulata undulata)*, Hardouin *et al.* (2015) found a sex-specific effect of individual inbreeding coefficient on PRD. We are not aware of any other studies examining the role of internal state, or early environmental effects, on subsequent PRD, despite the obvious potential for these to be important factors.

Here, we use radio tracking data from 55 individuals of an endangered passerine, the New Zealand hihi (*Notiomystis cincta*) to two release areas, to examine the role of internal state in individual variation in PRD across three phases:

- initial PRD phase (the immediate movements after release at a new site)
- exploratory phase (subsequent exploratory movements at a new site prior to settlement)
- settlement phase (end of exploratory movements and settlement at first breeding location)

Given the importance of personality in natal dispersal patterns (Dingemanse *et al.*, 2003; Duckworth and Badyaev, 2007; Cote *et al.*, 2010a), and the role of the early natal environment in influencing personality (Chapter 2; Krause *et al.*, 2009; Noguera *et al.*, 2015) we focus on these aspects of internal state, and compare their influence on PRD with that of the physical condition of the individual at the time of release. We also examine the effect of genetic quality on PRD. We expect that all factors will influence PRD, and that the effects of these will be sex-specific and vary between the initial PRD phase and subsequent exploratory phase. Finally, we also examine the relationship between early PRD movements and later breeding site selection (i.e., the settlement phase).

Methods

Study species

The hihi is an endangered New Zealand passerine (Vulnerable on the IUCN Red List; IUCN, 2013) that has been subject to multiple reintroduction attempts (Ewen *et al.*, 2013b). Reduced to a sole island population by the 1880s (Hauturu/Little Barrier Island), hihi now persist at additional reintroduction sites including two islands (Tiritiri Matangi and Kapiti), and three mainland reserves (Karori Wildlife Sanctuary, Maungatautari Ecological Island and Bushy Park). All populations are reliant on management, including maintenance of an environment free from mammalian predators (all populations), as well as provision of supplementary food (all reintroduced populations; Chauvenet *et al.*, 2012) and artificial nest boxes (all reintroduced populations except Maungatautari and Kapiti). Reintroduction attempts have also been made to four other areas, including one mainland reserve (Ark in the Park), but were not successful. The increasing focus of hihi recovery efforts is towards the mainland, where mature forest (thought to be preferred habitat of hihi; Makan *et al.*, 2014) is primarily found. One complication from reintroduction to the mainland (c.f. islands) is the increased potential for dispersal away from the release area. Individuals lost from the release area due to dispersal may effectively represent mortality events that compromise conservation efforts. Understanding what influences the extent of dispersal has therefore become a priority area of research for hihi recovery (Ewen *et al.*, 2013b). We monitored the initial post-release period of two translocations to mainland areas through intensive radio tracking, and mapped first-breeding locations at one of these areas, to address our research questions.

Study sites and translocations

Ark in the Park

Ark in the Park is a mainland forest restoration area (~1100 ha in 2007) within the larger Waitakere Ranges (~13,000 ha contiguous forest), west of Auckland, New Zealand (36°53'05.5"S 174°31'19.1"E, Figures 3.1, 3.2). The restoration area is a mix of original mature kauri (*Agathis australis*) forest and modified podocarp-broadleaf forest, and the restoration involves control of invasive mammals (Bellingham *et al.*, 2009). Seven supplementary feeder stations were established for hihi, all within 500 m of the release site.

Fifty-nine hihi (50 juveniles and nine adult males) were translocated to Ark in the Park from Tiritiri Matangi Island in February and June 2007 (Richardson *et al.*, 2015a). This was the first translocation of hihi to the area. Twenty-one of the juveniles released (and four adults, excluded from this analysis) carried body-mounted Holohil BD-2 radio transmitters (0.75-1.2 g, expected battery life 21-74 days), and were monitored intensively for up to eight weeks post-release. All birds had been colour banded in the nest on Tiritiri Matangi Island, and at the time of translocation were weighed, had tarsus length measured, and the number of fault bars on rectrices of each juvenile counted (the latter as a measure of early natal condition; Riddle, 1908; Fitzpatrick and Price, 1997). All had a blood sample taken for disease-screening purposes, and to enable a white blood cell count, haematocrit score, and heterophil:lymphocyte ratio to be calculated as additional measures of condition (Ewen *et al.*, 2012). Pedigree-based inbreeding coefficients were available for most individuals from an associated project (for details see Brekke *et al.*, 2011; 2013; 2015).

All translocated hihi were held in captivity at the source site for 9-14 days while disease screening results were awaited. Half were then held in captivity at the release site for an additional 2-4 days as a delayed-release strategy, while the other half were released immediately (Richardson *et al.*, 2015a).

Maungatautari Ecological Island

Maungatautari Ecological Island (henceforth “Maungatautari”) is a ~3400 ha reserve in the Waikato region of New Zealand’s North Island (38°01°00°S 175°34°00°E, Figures 3.1, 3.3). Maungatautari is a volcanic cone (797 m a.s.l) covered primarily in mixed podocarp/broadleaf forest, largely surrounded by pasture (McQueen *et al.*, 2004). A predator-exclusion fence was completed around the forest edge in 2006 and all invasive mammals except mice (*Mus musculus*) and small numbers of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) were eradicated. Six supplementary feeder stations were established for hihi, all within 150 m of the release site.

Hihi were first translocated to Maungatautari in 2009, with 79 birds (70 juveniles and nine adults) released in 2009 and 37 juveniles in 2010 (Ewen *et al.*, 2011). These individuals were not radio tracked after release, but subsequent monitoring showed at least 42 breeding adults were established by 2010/11 (a combination of translocated birds and locally-bred recruits; Appendix A).

In April 2011, a further 39 juvenile hihi were translocated from Tiritiri Matangi Island to Maungatautari, and these were radio tracked following release. All of these had been colour banded in the nest, and at the time of translocation the same measures were obtained as for the Ark in the Park translocation. All were held in captivity for 5-10 days at the source site while disease screening results were awaited and all were released immediately at the release site. All 39 juveniles were fitted with tail-mounted Holohil BD-2 radio transmitters (0.62-0.75 g, expected battery life 21-28 days); one lost the transmitter prior to release and is excluded from this analysis.

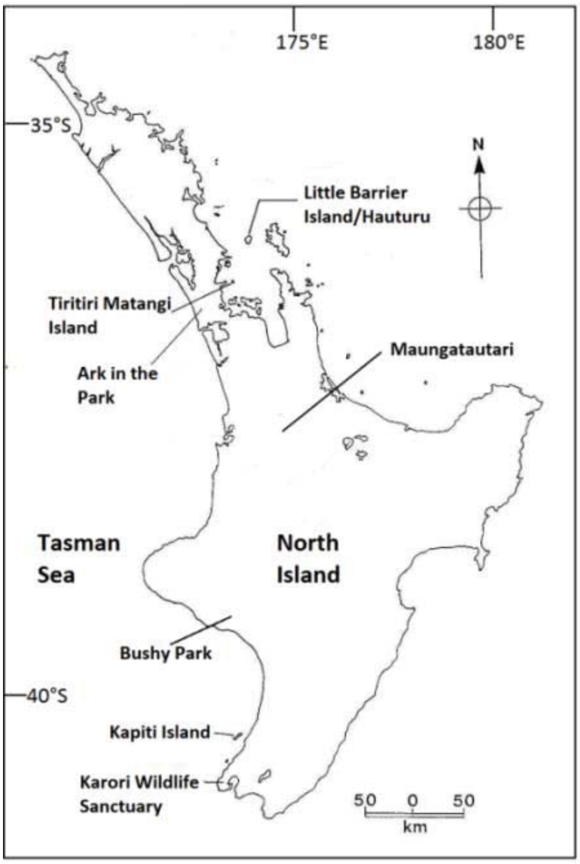


Figure 3.1 Map of the North Island of New Zealand, showing location of the remnant hihi population (Little Barrier Island/Hauturu), persisting reintroduced populations as of 2015 (Tiritiri Matangi and Kapiti Islands, Maungatautari, Karori Wildlife Sanctuary and Bushy Park), and one failed reintroduction (Ark in the Park).

Natal nutrition experiment

All of the hihi translocated to Maungatautari in 2011 were subject to experimental supplementary feeding in the nest on Tiritiri Matangi Island, enabling examination of the effect of natal nutrition on PRD. The experimental design is described in detail in Walker *et al.* (2013a). In brief, all individual nestlings were assigned to one of four treatment groups (both within- and between-nests, either N+C+, N-C+, N+C- or N-C-), with N+ nestlings fed a high protein dietary supplement (Wombaroo^{TM} Lorikeet and Honeyeater Food, Wombaroo Food Products, Glen Osmond, SA, Australia), and N- a control supplement (sugar water). C+ nestlings received this supplement enhanced with carotenoids (lutein and zeaxanthin in the form of OroGLO® liquid; Kemin Industries, Des Moines, IA, USA), and C- without. Carotenoids are important biomolecules that can be obtained only through dietary means, and have previously been linked to a range of health benefits in hihi (Ewen *et al.*, 2006; Ewen *et al.*, 2008; Thorogood *et al.*, 2008; Ewen *et al.*, 2009) as well as in other species including humans (e.g. Johnson, 2002). In the Walker *et al.* (2013a) study, a sex-specific effect of the high protein diet was found on nestling growth parameters, and an interactive effect between the high protein diet and carotenoid supplement on survival to fledging, but no effect of nestling dietary treatment was detected on survival from fledging to recruitment.

Personality testing

Personality tests were performed for all juveniles translocated to Maungatautari in 2011, between one and two months prior to translocation *in situ* at the source site (further detail is presented in Chapter 2). We tested birds in a specifically designed cage (150 x 50 x 50 cm) similar to that used in captive tests, with a removable divider across the middle, and escape hole at each end, modified from that used by Herborn *et al.*

(2010). Birds were captured in mist nets and then released into the cage. After five minutes, the observer (KMR) would approach the cage from the back, and remove the divider. After another five minutes, the escape hole on the opposite side to the bird was opened. If the bird remained after five minutes, the front doors would be left open until the bird left. All tests were filmed using a Canon SX20 camera on a tripod set up ~2-3 m in front of the cage. Footage was subsequently viewed using Windows Media Player. This footage was used to calculate the following personality scores:

- Activity score: the number of movements (hops or flights) made by the bird in the first five minutes in the cage.
- Boldness: the latency (seconds) of the bird to move to the "novel" side of the cage after removal of the divider.
- Exploratory score: the number of movements made on the "novel" side of the cage minus the number of movements made on the “familiar” side (as per Herborn *et al.*, 2010).
- Latency to escape: the latency (seconds) for the bird to escape the cage in the third five minute period.
- Acclimation time: the time between release into the cage and the first body shake. We noted while viewing film footage that almost all birds underwent an initial very high movement phase (presumably an attempt to escape), but after a varying period of time would settle onto one of the perches, shake and ruffle their body feathers, and then sit still and survey the surroundings briefly before resuming movement. There was considerable variation among individuals in the time taken for this to occur, hence we measured this, and termed it "acclimation time".

We noted during these tests that individual responses in the hand varied during mist net extraction, and considered this may represent variation in personality type (sensu Pascual and Senar, 2014). Hence during subsequent recapture for translocation we recorded the response of the bird within the first 30 seconds of being removed from the net. Individuals that did not struggle or distress-call were assigned a handling score of "0", individuals that struggled but did not distress-call were recorded as "1", and individuals that both struggled and distress-called were recorded as "2". No bird distress-called without struggling.

Post-release monitoring

Ark in the Park 2007

The primary focus of post-release monitoring was detecting dispersal of individuals outside of the restoration area, and retrieving mortalities; however we were able to detect dispersal distances for the majority of birds within the first week. We walked along set tracks within the Ark in the Park area at least every second day to detect telemetry signals from the radio-tagged birds. Searches were also carried out beyond the restoration area, up to 6 km from the release site, to detect radio-tagged individuals that had left the restoration boundaries. In addition we monitored each supplementary feeder station weekly.

Maungatautari Ecological Island 2011

Post-release monitoring after this translocation aimed to obtain detailed dispersal data for each individual. We used existing tracks established at Maungatautari for detecting invasive mammalian predators. These form a network of tracks across the reserve and are designed to be no more than 200 m apart. We aimed to locate each bird at least every other day, but in practice this varied considerably between individuals, with some located almost daily, and others only a small number of times across the four week period despite extensive searches. Searches were also conducted outside the reserve, with a focus on the isolated forest patches up to 16 km away. Supplementary feeders were monitored at least twice weekly.

Breeding territories were located each year for hihi at Maungatautari as part of a larger project between 2010/11 and 2012/13. Each season the reserve was thoroughly searched using the same tracks as in the post-release monitoring. The majority of territories were found between September and early November when male calling rates are highest. We considered male hihi to be resident to a location if they were identified at least three times there during the breeding season, and female hihi resident if they were observed at the location engaged in breeding behaviour (e.g. nest building, incubating, or feeding chicks), or otherwise observed at the same location at least twice during the breeding season (see Chapter 4 for further detail).

Data analysis

Dispersal data

The Maungatautari 2011 dispersal data included a combination of known locations (from visual sightings) over the four weeks of telemetry monitoring and estimated locations from triangulated data. We excluded data for three of the 38 radio tagged birds at Maungatautari from all analyses: one bird as only one location estimate could be generated during the four week period, and two as only weak signals with an irregular pulse were obtained during the four week period. All three birds were detected at the end of the four week period, and two were sighted several months after the initial four week period, hence it is unlikely that the lack of data for these individuals was due to dispersal outside of the reserve.

We used LOAS software (Ecological Software Solutions Inc., Sacramento, CA) to estimate locations from triangulated data using a maximum likelihood estimator. We only used bearings with intersections, excluded intersections that were more than 1 km from the observation points, and only data obtained within a 2 h period. This resulted in 241 locations for 35 individuals (mean 7 locations per bird over 28 days), with gaps of no more than 6 days between individual locations.

The Ark in the Park data were less detailed for individual birds; however we were able to estimate locations for 17 of the juveniles one week after release, using the same methods as above. Of the remaining four, two were detected in the first two days after release moving rapidly from the release site, and then not detected again, and a third was never detected. All three of these transmitters were in good working order at the time of release. We thoroughly searched the area within 2 km of the release site for at least six weeks after release (Richardson *et al.*, 2015a) and frequently sighted both tagged and non-tagged individuals, but never these three. Therefore we believe that these three birds dispersed at least 2 km from the release site within the first week. The fourth bird died within two days of release (~1.8 km from the release site), and was excluded from the analysis.

Modelling of covariate effects

We calculated dispersal distances in the initial PRD phase (one week post-release, data from both sites, n=55) and subsequent exploratory phase (four weeks post-release, Maungatautari data only, n=33, as another 2 transmitters had failed by this stage). We fitted generalised linear models with an exponential distribution and log-link function in WinBUGS 1.4 (Lunn *et al.*, 2000) to examine the effect of covariates on dispersal distance from release site in both the initial and exploratory phase. We initially examined the Ark in the Park data separately, to test for an effect of the different release dates (February and June) and release strategy (immediate and delayed release). As we did not find an effect, we did not include these factors in subsequent models and analysed data from the two sites together.

We included the following as covariates: sex, early natal condition (number of fault bars, C and N), condition at time of release (weight:tarsus, weight change during captivity period, white blood cell count, haematocrit score, heterophil:lymphocyte), inbreeding coefficient and personality (activity score, exploratory score, acclimation time, boldness, escape latency and handling score). As boldness and escape latency both displayed a distinctly bimodal distribution we rescored these to 1 (did not move to novel side/shy, or did not escape), or 0 (did move to novel side/bold, or did escape). We also included site as a fixed effect for analysis of the initial phase. We first ran a constant model and then added covariates one at a time. As we found a significant main effect of sex in the exploratory phase, we included sex in all subsequent models with dispersal distance to four weeks as the response variable. We included site as a main effect in models for C and N, to account for Ark in the Park birds receiving no nutritional treatment. As the effects of these supplementations are known to be sex-specific (Walker *et al.*, 2013a, Chapter 3), as can those of personality (e.g. Dingemanse, 2004; Pascual and Senar, 2014; van Overveld *et al.*, 2014), we tested for an interaction with sex for all food supplementation and personality covariates. We also tested for an interaction between C and N as this was previously found to be significant for other traits (Walker *et al.*, 2013a). Where missing values were present (missing values were present for 4% of individuals for inbreeding coefficients, 5-18% for haematological parameters, and 3-9% for personality variables), we imputed them by sampling from either a normal, Bernoulli, or Poisson distribution as appropriate (Nakagawa and Freckleton, 2008). Where dispersal distance was only known to be > 2000 m, we used right censoring (Link and Barker, 2010). For all models there was burn in of 10,000 samples, and we then introduced another 100,000 samples after convergence was reached. Alternative models were compared using DIC (Deviance Information Criteria) values (Spiegelhalter *et al.*, 2002). As models estimating missing values from a non-normal distribution could not generate DIC values, we also divided the mean dispersal distance estimated under the highest covariate score by the mean dispersal distance estimated under the lowest covariate score to generate comparable effect sizes between models.

We then examined the effect of the same covariates on the multiple exploratory movements of individuals over the first four weeks, using only the Maungatautari data (n=35). We fitted data to generalised linear mixed models with an exponential distribution and log-link function as above. However, this time we also included a random effect of individual and a fixed effect of time since release, since individuals were located multiple times at different times after release. Because birds were not always located daily, we also included a fixed effect distinguishing 1-day intervals from longer intervals (preliminary analysis suggested no difference among the longer intervals). We first ran a constant model and then added covariates one at a time, including interactions between sex and feeding treatments and personality scores, as well as an interaction between C and N.

Results

All model output is presented in Appendices 3.1-3.3 with DIC values and effect sizes.

Sex-specific differences

We observed considerable variation among individuals in post-release dispersal movements at both sites. In the initial phase (to one week post-release), juvenile male hihi at Ark in the Park dispersed a mean of at least 1323 m (min. 300 m, max. > 2000m) and juvenile females a mean of 1679 m (min. 300 m, max. 4260 m) (Figure 3.2). Dispersal distances in the initial phase were slightly higher at Maungatautari, with juvenile males dispersing a mean of 1750 m (min. 30 m, max. 4073 m), and juvenile females a mean of 2155 m (min. 500 m, max. 4763 m) (Figure 3.3). By the exploratory phase (four weeks post-release, Maungatautari only), the distances from release site for juvenile males had decreased to a mean of 1307 m (min. 167 m, max. 4754 m), and for juvenile females slightly increased to a mean of 2520 m (min. 461 m, max. 5345 m) (Figure 3.3).

Personality traits

We found no strong effects of any of our personality scores in the distance moved in the initial phase (Table 3.1), but a weak effect of activity scores, with hihi with higher activity scores tending to disperse shorter distances (Figure 3.4a). There was also a tendency for males that distress-called upon capture to disperse farther than those that did not.

Escape latency was related to dispersal distance in the exploratory phase, with those that found the escape hole during the personality test tending to be closer to the release site after four weeks than those that did not escape (Figure 3.5a). There was a strong effect of handling score on exploratory phase movements, with distress-callers of both sexes exhibiting greater movement during this time period (Figure 3.6a).

Table 3.1 Summary of covariate effects on post-release dispersal behaviour of hihi released at Maungatautari in the initial and exploratory phases. ✔=strong effect[1], ✓=weak/marginal effect[2], *=interaction with sex.

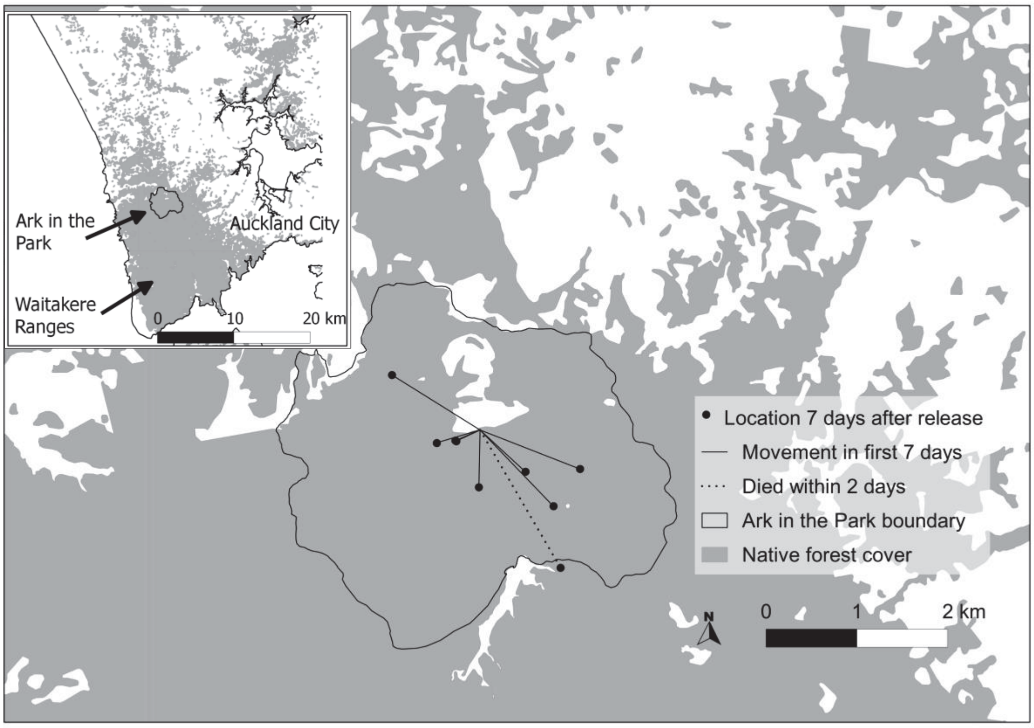
		Initial phase (net distance to 1 wk post-release)	Exploratory phase (net distance to 4 wks post-release)	Exploratory phase (multiple movements in first 4 wks post-release)
	Sex		✔	
	Site			
	Inbreeding coefficient			✔
Early natal condition	Number of fault bars	✓		
	Carotenoid (C) supplement			
	Protein (N) supplement		✔*	
Condition at time of release	Weight:tarsus			
	Weight change in aviary			
	Haematocrit score			
	Heterophil: lymphocyte			
	White blood cell count			
Personality traits	Activity score	✓		
	Acclimation time			
	Exploratory score			
	Boldness			
	Escape latency		✔	
	Handling score	✔*		✔

---

[1] Strong effect = including variable in model results in DIC lower than that of constant model, or an effect size of >4.

[2] Weak effect = including variable in model results in ΔDIC <0.2, but not lower than that of constant model.

a)



b)

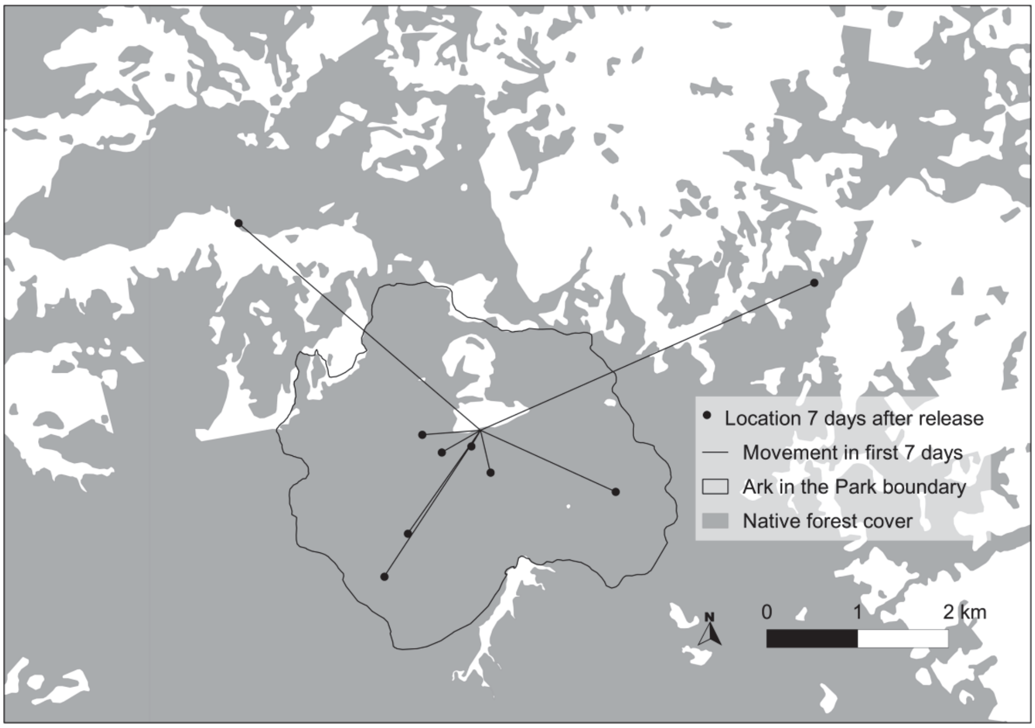
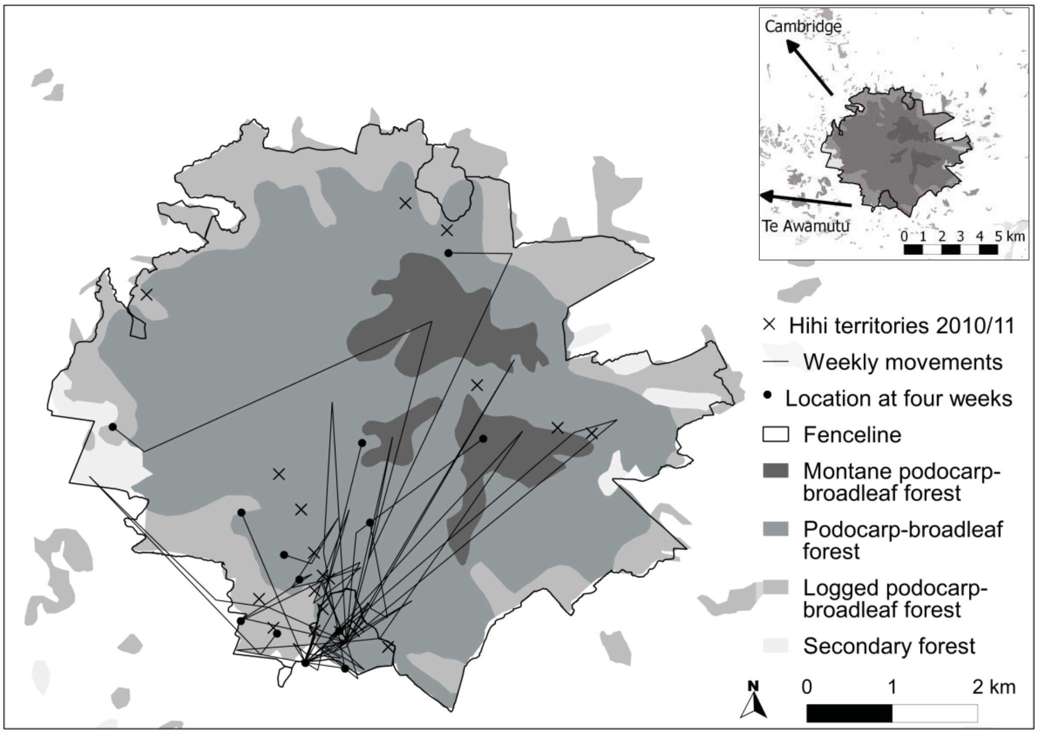


Figure 3.2 Initial post-release dispersal of a) male hihi and b) female hihi translocated to Ark in the Park in 2007. Lines represent dispersal from release site to one week post-release.

a)



b)

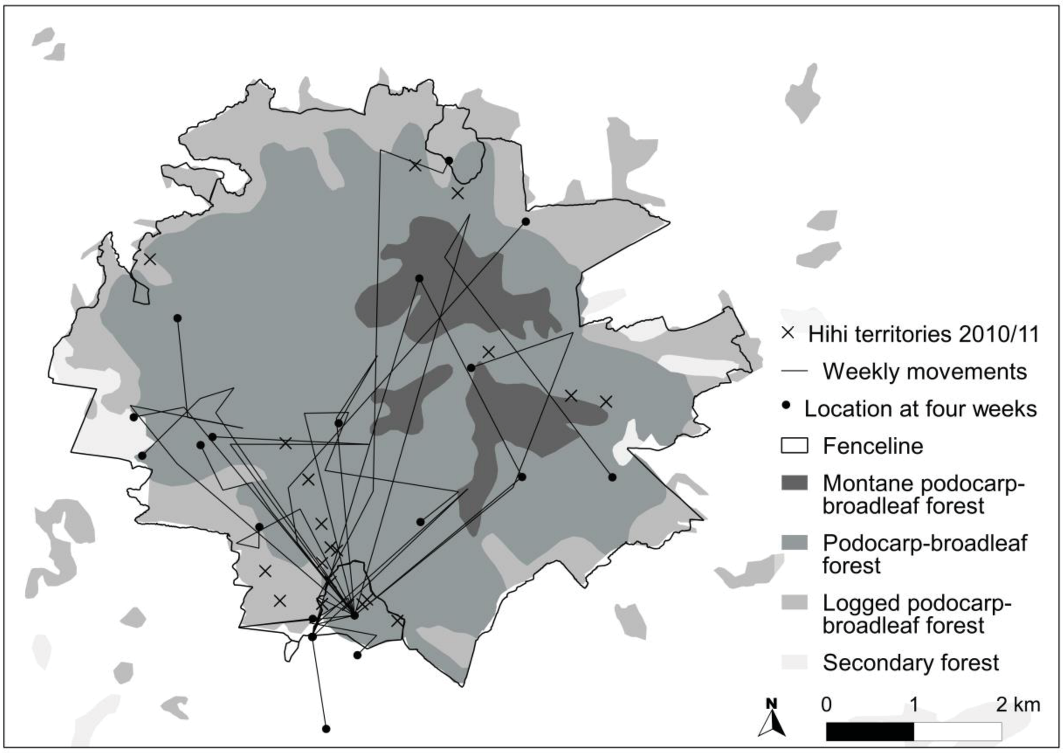


Figure 3.3 Initial and exploratory post-release dispersal of a) male hihi and b) female hihi translocated to Maungatautari in 2011. Lines represent weekly movements from release site, and the dot represents last known location for each individual (between three and four weeks post-release).

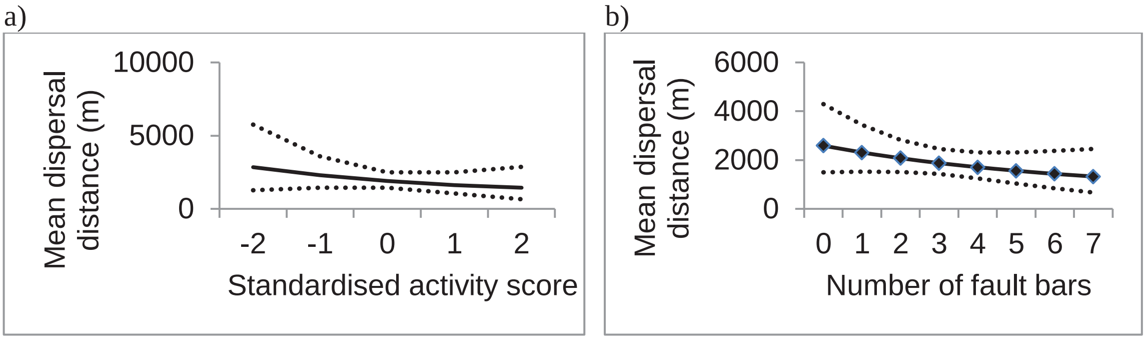


Figure 3.4 Estimates of mean dispersal distance (m) from generalised linear models examining relationship between dispersal distance in the **initial phase** (one week post-release) and a) standardised activity score, and b) number of tail fault bars. Dotted lines denote 2.5% and 97.5% credible limits.

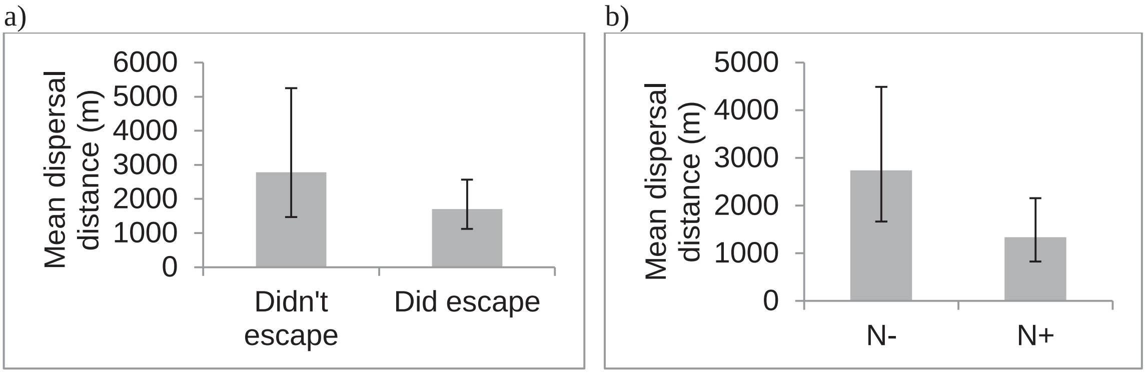


Figure 3.5 Estimates of mean dispersal distance (m) from generalised linear models examining relationship between dispersal distance in the **exploratory phase** (four weeks post-release), and a) escape latency during personality test and b) protein supplement in nest (at Maungatautari 2011). Error bars denote 2.5% and 97.5% credible intervals.

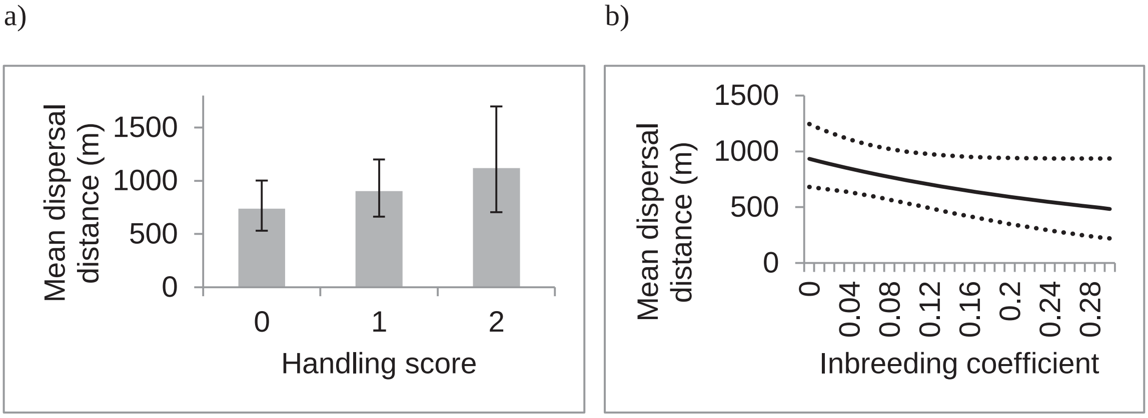


Figure 3.6 Estimates of mean dispersal distance (m) from generalised linear mixed models examining relationship between **exploratory movements** in the first four weeks and a) handling score (0=no struggle, 1=struggled, 2=struggled and distress-called), and b) *f* value. Error bars/dotted lines denote 2.5% and 97.5% credible intervals/limits.

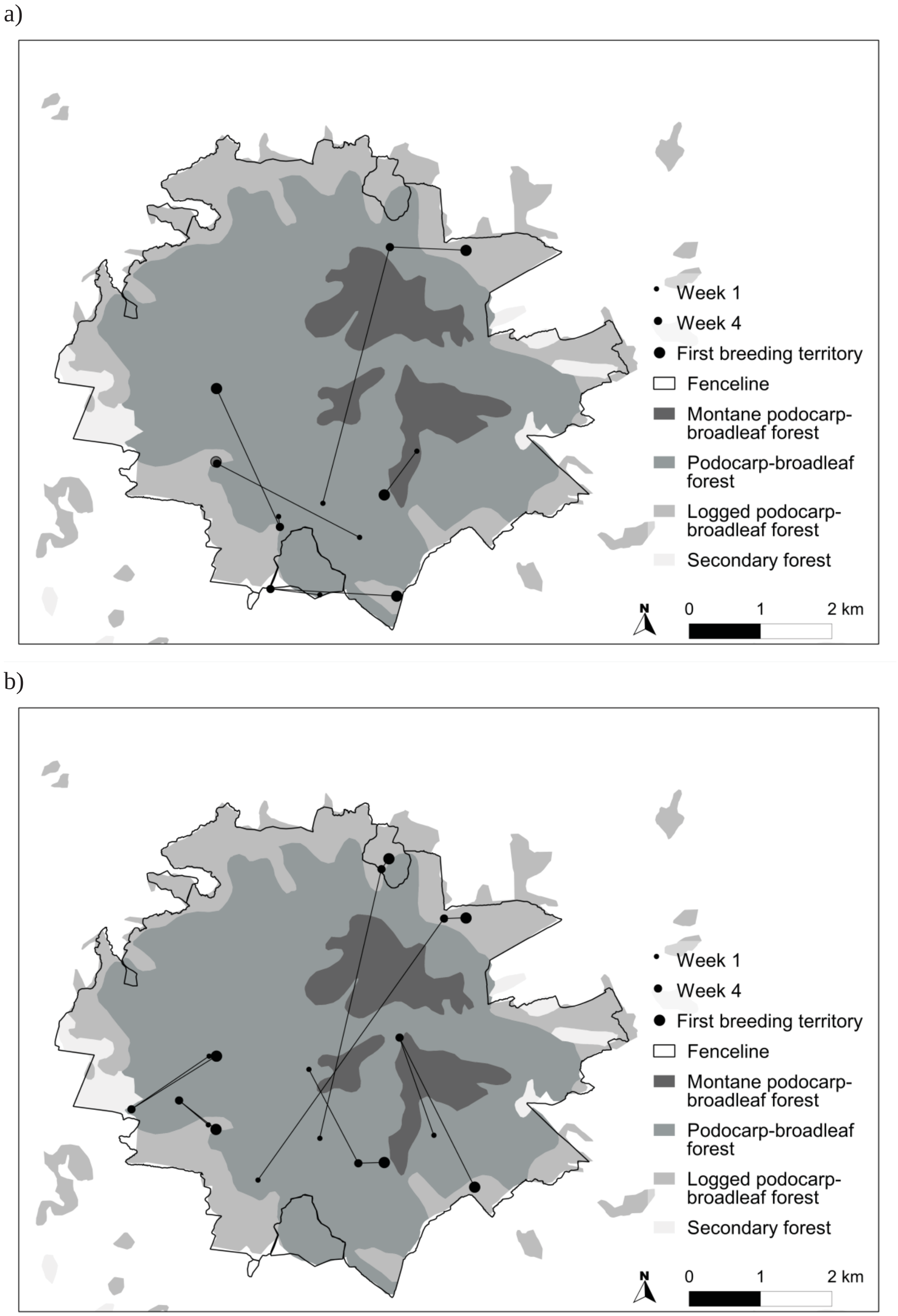


Figure 3.7 Individual locations during initial and exploratory post-release dispersal, and territory location six months later, for hihi translocated to Maungatautari Ecological Island that survived and bred in the 2011/12 breeding season for a) males and b) females.

Inbreeding effects

There was an effect of degree of inbreeding on exploratory phase movements, with hihi with higher *f* values exhibiting reduced movement during this time period compared to those with lower *f* values (Table 3.1, Figure 3.6b). However, inbreeding did not affect net distance dispersed in either the initial or exploratory phase.

Early natal nutritional environment

There was a tendency for dispersal distance in the initial phase to be shorter for juveniles with more tail feather fault bars (Table 3.1, Figure 3.4b). Protein supplementation in the nest also had a strong effect on dispersal distance in the exploratory phase, with those receiving the supplement located closer to the release site after four weeks than those that had not received the supplement (Figure 3.5b). This effect was present in both sexes, but was stronger in males. Exploratory phase movements were also influenced by protein supplementation, with those receiving the supplement having reduced movements compared to those that did not.

Condition

We did not detect any effect of weight:tarsus ratio, weight change during captivity, or any of the haematological parameters on dispersal behaviour in the initial or exploratory phase (Table 3.1).

Early PRD movements and the settlement phase

15 of the 38 hihi radio tracked at Maungatautari were known to have survived from release in April 2011 to the 2011/12 breeding season. Of these, we found the territory of

6 of 7 females (the 7th female bred successfully, but location is only known approximately), and 5 of 8 males (the remaining 3 were thought to be floater males).

On average, male breeding territories were 2036 m (min. 796 m, max. 4072 m) away from their location one week post-release, and 1249 m (min. 29 m, max. 2135 m) from their location four weeks post-release (Figure 3.7a). Female territories were on average 1930 m (min. 106 m, max. 4673 m) from their location one week post-release, and on average 881 m (min. 193 m, max. 2337 m) from their location four weeks post-release (Figure 3.7b).

Discussion

Our results demonstrate considerable within-species variation in PRD behaviour at release areas with opportunities for relatively large-scale dispersal. This study is the first to show genetic, phenotypic and ontogenetic effects similar to those found in natal dispersal studies. We also show these effects vary across the different phases of PRD, and find a strong, sex-specific link between initial PRD and settlement.

Sex-specific differences

Dispersal distances varied considerably across both sexes - whilst some individuals remained within close proximity to the release site, others dispersed at least as far as 5.3 km within the first four weeks. Overall, females tended to disperse further, but this difference was not significant until four weeks post-release. Visual inspection of dispersal maps suggested that, at Maungatautari, a number of males that had dispersed in the first week then returned to the release site by the fourth week, in contrast to females that tended to be more settled by this time. This movement of males may represent a higher level of exploration of the release area (especially given the constraints of the forest boundary that appeared to prevent movement outside of the reserve), or a social effect given the higher density of resident birds near the release site.

Potentially, the presence of supplementary feeders close to the release site may have played a role, but despite intensive monitoring of these feeders we only observed two of the recently released birds using the feeders during this time, and these only sporadically. We suspect the social effect of the resident birds, and in particular the presence of creches of resident juvenile hihi near the release site played a stronger role. The sex-specific difference in the return to the release site may reflect the differences between male and female mating strategies in hihi. Hihi have high levels of extra-pair paternity (Ewen *et al.*, 1999; Brekke *et al.*, 2013), and information about conspecifics (e.g. breeding locations, quality) presumably enhances male reproductive success. Females, on the other hand, probably benefit more from remaining more philopatric outside of the breeding season and gaining information about resources rather than conspecifics.

Personality effects

Our study is the first to demonstrate an effect of personality on PRD. We show that males that distress-call upon capture (generally thought to be at the "proactive" end of the personality spectrum; Groothuis and Carere, 2005; Cockrem, 2007; Pascual and Senar, 2014), tend to disperse greater distances initially, and that both sexes that distress-call exhibit higher overall exploratory phase movements. However, we also found that individuals with lower activity scores, and slow escape times (generally thought to be at the "reactive" end of the personality spectrum), also tended to disperse further in the initial and exploratory phase respectively. There was no correlation among our personality variables (Chapter 2; including between handling score, data not presented in this thesis), in contrast to Pascual and Senar's (2014) finding that male Eurasian siskins (*Carduelia spinus*) that distress-called had higher exploratory scores as well as being more dominant and aggressive. Distress-calling has been shown to be highly repeatable (Perrone, 1980; Koenig *et al.*, 1991), as well as linked to stress response (Blumstein *et al.*, 2006), and is potentially a useful measure of personality, but the relationship with other personality scores is not yet well understood across multiple species. Ontogenetic manipulations in great tit (*Parus major*) studies have found that personality characteristics usually belonging to the same end of the spectrum can become uncoupled as an adaptive response to environmental conditions (reviewed in Groothuis and Carere, 2005), and it is possible that the nestling feeding experiments in our study may have reduced the correlation between otherwise related personality variables. Additionally, different measures of personality presumably reflect different aspects of behavioural variation, rather than a simple proactive-reactive dichotomy. Our results may reflect this, as may possible linkages between personality and other traits (e.g. social aspects of personality such as dominance, aggression that we were not able to measure) that could have affected interactions with conspecifics and hence dispersal distances (e.g. van Overveld *et al.*, 2014; Aguillon and Duckworth, 2015).

Inbreeding effects

We found a strong effect of inbreeding coefficient on exploratory phase movements, with inbred individuals tending to move less during this four week period. Correlations have been found between inbreeding and a variety of life history traits (reviewed in Keller and Waller, 2002), and there is evidence that inbred individuals are less able to cope with the effects of environmental stress (Crnokrak and Roff, 1999; Keller and Waller, 2002). The relationship with spatial behaviour is less commonly investigated, but three studies have shown spatial behaviour to be related to inbreeding or homozygosity. Garten (1977) found exploration in male oldfield mice *(Peromyscus polionotus)* decreased with increased homozygosity, Cain *et al.* (2014) found home range sizes of male eastern black rhinoceros *(Diceros bicornis michaeli)* decreased with homozygosity, and Hardouin *et al.* (2015) found a sex-specific effect of inbreeding coefficient on PRD distances of North African houbara bustard (inbred males tended to disperse further). In our study, the effect was not clearly sex-specific, but appeared slightly stronger in females. Taken in conjunction with previous studies, our results suggest that effects on spatial behaviour are one potential mechanism by which high inbreeding coefficients can reduce individual fitness. This result has implications for the ability of such individuals to cope with translocation, which is a stressful event (Dickens *et al.*, 2010). We did not assess the effect of inbreeding coefficient on post-release survival in our study, but consideration of the interactions between differential dispersal, and possible differential survival, of translocated individuals warrants further research.

Early natal nutritional environment

The early natal environment influences individual quality and behaviour across multiple life stages (reviewed in Lindström, 1999), and here we demonstrate its effect on PRD. It has already been established that receiving a nutritional protein supplement in the nest had a range of sex-specific effects on the juveniles in our study population, with primarily negative effects in males and somewhat positive effects in females, as well as sex-specific effects on personality scores. Our results suggest a link between individual condition (as dictated by early natal effects) and PRD, with "better" individuals dispersing further and exploring more in the initial and later exploratory phases of PRD. Together with our finding that more inbred individuals have reduced dispersal, this could raise concern at a release area where dispersers were effectively lost to the population, as it would represent loss of the higher quality individuals.

Do early PRD movements predict decisions in the settlement phase?

Our results suggest that early movements (initial and exploratory phases of PRD) provide some information about the eventual settlement phase of translocated hihi, and this appears to be particularly the case for females. All but one of the females that survived to breed were located within 400 m of their first nest site in the first four weeks after release, whereas of the breeding males, only one was within 750 m during this time period. This suggests that eventual breeding site selection is primarily guided by the movements of female hihi in the first few weeks post-release, and that female exploration of release areas is more limited than that of males. This has several implications. First, it provides some direction for monitoring reintroduced populations, as female movements over the first few weeks (the lifespan of small transmitters) appear to provide useful guidance for finding later breeding sites. Second, if selection decisions are made with limited exploration of available habitat, this has implications for habitat selection at the population level. Our results raise the question of to what degree these early movements reflect informed habitat selection vs random, non-directional movement of stressed individuals. Results from another aspect of this study (Chapter 4) suggested that habitat selection decisions of hihi recently released at this site were not related to proximity to conspecifics, release site, or supplementary feeders, and were only weakly related to physical characteristics of the environment (primarily stream proximity) that appear to characterise overall hihi habitat selection at Maungatautari.

In summary, our study represents the first detailed investigation of drivers of PRD. As with studies of natal dispersal, we find multiple factors influencing individual variation, with personality traits, early natal condition and genetic quality converging to shape how individuals behave immediately after translocation.

Appendix 3.1 Results from generalised linear models assessing effect of individual covariates on dispersal distance in the initial (one week) post-release phase at both Ark in the Park and Maungatautari. Best models are in bold.

	pD	**DIC**[b]	**ΔDIC**[c]	**Effect size**[d]	
Constant	1.02	888.30	0.00	NA	
Number of fault bars	1.95	888.50	0.20	0.58	
Activity score	2.06	888.98	0.68	0.68	
Acclimation time	1.72	889.43	1.13	1.69	
Haematocrit score	1.92	889.52	1.22	1.86	
Exploratory score	1.71	889.72	1.42	1.24	
Heterophil:lymphocyte	1.94	889.98	1.68	1.92	
Weight:tarsus	1.98	889.80	1.50	1.67	
White blood cell count	1.93	889.83	1.53	3.26	
Site (Ark/Maungatautari)	1.97	889.90	1.60	1.22	
Sex	1.98	890.00	1.70	0.92	
Weight change in aviary	2.00	890.30	2.00	1.16	
Activity score + sex	3.09	890.55	2.25	0.63	
Acclimation time + sex	2.69	891.32	3.02	1.58	
Exploratory score + sex	2.70	891.47	3.17	1.22	
C[1] + site	3.01	891.90	3.60	1.35	
N[1] + site	2.98	891.90	3.60	1.24	
Activity score * sex	3.80	891.94	3.64	0.93	Female
				0.69	Male
Acclimation time * sex	3.35	892.64	4.34	2.09	Female
				2.09	Male
Exploratory score * sex	3.35	892.74	4.44	1.64	Female
				1.67	Male
C[1] + sex + site	3.95	893.54	5.24	1.23	
N[1] + sex + site	3.96	893.71	5.41	1.08	
N[1] * sex + site	4.89	894.83	6.53	0.88	Female
				1.47	Male
C[1] * sex + site	4.93	895.27	6.97	1.59	Female
				1.10	Male
C[1] * N[1] + site	4.98	895.78	7.48	1.23	C-
				0.98	C+
Handling score	NA	NA		1.73	
Boldness	NA	NA		1.22	
Escape latency	NA	NA		0.83	
f[1]	NA	NA		0.93	
Handling score + sex	NA	NA		1.72	
Handling score * sex	**NA**	**NA**		**1.05**	**Female**
				4.13	**Male**
Boldness + sex	NA	NA		1.20	
Boldness * sex	NA	NA		1.09	Female

				1.37	Male
Escape latency + sex	NA	NA		0.82	
Escape latency * sex	NA	NA		0.90	Female
				0.76	Male

[a] pD = Effective number of parameters (mean of posterior deviance minus mean of posterior distribution.

[b] DIC = Deviance information criterion, where lower DIC means higher predictive value.

[c] ΔDIC = Difference in DIC from that of best model.

[d] Effect size = Mean dispersal distance estimated under highest covariate score divided by mean dispersal distance estimated under lowest covariate score.

[1] C refers to carotenoid supplement in nest, N refers to protein supplement in nest,
f refers to pedigree-based inbreeding coefficient.

Appendix 3.2 Results from generalised linear models assessing effect of individual covariates on dispersal distance in the exploratory (four weeks) post-release phase at Maungatautari. Best models are in bold.

	pD[a]	DIC[b]	ΔDIC[c]	Effect size[d]	
N^1 + sex	**2.95**	**561.36**	0.00	**0.52**	
N^1 * sex	3.94	562.60	1.24	0.70	Female
				0.37	Male
Escape latency + sex	2.94	563.83	2.47	0.68	
Sex	1.99	564.61	3.25	0.55	
Weight:tarsus + sex	2.90	564.89	3.53	0.21	
Acclimation time + sex	3.00	565.42	4.06	1.16	
White blood cell count + sex	2.95	565.44	4.08	1.58	
Escape latency * sex	3.92	565.47	4.11	0.78	Female
				0.48	Male
Heterophil:lymphocyte + sex	2.96	565.57	4.21	0.65	
Haematocrit score + sex	2.99	565.66	4.30	1.74	
Acclimation time * sex	3.95	565.73	4.37	1.06	Female
				0.74	Male
Weight change in aviary + sex	2.95	566.11	4.75	1.61	
Constant	1.00	566.12	4.76	NA	
Number of fault bars + sex	2.93	566.18	4.82	1.71	
Activity score + sex	2.96	566.25	4.89	2.83	
Exploratory score * sex	3.90	566.27	4.91	0.76	Female
				1.50	Male
f^1 + sex	2.95	566.54	5.18	0.82	
Exploratory score + sex	2.95	566.55	5.19	0.92	
Handling score + sex	2.96	566.41	5.05	1.58	
C^1 + sex	2.97	566.59	5.23	1.03	
C^1 * N^1	3.97	567.94	6.58		
Activity score * sex	3.91	568.10	6.74	1.14	Female
				1.36	Male
C^1 * sex	3.94	568.26	6.90	1.38	Female
				0.90	Male
Handling score * sex	3.91	568.37	7.01	1.15	Female
				1.21	Male
Boldness + sex	NA	NA		0.83	
Boldness * sex	NA	NA		0.80	Female
				0.76	Male

[a] pD = Effective number of parameters (mean of posterior deviance minus mean of posterior distribution.

[b] DIC = Deviance information criterion, where lower DIC means higher predictive value.

[c] ∆DIC = Difference in DIC from that of best model.

[d] Effect size = Mean dispersal distance estimated under highest covariate score divided by mean dispersal distance estimated under lowest covariate score.

[1] C refers to carotenoid supplement in nest, N refers to protein supplement in nest,
f refers to pedigree-based inbreeding coefficient.

Appendix 3.3 Results from generalised linear mixed models assessing effect of individual covariates on exploratory movements in the first four weeks post-release at Maungatautari. Best models are in bold.

	pD^a	**DIC^b**	**ΔDIC^c**	**Effect size^d**	
Handling score	**19.51**	**3787.49**	0.00	**1.54**	
f^1	18.71	3787.67	0.18	0.53	
f^1 * sex	19.33	3787.99	0.50	0.20	Female
				0.55	Male
Constant	19.60	3788.07	0.58		
N^1	19.78	3788.24	0.75	0.80	
Handling score + sex	20.33	3788.27	0.78	2.19	
f^1 + sex	19.11	3788.54	1.05	0.50	
White blood cell count	20.04	3788.63	1.14	0.78	
Weight change in aviary	20.08	3788.70	1.21	1.77	
Number of fault bars	18.81	3788.77	1.28	0.55	
Acclimation time	20.21	3788.77	1.28	1.03	
Sex	20.47	3789.00	1.51	1.05	
Weight:tarsus at capture	20.30	3789.02	1.53	1.25	
N^1 + sex	20.58	3789.10	1.61	0.85	
C^1	20.47	3789.10	1.61	0.97	
Exploratory score	20.54	3789.11	1.62	1.12	
N^1 * sex	21.21	3789.18	1.69	0.66	Female
				0.99	Male
Heterophil:lympocyte	20.39	3789.29	1.80	1.21	
Activity score	20.04	3789.34	1.85	0.84	
Handling score * sex	21.18	3789.37	1.88	1.56	Female
				1.76	Male
Acclimation time + sex	21.04	3789.78	2.29	2.90	
C^1 + sex	21.35	3789.82	2.33	1.02	
Acclimation time * sex	20.79	3789.96	2.47	2.24	Female
				0.66	Male
Exploratory score + sex	21.38	3790.05	2.56	1.62	
N^1 * C^1	21.52	3790.17	2.68	0.83	C-
				0.82	C+
Activity score + sex	21.08	3790.32	2.83	1.14	
C^1 * sex	21.79	3790.67	3.18	1.17	Female
				0.85	Male
Activity score * sex	21.81	3790.86	3.37	1.15	Female
				0.74	Male
Exploratory score * sex	19.37	3791.23	3.74	0.62	Female
				4.28	Male
Boldness	NA	NA		0.96	
Escape latency	NA	NA		0.81	
Boldness + sex	NA	NA		1.01	
Escape latency + sex	NA	NA		0.85	

Boldness * sex	NA	NA		0.94	Female
				1.02	Male
Escape latency * sex	NA	NA		0.74	Female
				0.91	Male
Haematocrit score	NA	NA		1.16	

[a] pD = Effective number of parameters (mean of posterior deviance minus mean of posterior distribution.

[b] DIC = Deviance information criterion, where lower DIC means higher predictive value.

[c] ΔDIC = Difference in DIC from that of best model.

[d] Effect size = Mean dispersal distance estimated under highest covariate score divided by mean dispersal distance estimated under lowest covariate score.

[1] C refers to carotenoid supplement in nest, N refers to protein supplement in nest,
f refers to pedigree-based inbreeding coefficient.

Appendix 3.4 Hihi dispersal in non-forested habitat

Of the 55 juveniles we radio tracked at both sites, we only recorded one individual (female YG-WM, Figure 3.8) dispersing any significant distance from forest habitat, although we cannot be sure that other individuals did not carry out similar occasional movements. This female travelled ~1 km from the forest boundary through a partially forested gully network, crossing ~100 m of tree-less farmland and then crossing a main road (Arapuni Road) to reach a rural residential garden. Visual observations were made of this female at approximately 30 minutes before sunset, 20 days after release, and she was subsequently radio tracked back towards the forest by nightfall. While it was not possible to determine an accurate location estimate for her after this, signals were detected from within the forest boundary up to 29 days after release, after which no further signals were detected, nor was this female sighted again. The Ark in the Park release site is adjacent to a golf course (represented by the white area directly above the release site in Figure 3.1), and we frequently sighted hihi flying across open areas (~100 m) to feed on flowering pohutukawa that had been planted in the middle of the course (Richardson, 2009).

These results suggest that hihi are largely confined to forest habitat and do not readily show a willingness to leave these areas. However, they have the ability to cross open areas of at least 100 m, and potentially further if aided by trees within the landscape. It would be useful to examine the degree to which this occurs beyond the first few weeks, particularly in natal dispersal.

Figure 3.8 Movements of female YG-WM at 20 days after release. Arrows show approximate route taken to disperse from (and back to) reserve, dashed line represents 100 m across open pasture.

CHAPTER 4

Habitat selection in a reintroduced population: social effects differ between natal and post-release dispersal

---

This chapter is published as: Richardson, K.M. and Ewen, J.G. 2015. Habitat selection in a reintroduced population: social effects differ between natal and post-release dispersal. *Animal Conservation*, in press.

Co-authors and their respective contributions are as follows:

John Ewen (Zoological Society of London), co-supervisor - assistance with study design, institutional support for field work and data analysis, comments on manuscript.

Abstract

Understanding the factors driving dispersal behaviour and habitat selection in reintroduced populations can be critical to reintroduction success. Social factors in particular can influence habitat selection, for example through conspecific attraction, and this can have both positive and negative effects on reintroduction success, particularly where multiple releases occur. In addition, little is known about how habitat selection differs between natal and post-release dispersal within species. Often it is assumed that information from a species' natal dispersal preferences and patterns can act as a guide for predicting post-release dispersal behaviour, but no studies to date have examined this.

We examined the factors influencing habitat selection during both natal and post-release dispersal in a reintroduced hihi (*Notiomystis cincta*) population using species distribution models. We demonstrate a strong social effect in habitat selection of natal dispersers bred at the release area (largely the offspring of founders); yet find no detectable social effect in habitat selection of juveniles translocated two years after the first releases occurred. In addition, we establish that environmental factors are important in habitat selection in both groups. We suggest 1) that consideration of social effects and conspecific attraction should play a role in planning reintroduction release strategies, especially if reinforcement releases are considered necessary, and 2) that it may not always be appropriate to assume post-release dispersal in reintroduced populations will be driven by the same factors that influence natal dispersal.

Introduction

The importance of understanding dispersal behaviour in reintroduction biology is well recognised (reviewed in Le Gouar *et al.*, 2012). Habitat selection is a vital component of dispersal, with dispersing individuals expected to respond to features of the habitat and demonstrate active selection of certain areas over others (Matthysen, 2012). Definitions of what comprises "habitat" have varied widely in the literature (Hall *et al.*, 1997; Armstrong and Seddon, 2008), with some authors limiting habitat to the physical characteristics of the environment (e.g. Jones, 2001), and others including biological factors such as interspecific and intraspecific competition, and interactions with predators and parasites. Here, we use the latter definition, and consider habitat as defined by Osborne and Seddon (2012): “a species-specific complex of interacting physical and biotic components, including other species”.

Social factors can be an important influence on post-release habitat selection behaviour and dispersal, and can inform on decisions around release methodology, particularly the effect of multiple releases. The presence of conspecifics can act as a cue for habitat quality, providing a guide to enable dispersers to select optimal habitat (Serrano *et al.*, 2003; Parejo *et al.*, 2007; Martin *et al.*, 2008; Harrison *et al.*, 2009). Conspecific attraction can lead to negative density-dependent relationships to dispersal propensity (Matthysen, 2012), and can limit expansion of reintroduced populations, or result in clusters of individuals. In cases where residents are present in sub-optimal habitat, conspecific attraction can act as an ecological trap to translocated individuals and prevent expansion into more optimal habitat (Mihoub *et al.*, 2011). Conversely, conspecific repulsion can increase dispersal of newly reintroduced individuals, resulting in geographical isolation from the intended release area.

It is important to carefully consider the objectives behind multiple releases (or reinforcements) to ensure the potential effects of conspecific attraction or repulsion are considered at the planning stage. For example, many reintroductions are undertaken as a series of releases over time - often because of logistical constraints in releasing the appropriate number of individuals simultaneously, because of limiting factors in the numbers available for reintroduction, or because of concerns over impacts of harvesting from source populations (Griffith *et al.*, 1989; Armstrong and Seddon, 2008; Tracy *et al.*, 2011). Frequently, it is assumed that survival and dispersal probabilities will remain constant between releases. However, evidence to date suggests that this is not always the case (Støen *et al.*, 2009; Le Gouar *et al.*, 2012), and quantifying the changes in these probabilities between subsequent releases can have important ramifications for planning of release strategies. Additionally, reinforcements can sometimes occur for purposes other than bolstering numbers, such as attempting to introduce new genetic material to the population (Tracy *et al.*, 2011; Weiser *et al.*, 2013; Weeks *et al.*, 2015). Successful integration of these later-released individuals into the population can be undermined by density dependent (Armstrong *et al.*, 2005) or behavioural barriers (Mihoub *et al.*, 2009; Mihoub *et al.*, 2011; Parker *et al.*, 2012a) due to presence of conspecifics.

Here, we examine the habitat selection behaviour of dispersing hihi (*Notiomystis cincta*), during the initial years after release of an establishing population in a large reserve free of introduced mammalian predators. Reintroduction is the primary conservation action used in hihi recovery, yet we remain uncertain about habitat requirements and preferences of hihi, basing our knowledge predominantly on habitat comparisons to the one remnant island population (Ewen *et al.*, 2013b). Generally speaking, some increasing level of habitat complexity (particularly vegetation structure and diversity) is linked with improved site suitability (Makan *et al.*, 2014), hence recent reintroductions have looked to the mainland where such habitat is found. In contrast to islands targeted for early hihi reintroductions, mainland attempts are vulnerable to individuals dispersing from the release site, and the first mainland reintroduction of hihi to a large, mature forest site failed at least partially for this reason (Richardson, 2009). We have little information about the role of conspecific attraction in hihi, both in habitat selection of dispersing juveniles as the population establishes, and of dispersing individuals released during reinforcement translocations. Despite this, these types of translocations are frequently undertaken; hence understanding the effect of already established conspecifics is of importance to assess the effectiveness of translocation strategies.

In this study, we firstly examine which, if any, physical characteristics of the environment can predict preferred habitat for hihi at our mature forest release area, and secondly, compare how conspecifics influence dispersal and habitat selection between resident juveniles (those hatched at the release area from birds translocated there initially: natal dispersers) and juveniles released in reinforcement translocations (post-release dispersers).

Methods

Study species

The hihi is an endangered New Zealand passerine (Vulnerable on the IUCN Red List; IUCN, 2013) that has been subject to multiple reintroduction attempts (Ewen *et al.*, 2013b). Reduced to a sole island population by the 1880s (Hauturu/Little Barrier Island), hihi now persist at additional reintroduction sites including two islands (Tiritiri

Matangi and Kapiti), and three mainland reserves (Karori Wildlife Sanctuary, Maungatautari Ecological Island and Bushy Park). All populations are reliant on management, including maintenance of an environment free from mammalian predators (all populations), as well as provision of supplementary food (all reintroduced populations; Chauvenet *et al.*, 2012) and artificial nest boxes (all reintroduced populations except Maungatautari and Kapiti).

Study site

Maungatautari Ecological Island (henceforth “Maungatautari”, Figures 4.1, 4.2) is a ~3400 ha reserve in the Waikato region of New Zealand’s North Island (38°03′08″S 175°33′58″E). Maungatautari is a volcanic cone (797 m) covered primarily in mixed podocarp/broadleaf forest, largely surrounded by pasture, creating a “mainland island” effect (McQueen *et al.*, 2004). A predator-exclusion fence was completed around the forest edge in 2006 and all invasive mammals except mice (*Mus musculus*) and small numbers of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) have now been eradicated. A total of 11 endemic species have now been reintroduced (Smuts-Kennedy and Parker, 2013), of which seven are listed as Endangered or Vulnerable on the IUCN Red List (IUCN, 2013).

Hihi reintroductions to Maungatautari 2009-2011

Hihi were first released in 2009, with two translocations occurring in March. The released birds consisted of 59 juveniles from Tiritiri Matangi Island and 20 (a mix of adults and juveniles) from Hauturu/Little Barrier Island (Ewen *et al.*, 2011). A mark-recapture survey in early 2010, in combination with later field research, suggested 26-41 (33-52%) of these survived to the first breeding season (October 2009, seven months post-release) (Ewen *et al.*, 2011).

Two further releases of juvenile hihi occurred from Tiritiri Matangi Island in 2010 (37 birds) and 2011 (39 birds). Subsequent monitoring indicated a minimum of 17 from the 2010 translocation survived to their first breeding season (46%), and a minimum of 15 from the 2011 translocation (38%) (Appendix A). By the 2011/12 breeding season approximately 71 adult hihi were present at the site (Appendix B), comprising a mix of the original translocated hihi (38) and locally-bred birds (33). Six supplementary feeders are provided, all within 150 m of the release site, and these are utilised by some, but not all, of the birds present.

Post-release monitoring and location of breeding territories

All 155 translocated individuals were colour banded and genotyped prior to translocation. The majority of locally-bred recruits between 2009/10 and 2011/12 were captured by mistnetting (49 birds) or catching in cages at supplementary feeder stations (27 birds). All were colour banded as well as being genotyped to assign parentage (Chapter 5).

To answer our first question, testing whether physical characteristics of the environment (e.g. vegetation type, aspect, proximity to stream) could be used to predict preferred habitat, we used data from all active hihi breeding territory locations between 2010/11 and 2012/13. Breeding sites were located by comprehensive searches of the reserve using the existing monitoring line network (Figure 4.2) established for detecting mammalian pest presence, as well as following up reported hihi sightings from pest monitoring staff and local volunteers. These monitoring lines are distributed evenly across the reserve and designed to be no more than 200 m apart, although there are some larger gaps. We therefore consider that the reserve was searched evenly across habitat types.

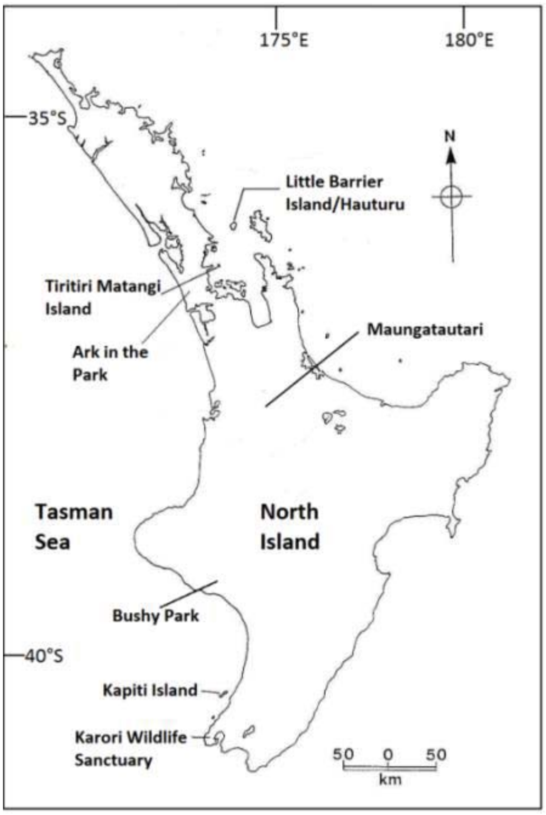


Figure 4.1 Map of the North Island of New Zealand, showing location of the remnant hihi population (Little Barrier Island/Hauturu), persisting reintroduced populations as of 2015 (Tiritiri Matangi and Kapiti Islands, Maungatautari, Karori Wildlife Sanctuary and Bushy Park), and one failed reintroduction (Ark in the Park).

Monitoring was carried out from October 2010-February 2011 (by one full-time field worker and additional volunteers), September 2011-March 2012 (two full-time field workers and additional volunteers), and September-December 2012 (two full-time field workers and additional volunteers). The majority of territories were located in late September through to mid-November when hihi males are most vocal and hihi females are most detectable. Most lines were walked at least once during this peak calling time by experienced personnel, and all were covered by staff or volunteers during this time. We considered male hihi to be resident to a location if they were identified at least three times in the same location during the breeding season, and female hihi if they were observed engaged in breeding behaviour (e.g. nest building, incubating, or feeding chicks), or otherwise observed at the same location at least twice during the breeding season. Breeding locations were found up to 80 m away from monitoring lines by listening for hihi calls during searches, and using playback of male calls. However, about 500 ha of the 3400 ha reserve fell more than 80 m from a monitoring line (Figure 4.2). Therefore in 2011/12 and 2012/13 these areas were searched using the same methods (listening and call playback) but no resident hihi were found. This methodology resulted in active breeding territories being identified in 34 different locations, some of which were utilised over multiple seasons and others only once.

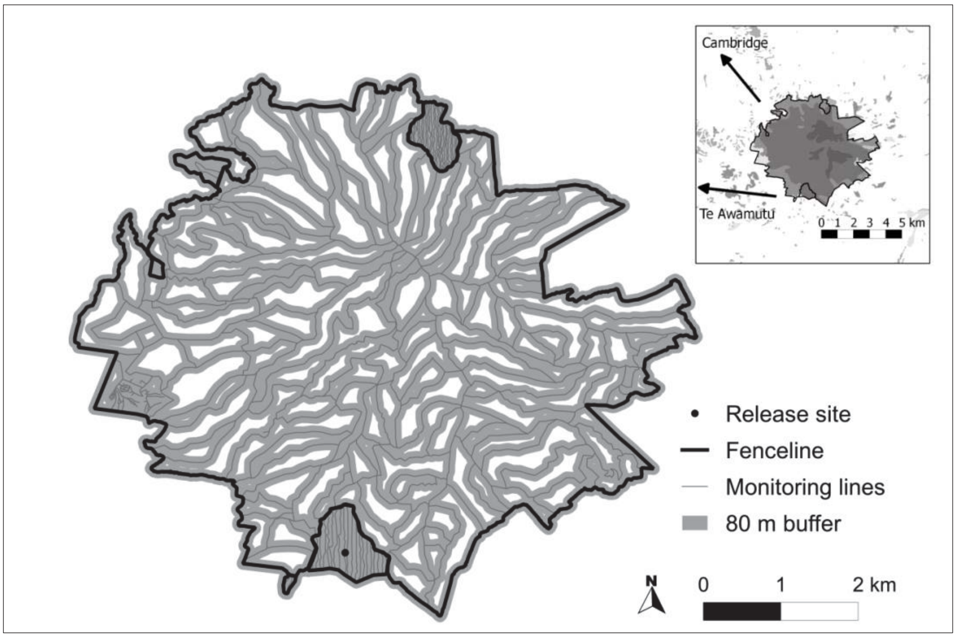


Figure 4.2 Map of Maungatautari Ecological Island showing monitoring lines with 80 m buffer either side, and release site for translocation of hihi between 2009 and 2011. Hihi were detectable at least 80 m from a monitoring line; hence grey areas show areas well covered during territory searches (approx. 85% of the site).

For our second question, determining if there is a social effect in habitat selection behaviour during natal and post-release dispersal, we used data from the 2011/12 season only, specifically looking at differences in breeding territory selection between first-year hihi bred at the reserve in 2010/11, and first-year hihi that had been translocated that year (April 2011). 34 first-year hihi were known to be present at the beginning of the breeding season (October 2011), and 25 of these were identified at a breeding territory during the season (Table 4.1). The remaining nine individuals were either floater males that remained unpaired (Brekke *et al.*, 2015) or never identified at a territory. Of the 25 identified at a territory, 15 were locally bred from the 2010/11 cohort, and 10 had been recently translocated to the reserve in April 2011. In addition to these first-year birds, a further 29 adults in their second or third season were identified at 19 territories that had also been occupied the previous season. The locations of these 19 territories were used to calculate distance to conspecific territory for use in the modelling below (Figure 4.3f).

Table 4.1 Known territorial hihi present at Maungatautari at start of 2011/12 breeding season (October 2011), by age and sex, and resident/release status.

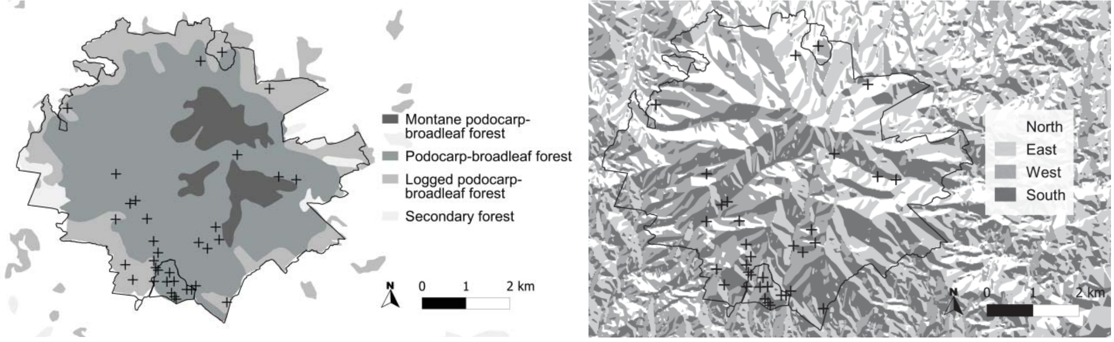
Age	Male	Female	Total
Resident adults 2+	16	13	29
First year residents, bred at reserve in 2010/11 season	7	8	15
First year, translocated to reserve in April 2011	5	5	10

Species distribution modelling

We applied species distribution modelling methods (Guisan and Thuiller, 2005) to examine the effect of both environmental and social factors on breeding location selection for reintroduced hihi at Maungatautari. We used maximum entropy models (MaxEnt, see Phillips *et al.*, 2006; Merow *et al.*, 2013) as our data were presence-only, and it is possible that some areas explored did contain breeding hihi that were not identified, although we believe this number to be very low (< 5 per season, based on sightings of birds at supplementary feeders and subsequent genotyping of juveniles (Chapter 5). All analyses were carried out using the ‘dismo’ package in R v. 3.01 (R Development Core Team, 2013).

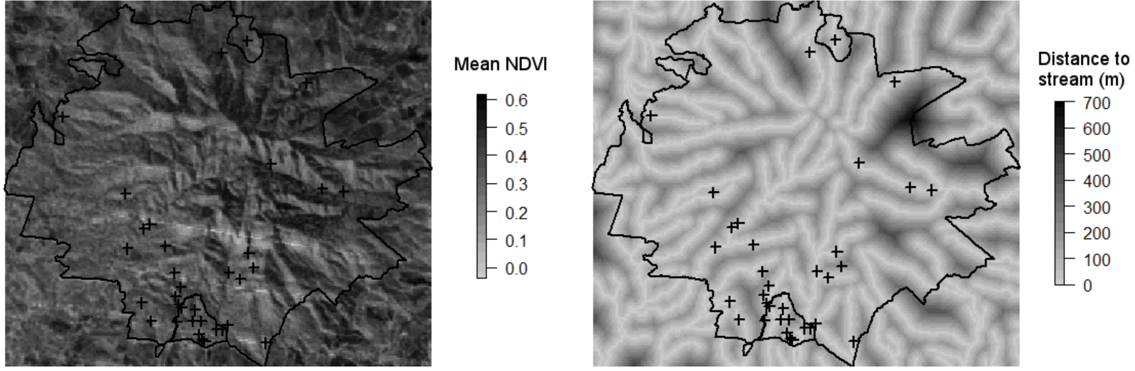
To investigate whether physical characteristics could be used to predict preferred habitat, we treated the 34 independent territory locations found during the study period (2010/11-2012/13) as our presence data, and first used the following environmental variables as possible predictors (m1; see Table 4.2): vegetation class (four classes: podocarp-broadleaf forest, montane podocarp-broadleaf forest, logged podocarp-broadleaf forest and secondary forest), aspect (0-359 degrees), primary productivity (using mean Normalised Difference Vegetation Index (NDVI) values derived from Landsat 7 & 8 data across the reserve during the study period (Pettorelli *et al.*, 2005) and distance to nearest stream (Figures 4.3a-d). We then re-ran the same analysis but this time included distance to release site/supplementary feeders (Figure 4.3e) as an additional environmental variable (m2), as we suspected that both of these factors could influence breeding site selection. As the supplementary feeders are within close proximity of the release site it was not possible to distinguish between the effects of release site vs effect of supplementary feeder location.

For our second question, we used the same environmental variables as in the first analyses (including distance to release site), but included an additional social variable, distance to conspecific territory (Figure 4.3f, as described above). We generated two models, one using the location of first-year hihi bred at the reserve as presence data (natal dispersers, m3), and the other using the location of first-year hihi translocated to the reserve that year (post-release dispersers, m4).



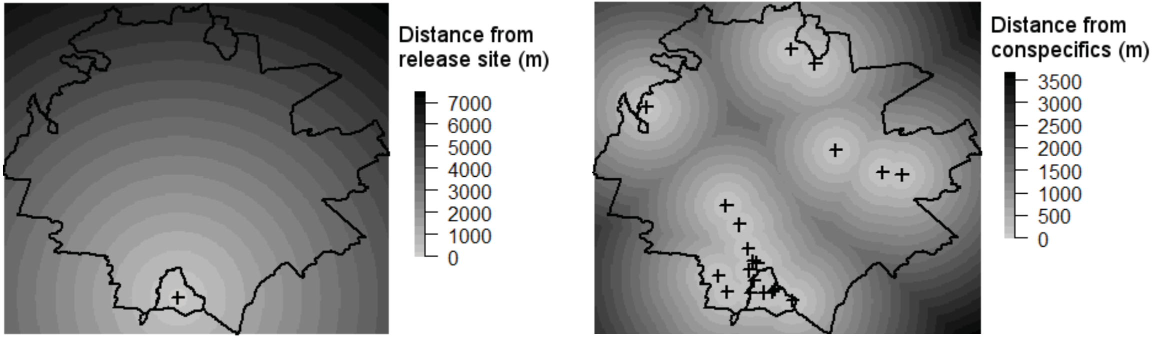
a) Vegetation class

b) Aspect



c) Primary productivity (mean NDVI)

d) Distance to streams



e) Distance from release site

f) Distance to conspecific territory

Figure 4.3 Environmental variables used in species distribution models, with maps demonstrating variation across the release area, Maungatautari Ecological Island, for each variable. Outlined area shows predator-exclusion fence, (a-d) cross represents location of hihi territories found 2010/11-2012/13 used as presence data in m1 and m2, (e) cross indicates release site, (f) cross represents existing second- and third-year hihi territories in 2011/12 season used to calculate distance to conspecifics in m3 and m4.

Table 4.2 Maximum entropy models used in analysis, with source of presence data listed and possible predictors used in each analysis.

Model	Presence data (n)	Environmental variables	Social variables
m1	All hihi breeding territory locations 2010/11 to 2012/13 (34)	Vegetation class Aspect Primary productivity Distance to stream	None
m2	All hihi breeding territory locations 2010/11 to 2012/13 (34)	Vegetation class Aspect Primary productivity Distance to stream Distance to release site	None
m3	First-year hihi breeding territories 2011/12 – hihi bred at reserve 2010/11 (15)	Vegetation class Aspect Primary productivity Distance to stream Distance to release site	Distance to conspecific territory (based on 19 territory locations)
m4	First-year hihi breeding territories 2011/12 – hihi translocated to reserve 2011 (10)	Vegetation class Aspect Primary productivity Distance to stream Distance to release site	Distance to conspecific territory (based on 19 territory locations)

Results

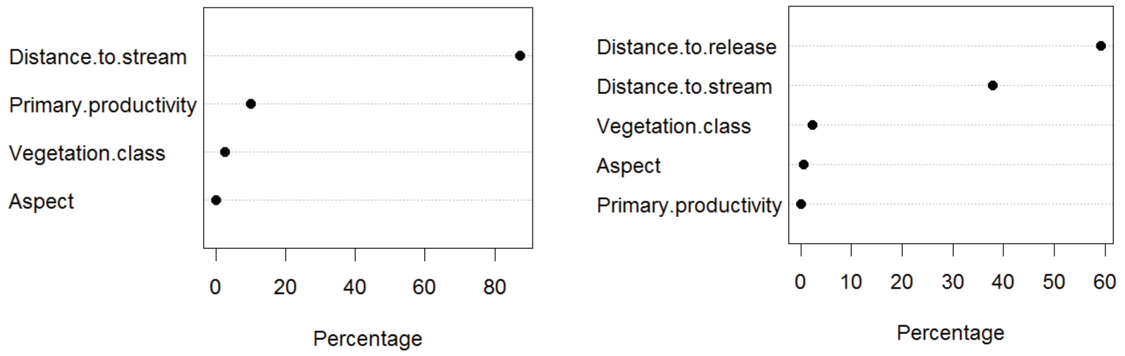
Physical characteristics as predictors of preferred habitat

We demonstrated an effect of some of our environmental characteristics on hihi habitat selection at Maungatautari (Figures 4.4a, b; 4.5a, b). In the first few years following release, hihi have primarily selected breeding territories within 150 m of a stream, and closer to the release site/supplementary feeders than expected by chance (most within 3 km). There was also a slight tendency for hihi to select podocarp-broadleaf forest over montane and logged podocarp-broadleaf forest and secondary forest; however these factors contributed relatively little under either model in comparison to distance to stream (Figure 4.4a, b). Aspect did not influence territory selection in either model. Primary productivity appeared to have a weak influence under m1 (with lower primary productivity being preferred habitat) but this effect disappeared when distance to release site was also included (Figure 4.4a, b).

Comparison between natal and post-release dispersal

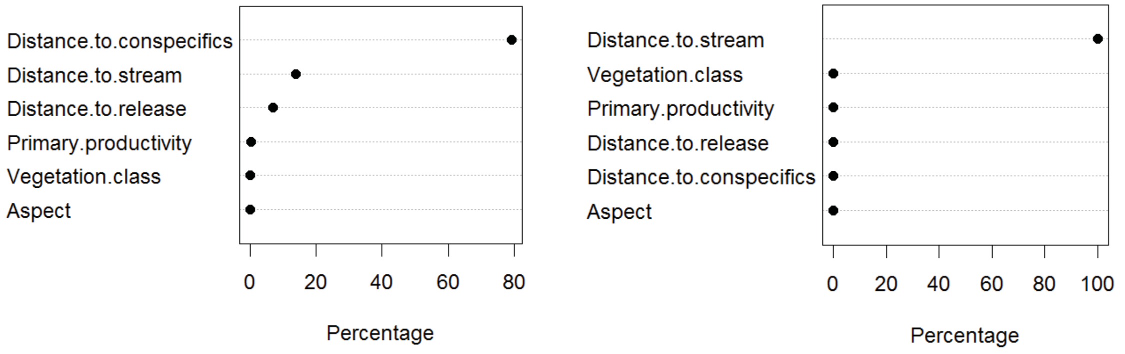
There was a striking difference in habitat selection predictors between first-year hihi hatched at our study site (natal dispersers) and first-year hihi recently translocated there (post-release dispersers) (Figures 4.4c, d; 4.5c, d). Natal dispersers appeared most strongly driven by social factors, with proximity to a conspecific territory being the most influential factor of those tested (majority within 500 m). Distance to stream and distance to release site were less influential factors but still important, and aspect, vegetation class and primary productivity had no influence. The predictive map generated from the maximum entropy model (Figure 4.5c) clearly demonstrates the stronger social effect in territory selection for natal dispersers.

In contrast, social factors do not appear to be significant in territory selection for the post-release dispersers. Distance to streams appears to be the only environmental variable influencing territory selection in this group, but less strongly than previously with the majority within 500 m rather than 150 m (Figures 4.4d, 4.5d). Interestingly, distance to release site/supplementary feeders did not affect territory selection for post-release dispersers, despite it being one of the most significant influences overall for all birds at the reserve (Figure 4.4b).



a) Percentage variable contribution of environmental characteristics, not including distance to release site (m1), n=34.

b) Percentage variable contribution of environmental characteristics, including distance to release site (m2), n=34.



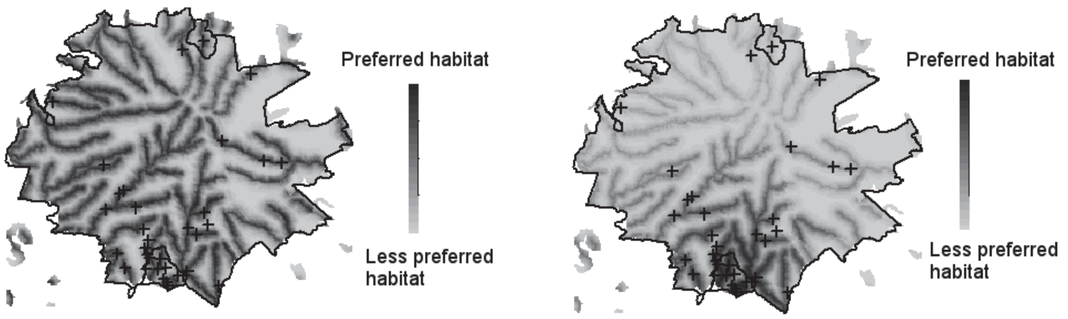
c) Percentage variable contribution of environmental and social characteristics – natal dispersers (m3), n=15.

d) Percentage variable contribution of environmental and social characteristics – post-release dispersers (m4), n=10.

Figure 4.4 Percentage variable contribution from maximum entropy species distribution model examining habitat preference in hihi at Maungatautari.

a) Predictive map based on environmental characteristics, not including distance to release site (m1), + = all territories 2010/11 to 2011/12.

b) Predictive map based on environmental characteristics, including distance to release site, (m2), + = all territories 2010/11 to 2011/12..



c) Predictive map based on environmental and social characteristics – natal dispersers (m3), '+' = conspecific territories 2011/12.

d) Predictive map based on environmental and social characteristics – post-release dispersers (m4), '+' = conspecific territories 2011/12.

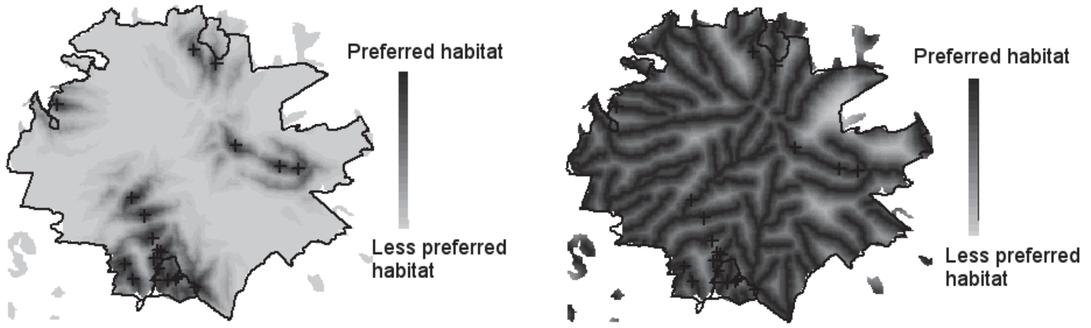


Figure 4.5 Predictive maps from maximum entropy species distribution models, predicting preferred breeding habitat for hihi at Maungatautari. Outlined area shows predator-exclusion fence.

Discussion

There were striking differences between habitat selection patterns in resident and recently translocated first-year individuals that may have implications for the establishment of reintroduced populations. We found a strong effect of conspecific attraction in the breeding territory selection of natal dispersers, but no effect of conspecific attraction was detected in recently translocated individuals. In addition, we have identified environmental variables that play a role in breeding territory selection in hihi in mature forest habitat.

Habitat selection in hihi

Our results provide the first assessment of hihi habitat preferences in a reintroduced population, and suggest that habitat selection is non-random. Proximity to a stream is the primary environmental variable predicting breeding territory occurrence. A strong effect of either distance to release site or to the established supplementary feeders is evident, but the results suggest this may only be important in the early stages of population establishment as it was not a significant factor for natal dispersers, or for the post-release dispersers from the last release. Both vegetation class and primary productivity had a weak effect, and incorporating additional data into the model as the population grows may help determine if this is a real effect, or an artefact of small sample size.

It is difficult to ascertain the mechanisms linking hihi preference to stream proximity from our data. At Maungatautari, the majority of hihi nests were located in pukatea (*Laurelia novae-zelandiae*), an endemic slow-growing tree which often has multiple natural cavities and typically occurs in swampy areas or close proximity to streambeds.

However, potentially suitable cavities also occurred in other tree species that are found away from streambeds, and further investigation would be needed to determine if stream proximity is linked to availability of suitable nest cavities, or other factors such as vegetation complexity or food availability.

Habitat selection in natal vs post-release dispersers

We demonstrated a clear difference in habitat selection patterns between natal and post-release dispersers, suggesting that making inferences about post-release dispersal behaviour from natal dispersal data may not always provide reliable information.

We found that natal dispersers were strongly influenced by presence of conspecifics in selection of breeding territories. Natal dispersal data collect as part of this project (Chapter 5) strongly indicates this conspecific attraction is not explained by natal philopatry, hence we believe it reflects active selection of natal dispersers (the mean natal dispersal distance was 1.3 km during our study period, with the closest recorded distance between territories ~150 m; Chapter 5). The absence of conspecific attraction in the recently translocated hihi is in clear contrast. We found neither a positive nor negative effect of distance to conspecifics on territory selection in this group, so there was no suggestion that recently translocated birds were actively avoiding residents, or were driven away by aggressive encounters.

Implications for reintroduction strategy

Our results highlight the importance of understanding the role that habitat selection can play in establishing reintroduced populations, in particular the effect of conspecifics. We emphasise the need to consider this from the outset in reintroduction planning, in particular where it is anticipated multiple releases may be required. It should not be assumed that individuals from subsequent releases will behave in a similar manner to those released first in the absence of conspecifics. In our study, it was hoped that resident birds would act as an anchor for new releases, hence increasing the probability of integration into the population and leading to more rapid population growth and maximising the probability of reintroduction success, and preventing individual birds from becoming isolated within a large area. Instead, our results suggest that while clustering of the resident population is apparent, integration of subsequently translocated birds is more problematic.

The wider implications for reintroduction strategy will largely be dependent on the context in which subsequent releases occur. Where reinforcements occur primarily to boost numbers, integration of new individuals into a population may not be immediately critical, and higher rates of dispersal may aid population expansion. However, in sites with high landscape connectivity, or adjacent to unmanaged areas, later releases may be less successful if later released individuals are less likely to settle near conspecifics. Where the objective for reinforcements is to boost genetic variability, integration of new individuals into the breeding population is key, and a lack of conspecific attraction in post-release dispersal may undermine the success of such translocation attempts unless integration is achieved in later generations.

As outlined by Mihoub *et al.* (2011), conspecific attraction has the potential to have both positive and negative effects on the establishment probabilities of a reintroduced population. Conspecific attraction is likely to lead to clusters of individuals in some areas, and if sub-optimal habitat were selected by the original individuals, this may lead to an ecological trap whereby the majority of the population resides in less optimal habitat. At our site, the effect on population growth is dependent on whether sub-optimal habitat was originally selected by hihi from the first release. Our results suggest that hihi are using some environmental indices to select habitat, which indicates non-random selection is occurring to some degree, but it is not possible to determine if the habitat selected is optimal based on available data.

Using species distribution modelling in monitoring reintroduced populations

Investigating how, or if, habitat preferences change at our study site as population densities increase will enhance our understanding of hihi habitat preference and adaptability. In particular this has relevance for predicting the carrying capacity of release areas and estimating population size. Predicted habitat with higher than 50% probability of occurrence (based on the map in Figure 4.5a) covered an area of 663 ha, about a fifth of the total available forest habitat at the reserve. Frequently, population estimates assume an equal density of individuals across an area, but this may only rarely be a true assumption. Ongoing monitoring of the Maungatautari population will determine if hihi restrict themselves to the predicted habitat, or if habitat selection patterns change as the density increases, and could provide information to assist in developing a stratified-sampling monitoring design.

Species distribution modelling has the potential to assist in monitoring reintroduced populations, particularly at release areas where there are logistical and/or constraints in resourcing species management. Refining, and testing, predictions about species habitat preferences may provide a guide to where best to focus effort on monitoring new and existing populations, and assist in generating population estimates where densities are known to vary spatially.

Conclusions

Overall, our results support the predictions made by Mihoub *et al.* (2011) that conspecific effects on habitat selection can have unexpected consequences on the establishment of reintroduced populations, and we suggest that differential habitat selection between releases may be an additional behavioural factor that can influence the success of reinforcement translocations. We recommend consideration of these factors during the earliest stages of reintroduction planning.

CHAPTER 5

Natal dispersal patterns in an establishing reintroduced hihi *(Notiomystis cincta)* population.

This chapter is intended for submission as a manuscript. Co-authors and their respective contributions are as follows:

John Ewen (Zoological Society of London), co-supervisor – assistance with study design, facilitation of collaboration within research group, comments on manuscript.

Patricia Brekke (Zoological Society of London) – genotyping of all hihi blood samples, provision of marker-based inbreeding coefficients, comments on manuscript.

Lydia Doerr (University of Wisconsin) – assistance with field work.

Kevin Parker (Massey University) – assistance with study design, comments on manuscript.

Doug Armstrong (Massey University), primary supervisor – assistance with study design, data analysis, comments on manuscript.

Abstract

Natal dispersal is known to be a complex behaviour influenced by multiple factors that are often sex-specific. Natal dispersal patterns are less well understood in reintroduced populations, particularly in the early years after release when densities are typically low. Here, we examine natal dispersal patterns in an establishing reintroduced population of an endangered passerine, the hihi (stitchbird, *Notiomystis cincta*), in the first three years after reintroduction to a large, mature forest reserve. We first examine natal dispersal distances and differences between the sexes, and second, the effects of individual differences in personality, early natal condition and the degree of inbreeding on natal dispersal distances.

We found natal dispersal distances to vary widely across both sexes in the first three years after release, with mean natal dispersal distances higher in males than females. There was a sex-specific effect of personality, with males that distress-called in the hand having greater natal dispersal distances than those that did not. We detected no effects of degree of inbreeding, and an ambiguous effect of early natal condition. Our results show that while clusters of individuals have established across the reserve, there is movement between these, primarily a consequence of male dispersal. Continuing to monitor natal dispersal patterns as populations establish beyond the initial years would provide further insights into the role of dispersal in shaping population settlement and establishment patterns.

Introduction

Natal dispersal is defined as the movement from the site of birth (or hatching) to the first breeding site (Matthysen, 2012). It is the primary mechanism by which gene flow occurs, and variation in dispersal behaviour has consequences at the individual, population, metapopulation and species level. The drivers of natal dispersal in reintroduced populations, and the effects of any behavioural variation, are less well understood, despite studies that have emphasised the potential for dispersal to play a strong role in reintroduction success, particularly in the early stages of habitat selection and population expansion (Mihoub *et al.*, 2009; Mihoub *et al.*, 2011). Population density is typically low in the early years of population establishment, and maximising recruitment of offspring into the new population critical. Therefore understanding dispersal movements of offspring of reintroduced animals is an important component to population establishment.

Increasingly it is recognised that the drivers of natal dispersal are many and complex, and occur over multiple stages – from the initial departure from the natal location, the exploratory or transience phase that follows, to settlement at the first breeding location (Clobert *et al.*, 2009), and the factors driving individual variation can influence each of these phases separately (e.g. del Mar Delgado *et al.*, 2010; van Overveld *et al.*, 2014). These complex, often sex-specific, interactions of multiple factors (Clobert *et al.*, 2009; Clobert *et al.*, 2012), have been placed into two broad categories, those related to internal state of the individual, and those related to the external environment. Internal state relates to individual traits, such as personality (e.g. Dingemanse *et al.*, 2003; Duckworth and Badyaev, 2007; Cote *et al.*, 2010a), genotype (e.g. Hardouin *et al.*, 2015), stress response (e.g. Belthoff and Dufty, 1998), morphology (e.g. O'Riain *et al.*, 1996; Massot and Clobert, 2000; Balbontín *et al.*, 2009) and condition (e.g. O'Riain *et al.*, 1996; Massot and Clobert, 2000; del Mar Delgado *et al.*, 2010). The external environment includes effects of habitat such as the structure and function of physical environment (e.g. Cruz-Angón *et al.*, 2008) as well as interactions with conspecifics, competitors, predators and parasites (e.g. Serrano *et al.*, 2003; Parejo *et al.*, 2007; Tschirren *et al.*, 2007; Martin *et al.*, 2008; Harrison *et al.*, 2009; Parejo and Aviles, 2011). Phenotypic traits linked to dispersal (in particular personality) are increasingly recognised to be driven by heritable factors, but with potential for mediation by a range of environmental factors, in particular the early natal environment (Duckworth, 2009; Krause *et al.*, 2009; Noguera *et al.*, 2015; Rowe *et al.*, 2015, Chapter 2).

In this study, we examine natal dispersal patterns in an establishing reintroduced population of an endangered passerine, the hihi (stitchbird, *Notiomystis cincta)*. Previous research in natal dispersal patterns of this species has been conducted in a closed island population (Tiritiri Matangi Island, 36°36’S, 174°53’E, 220 ha) where breeding individuals utilise artificial nest boxes. This earlier study found sex-specific density effects as the population established (Richardson *et al.*, 2010), with males the more dispersive sex in the first two years after initial release, and thereafter females. A male-biased sex ratio led to a decrease in female natal dispersal distances.

Here, we first expand on this previous study by examining natal dispersal distances (NDD), and differences between the sexes, in the first three years after reintroduction at a mature forest reserve more than 15 times the size of Tiritiri Matangi Island (Maungatautari Ecological Island, henceforth “Maungatautari”, 38°03′08″S 175°33′58″E, 3400 ha), where breeding takes place in natural nest cavities.

Second, we examine the effects of personality and early natal condition on natal dispersal distances. A concurrent aspect of the same study (Chapter 3) found multiple factors driving immediate post-release dispersal behaviour in this species, with effects of personality, early natal condition and genetic quality converging to shape spatial behaviour of individuals immediately after translocation. Here, we ask if these same factors drive natal dispersal patterns.

Methods

Study species

The hihi is an endangered New Zealand passerine (Vulnerable on the IUCN Red List; IUCN, 2013) that has been subject to multiple reintroduction attempts (Ewen *et al.*, 2013b). Reduced to a sole island population by the 1880s (Hauturu/Little Barrier Island), hihi now persist at additional reintroduction sites including two islands (Tiritiri Matangi and Kapiti), and three mainland reserves (Karori Wildlife Sanctuary, Maungatautari Ecological Island and Bushy Park). All reintroduced populations are reliant on management, including maintenance of an environment free from mammalian predators (all populations), as well as provision of supplementary food (all reintroduced populations; Chauvenet *et al.*, 2012) and artificial nest boxes (all reintroduced populations except Maungatautari and Kapiti). Hihi are typically socially monogamous, but have high frequencies of extra-pair paternity (Castro *et al.*, 1996; Ewen *et al.*, 1999; Brekke *et al.*, 2013), and breed from September to March each year. The majority of individuals breed at one year of age.

Study site

Maungatautari is a volcanic cone (797 m a.s.l.) in the Waikato region of the North Island of New Zealand. It is covered primarily in mixed podocarp/broadleaf forest, largely surrounded by pasture, creating a "mainland island" effect (McQueen *et al.*, 2004). A predator-exclusion fence was completed around the forest edge in 2006 and all invasive mammals except mice (*Mus musculus*) and small numbers of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) have now been eradicated. A total of 11 endemic species have been reintroduced (Smuts-Kennedy and Parker, 2013), of which seven are listed as Endangered or Vulnerable on the IUCN Red List (IUCN, 2013).

Hihi reintroductions to Maungatautari 2009-2011

Hihi were first released at Maungatautari in March 2009, when 79 birds were translocated from Tiritiri Matangi Island and Hauturu/Little Barrier Island (Table 5.1) (Ewen *et al.*, 2011). A mark-recapture survey in early 2010, in combination with later field research, suggested that 26-41 (33-52%) of these survived to the first breeding season (October 2009, seven months post-release) (Ewen *et al.*, 2011).

Two further releases of juvenile hihi occurred from Tiritiri Matangi Island in 2010 (37 birds) and 2011 (39 birds) (Table 5.1). Subsequent monitoring indicated a minimum of 17 individuals from the 2010 translocation survived to their first breeding season (46%), and a minimum of 15 individuals from the 2011 translocation (38%) (Appendix A). By the 2011/12 breeding season approximately 71 adult hihi were present at the site, comprising a mix of the original translocated hihi (38) and locally-bred birds (33) (Appendix B), with an estimated population growth rate of 1.2 (Appendix C). Six supplementary feeders are provided, all within 150 m of the release site (Figure 5.1), and these are utilised by some, but not all, of the birds present. All 155 translocated individuals were colour banded and genotyped prior to translocation (see below for further detail).

Table 5.1 Hihi released at Maungatautari, 2009-2011

Year (Source)	Adults	Juvenile males	Juvenile females	Total
2009 (Tiritiri Matangi Island)	0	31	28	59
2009 (Hauturu/Little Barrier Island)	9	7	4	20
2010 (Tiritiri Matangi Island)	0	18	19	37
2011 (Tiritiri Matangi Island)	0	20	19	39

Post-release monitoring and location of breeding territories

Intensive breeding monitoring and colour-banding of locally-bred birds was carried out between October 2010 and December 2012. Breeding territories were located by comprehensive searches of the reserve using the existing monitoring line network (Figure 5.1) established for detecting mammalian pest presence, as well as following up reported hihi sightings from pest monitoring staff and local volunteers. These monitoring lines are distributed evenly across the release area and designed to be no more than 200 m apart, although there are some larger gaps. We therefore consider the release area was searched thoroughly and evenly across habitat types. The majority of territories were located in late September through to mid-November when hihi males are most vocal and hihi females are most detectable. Most lines were walked at least once during this peak calling time by experienced personnel, and all were covered by staff or volunteers during this time. We considered male hihi to be resident to a location if they were identified at least three times there during the breeding season, and female hihi if they were observed engaged in breeding behaviour (e.g. nest building, incubating, or feeding chicks), or otherwise observed at the same location at least twice during the breeding season. Breeding locations were found up to 80 m away from monitoring lines by listening for hihi calls during searches, and using playback of male calls. However, about 500 ha of the 3400 ha reserve fell more than 80 m from a monitoring line (Figure 5.1). Therefore in 2011/12 and 2012/13 these areas were searched using the same methods as for the rest of the site, but no resident hihi were found.

Most of the locally-bred recruits from the 2009/10 (Year 1) to 2011/12 (Year 3) breeding seasons were captured, either by mistnetting (49 birds) or in cages at supplementary feeder stations (27 birds). These were all colour banded as well as genotyped to assign parentage (see below, Table 5.2). Male hihi can be aged in the hand up until the second year of age using plumage characteristics, but aging female hihi is more problematic. The majority of females were captured as juveniles at the end of the breeding season and were easily differentiated from adult females (a combination of plumage condition and behavioural characteristics). For females captured at other times of year we either aged them by inference from parentage (e.g. two females were caught in 2011 and sired by a male that was not translocated until 2010, and one female could not be aged so was excluded from further analyses).

At the time of capture we recorded the behaviour of the bird in the hand as a measure of personality (see Chapters 2, 3). Individuals that did not struggle or distress-call were assigned a handling score of “0”, individuals that struggled but did not distress-call were recorded as “1”, and individuals that both struggled and distress-called were recorded as “2”. No bird distress-called without struggling. We counted the number of fault bars on the tail feathers of each bird as a measure of natal condition. Hihi moult their first tail feathers at the end of the first breeding season, hence we could not collect these data for any individuals caught after this.

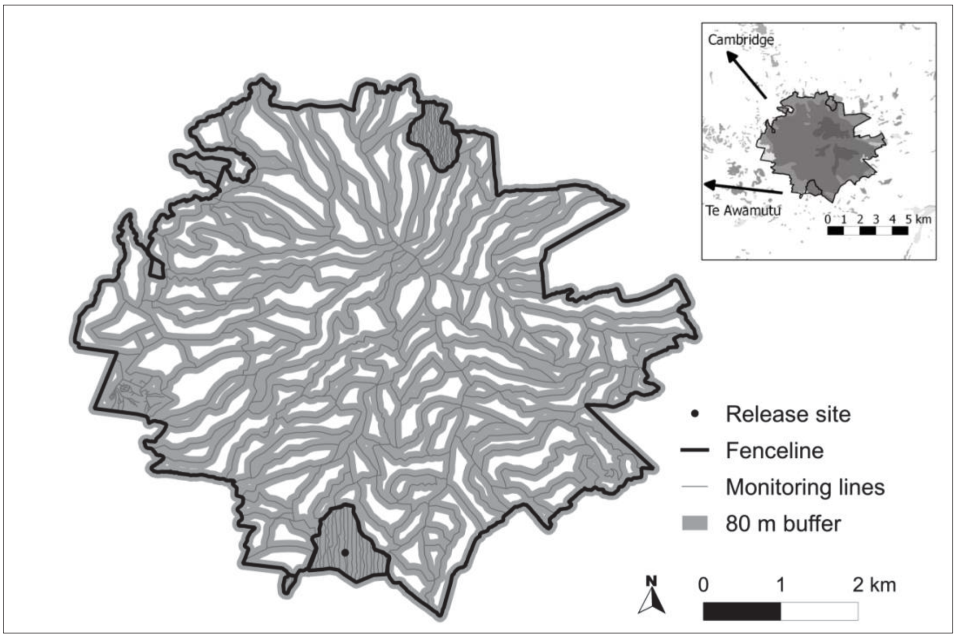


Figure 5.1 Map of Maungatautari Ecological Island (release area) showing monitoring lines with 80 m buffer either side, and release site for translocation of hihi between 2009 and 2011. Hihi were detectable at least 80 m from a monitoring line; hence grey areas show areas well covered during searches (approx. 85% of the release area).

Assignment of parentage and calculation of natal dispersal distances

We colour banded 76 locally bred hihi from 2009/10 until the end of 2012. Two of these were excluded from this analysis: one male from 2009/10 who was not blood sampled, and a female caught in early 2012 of unknown age (see above).

All individuals were genotyped at 19 highly polymorphic autosomal microsatellite loci (see Brekke *et al.*, 2009 for extraction and amplication details). To reduce genotyping errors (null or false alleles, allelic dropout and stutter), samples were amplified twice, or if not consistent, amplified until they were or excluded. Genotyping errors were estimated using Microchecker 2.2.3 (Van Oosterhout *et al.*, 2004). We then attempted to assign parentage to 74 of the locally-bred hihi using the maximum-likelihood software Colony 2.0 (Wang and Santure, 2009). Both sexes were defined as polygamous, and allele frequencies and genotyping error rates were provided. In 2009/10, parent candidate lists included all translocated individuals from 2009, in 2010/11 all translocated individuals from 2009 and 2010, and locally-bred birds from 2009/10, and in 2011/12 all translocated individuals from 2009, 2010 and 2011, and locally-bred birds from 2009/10 and 2010/11. The probability of the true parents being in the candidate lists was set at 0.99 for individuals from 2009/10, and 0.75-0.8 for 2010/11 and 2011/12. The lower probability in later years reflects our knowledge that unsampled (unbanded) resident putative parents were in the population during these seasons.

Table 5.2 Number of hihi banded, assigned maternity, and available natal dispersal distance (NDD) data by cohort, 2009/10-2011/12 at Maungatautari.

	Males			**Females**			**Total NDD**
Cohort	Banded	Maternity assigned	NDD available	Banded	Maternity assigned	NDD available	
2009/10	10	10	8	2	2	2	10
2010/11	17	13	8	11	7	5	13
2011/12	18	18	8	16	14	8	16
Total	**45**	**41**	**24**	**29**	**23**	**15**	**39**

We were able to assign maternity to 64 of the 74 offspring analysed (from 19 individual mothers, 16 of known territory location), and paternity to 69 (from 30 individual fathers), with > 95% confidence. Where we could not assign parentage, this was largely attributable to parentage by unbanded birds in the population. In 2010/11, we could not assign maternity to eight offspring, and Colony output suggested these offspring were from four individual females from the 2009/10 cohort (prior to the start of intensive banding efforts) that had not been genotyped and therefore were not in our candidate list. In 2011/12, we could not assign maternity to two individuals, both of which were captured in an area where two unbanded adult females were known to be present. Of the offspring (n=58) mothered by the 16 females we had located, 49% were fathered by the social male, 45% by a close neighbour (either paired or floater male), and 6% by males from a greater distance away or of unknown location.

Of the 64 offspring for which it was possible to assign maternity, 39 were both recruited into the breeding population, and then located at their first breeding territory. Natal dispersal distances were calculated by measuring the distance from the natal site (inferred by the breeding location of the mother) to the first breeding site.

Data analysis

We fitted generalised linear mixed models with an exponential distribution and log-link function in WinBUGS 1.4 (Lunn *et al.*, 2000) to examine the effect of covariates on natal dispersal distances. We began by running a constant model, and then introduced sex as a fixed effect, and a random effect of mother. We then considered fixed effects of cohort, handling score, inbreeding coefficient, and number of fault bars one at a time, and tested for interactions with sex. There was a burn in of at least 10,000 samples for each model, and we introduced another 100,000 samples after convergence was reached. Where missing values were present, we imputed them by sampling from either a normal or Poisson distribution as appropriate (Nakagawa and Freckleton, 2008). Alternative models were compared using DIC (Deviance Information Criteria; Spiegelhalter *et al.*, 2002). As models estimating missing values from a Poisson distribution could not generate DIC values, we also divided the mean dispersal distance estimated under the highest covariate score by the mean dispersal distance estimated under the lowest covariate score to generate comparable effect sizes between models.

Results

We found variation in natal dispersal patterns between individuals that differed by sex and personality type. Mean NDD was 1749 m for male hihi (range 0-5170 m) and 876 m for female hihi (range 0-3425 m) (Figures 5.2, 5.3). There was a significant interaction between sex and handling score, with the generalised linear mixed model estimating a mean NDD of 3472 m for males that distress-called in the hand, 1912 m for those that that struggled in the hand but did not distress-call, and 1141 m for those that neither struggled or distress-called (Figure 5.4). Number of fault bars had an ambiguous effect, with DIC not lowered but a large effect size, suggesting NDD was higher in birds with more fault bars. Cohort and inbreeding coefficient did not have a detectable effect on NDD (model comparisons and estimated effect sizes are presented in Appendix 5.1).

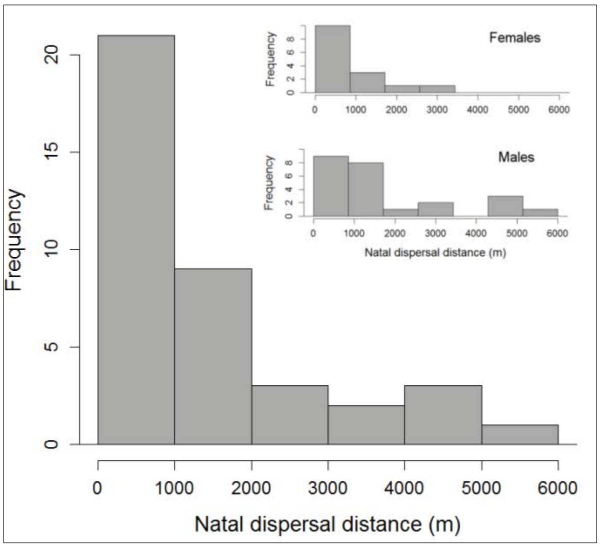
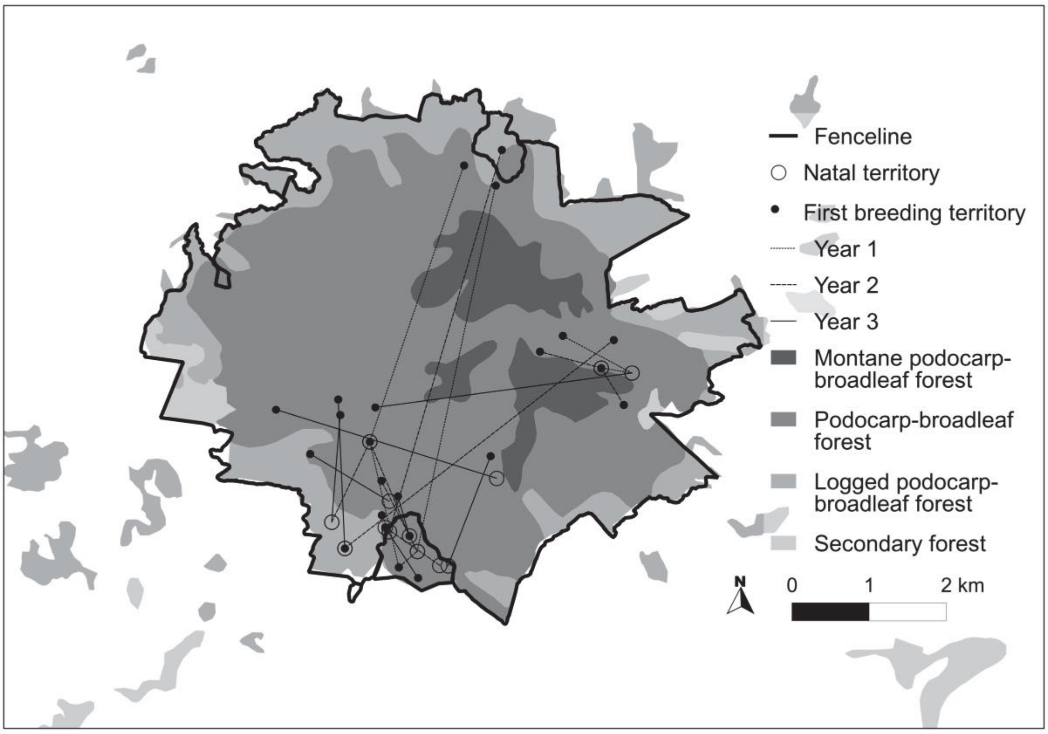


Figure 5.2 Natal dispersal distances of hihi at Maungatautari from 2009/10 (first breeding season after translocation) to 2011/12 (third breeding season after translocation).

a)



b)

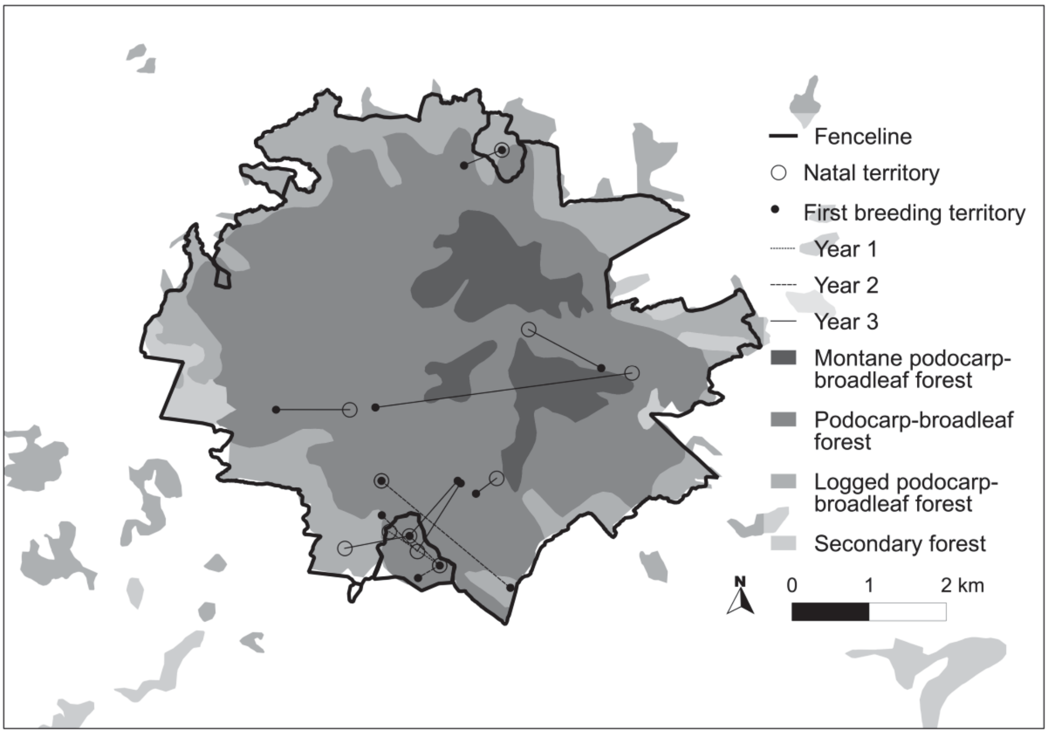


Figure 5.3 Map showing natal dispersal patterns at Maungatautari for juvenile a) males and b) females from 2009/10 to 2011/12 (first three breeding seasons after translocation).

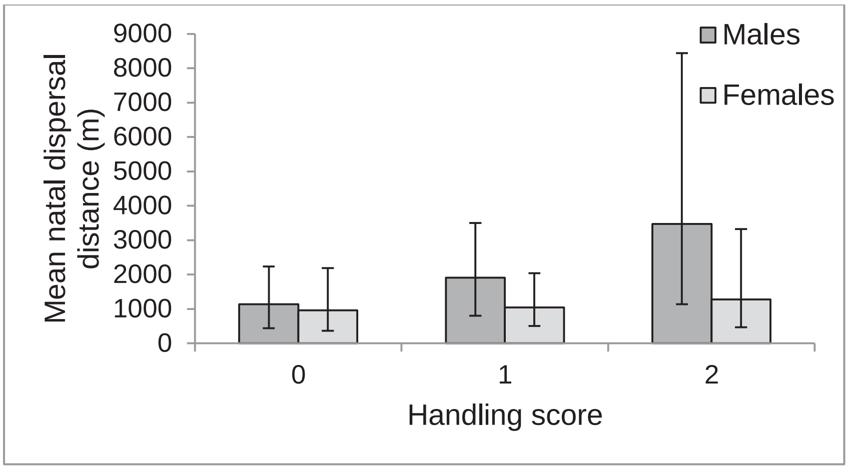


Figure 5.4 Mean natal dispersal distances estimated from generalised linear mixed model for male and female hihi with handling scores of 0) quiet, no struggle, 1) quiet, struggled, and 2) distress-called and struggled.

Discussion

We found considerable individual variation in NDD in the first three years of an establishing reintroduced hihi population. Male NDD was on average higher than female NDD, and we found effects of personality and early natal condition. The effects of personality on NDD mirrored our findings in a similar study on post-release dispersal, whereas the effect of condition was in contrast.

Effects of personality and condition

Our results suggest an effect of personality type on natal dispersal distance that is stronger in male hihi, similar to what was found in a previous analysis on post-release dispersal (Chapter 3). Males that gave distress-calls in the hand, thought to be at the "proactive" end of the personality spectrum (Groothuis and Carere, 2005; Cockrem, 2007; Pascual and Senar, 2014), dispersed greater distances both as juveniles moving away from the natal site, and as juveniles dispersing in the first few weeks after translocation. Due to logistical constraints, we could not examine other aspects of personality in juveniles bred at Maungatautari. However, our results provide further support to other studies that have shown a link between personality and natal dispersal patterns (Dingemanse *et al.*, 2003; Duckworth and Badyaev, 2007; Cote *et al.*, 2010a), with proactive individuals having greater dispersal tendencies.

There was no clear effect of inbreeding coefficient. This contrasts with our findings of effects on post-release dispersal, and could potentially be because the interaction between inbreeding and stress would be expected to be higher during post-release dispersal than natal dispersal (Crnokrak and Roff, 1999; Keller and Waller, 2002; Dickens *et al.*, 2010). It may also reflect the different measures used in this aspect of the study, i.e. the inbreeding coefficients used here were marker-based rather than pedigree-based (the latter are preferable, but were not available for this population). The result for early natal condition (as measured by number of fault bars on tail feathers grown in the nest) was more ambiguous, with a suggestion that poorer natal condition resulted in greater NDD. While this result is consistent with that of del Mar Delgado *et al.* (2010), interpretation is difficult in our case given the ambiguity of the result and lack of context as we had no measure of environmental variation across years that may have acted as an incentive (or otherwise) for dispersal each year.

Natal dispersal in an establishing hihi population

Our results bear both similarities and differences to natal dispersal patterns in this species on Tiritiri Matangi. Sex-specific differences are apparent at Maungatautari in the first three years of population establishment, with males having higher mean NDD than females. On Tiritiri Matangi, this was also the case for the first two years, but as population density increased female NDD also increased, and male NDD decreased. We were unable to examine sex ratio effects in the Maungatautari population, given the smaller dataset and shorter time period in comparison to that available for Tiritiri Matangi, but the population was known to be male-biased throughout our study period, particularly in 2011/12 (approximately 1.3:1 in 2010/11, 1.8:1 in 2011/12 and 1.2:1 in 2012/13). This male sex bias may have contributed to the lower female NDD we report in comparison to male NDD at Maungatautari, as was found in the Tiritiri Matangi population (Richardson *et al.*, 2010).

Additional birds were translocated into the population in autumn of both 2010 and 2011, artificially increasing density, and this may also have influenced NDD in locally-bred juveniles. However, another aspect of this study (Chapter 4) found the majority of the newly translocated birds did not pair with locally-bred birds, and settlement decisions could not be shown to be influenced by conspecific presence (in contrast to locally-bred birds that demonstrated strong conspecific attraction). Potentially this could be because locally-bred juveniles had already selected territories by autumn. Our observations of juveniles during the course of field work suggested that most left the natal site within a few weeks of fledging. Of those captured as juveniles, some were close to their eventual breeding sites, but not all, suggesting some variation in timing of settlement and exploration. The degree of exploration by juveniles, and how this varies by sex, condition and personality remains unknown and an avenue for further research.

Unsurprisingly, mean NDD was higher at Maungatautari than at Tiritiri Matangi which has less area. There was considerable variation between individuals of both sexes, with a small number of both males and females remaining to breed at their natal site, and the maximum dispersal distance > 5 km. Given that Maungatautari is constrained by the forest boundary and the greatest possible distance from known natal sites is ~6 km, it is likely that maximum NDD would be higher in unconstrained habitat.

Implications for reintroduction success

Another aspect of my study (Chapter 4) suggested that conspecific attraction plays a role in habitat selection of natal dispersers. Here, we clearly show that this is not a result of natal philopatry, but reflects active selection of territories close to conspecifics. By the end of 2012/13, clusters of individuals were apparent in four main areas at Maungatautari: 1) the southern area close to the release site and supplementary feeders, 2) the Mangaohoi catchment to the south-west, 3) the Mangakara catchment to the east, and 4) the Wairakau catchment to the north. Our study suggests that there is movement, and therefore potential for gene flow, between these clusters, primarily a consequence of male natal dispersal, although we did record one female who dispersed from Mangakara to Mangaohoi.

Hihi were known to be present at all of these locations by at least the end of the first breeding season, and this implies that the habitat selection that influenced the location of these breeding clusters occurred early in the establishment of the population. Our results from Chapter 3 demonstrated that female dispersal decisions are made within the first few weeks after translocation, and in conjunction with our results here and in Chapter 4 that suggest a strong effect of conspecific attraction in natal dispersal, this suggests that dispersal decisions made by female hihi in the initial post-release phase can have long-lasting multi-generational effects on the reintroduced population. These could be positive or negative – at large sites, conspecific attraction could act to reduce negative effects on natal dispersal outside of restoration areas, but conversely could lead to aggregation in sub-optimal habitat (Mihoub *et al.*, 2009; Mihoub *et al.*, 2011).

Understanding the degree to which this habitat selection reflects informed choice is critical to our understanding of habitat selection in reintroduced populations. Our results further highlight the importance of habitat selection strategies in the initial post-translocation phase, given its role in shaping future settlement patterns.

Appendix 5.1 Results from generalised linear mixed models assessing effects of individual covariates on natal dispersal distances of hihi at Maungatautari. Best models are in bold.

	pD[a]	**DIC[b]**	**ΔDIC[c]**	**Effect size[d]**
sex (re.m[e])	**3.57**	**645.60**	**0**	**2.06**
constant	1.00	645.81	0.21	NA
sex (re.m) + faults	4.65	646.15	0.55	3.37
sex (re.m) + cohort	4.49	647.30	1.70	1.27
sex (re.m) + f	4.47	647.49	1.89	
sex (re.m) + faults + faults*sex	5.58	647.90	2.31	1.08 (females)
				1.14 (males)
sex (re.m) + f + f*sex	5.58	648.83	3.23	1.02 (females)
				0.99 (males)
sex (re.m) + cohort + cohort*sex	5.51	649.27	3.67	1.25 (females)
				1.07 (males)
sex (re.m) + HS	NA	NA	NA	2.7
sex (re.m) + HS + HS*sex	**NA**	**NA**	**NA**	**1.2 (females)**
				1.77 (males)

[a] pD = Effective number of parameters (mean of posterior deviance minus mean of posterior distribution.

[b] DIC = Deviance information criterion, where lower DIC means higher predictive value.

[c] ΔDIC = Difference in DIC from that of best model.

[d] Effect size = Mean dispersal distance estimated under highest covariate score divided by mean dispersal distance estimated under lowest covariate score.

[e] re.m = random effect of mother

CHAPTER 6

Considering dispersal in reintroduction and restoration planning

---

This chapter is published as: Richardson, K. M., Doerr, V., Ebrahimi, M., Lovegrove, T. G. & Parker, K. A. 2015. Considering dispersal in reintroduction and restoration planning. In: Armstrong, D. P., Hayward, M. W., Moro, D. & Seddon, P. J. (eds.) *Advances in Reintroduction Biology of Australian and New Zealand Fauna.* CSIRO Publishing. Chapter 6, pp 59-72.

Co-authors and their respective contributions are as follows:

Veronica Doerr (CSIRO, Australia) – contributed approximately 15% of main text, in particular comment around dispersal and landscape-scale management from an Australian perspective. Contributed one boxed text (not presented here).
Mehregan Ebrahimi (Flinders University) – contributed one boxed text (not presented here).
Tim Lovegrove (Auckland Council) – contributed one boxed text (not presented here).
Kevin Parker (Massey University) – contributed approximately 5% of main text, substantial feedback on structure of chapter and editing of Table 1.

All co-authors have granted consent for the published chapter to appear in this thesis.

Abstract

Dispersal behaviour is a critical factor that can influence reintroduction success across multiple stages. To date, most attempts to deal with this issue have focused on either reducing or mitigating dispersal using various management tools, and solutions have focused on initial post-release dispersal without fully recognising or acknowledging the effects ongoing dispersal may have. We advocate for careful consideration of proposed sites for reintroduction, taking into account characteristics of the species (dispersal propensity and probability of mortality for dispersers), and assessments of both the release site and the surrounding landscape, including connectivity, linkages and invasive species management at the landscape scale. In some cases, existing knowledge may enable us to predict the effect of interactions between these species and site characteristics, enabling informed decisions to be made before reintroduction. We emphasise the need for reintroduction planning to incorporate an integrated landscape approach, viewing dispersal as a natural component of a species life history. Under integrated landscape management, the wider landscape beyond reintroduction sites could be managed, with the long-term goals of establishing self-sustaining populations and providing safe opportunities for dispersal and gene flow to recreate natural metapopulations.

Introduction

Dispersal behaviour can influence the success or failure of reintroductions in multiple ways, with interactions between factors making understanding and resolving these issues complex (Clobert *et al.*, 2012; Le Gouar *et al.*, 2012). Reintroductions can fail in the short term due to immediate dispersal of released individuals, and in the long term due to continued dispersal away from the reintroduction site. Conversely, reintroductions might also fail in the long term in the absence of management due to a lack of dispersal, and thus lack of long-term genetic and demographic exchange with other populations (Hanski, 1999; Jamieson and Lacy, 2012; Weeks *et al.*, 2015).

Individuals may disperse from release sites, or from the broader reintroduction site, as an adaptive response to explore and select optimal habitat. However, post-release dispersal may also involve a stress response and potentially produce or stimulate non-adaptive habitat selection or homing behaviour (Dickens *et al.*, 2010). Regardless of whether the behaviour itself may be an adaptive response, post-release dispersal can act to compromise reintroduction success across multiple stages at both the population and metapopulation level as outlined by Armstrong and Seddon (2008). In the establishment phase, post-release dispersal into the surrounding landscape can both reduce the size of the founder group and alter the composition of the founder group, either via loss of individuals to the population through dispersal-induced isolation, or higher levels of mortality to dispersing individuals. Dispersal can then continue to compromise persistence of populations through ongoing loss of individuals via dispersal away from the population (in particular natal dispersal of juveniles) or differential habitat selection (in response to either environmental or social factors; Mihoub *et al.*, 2011). These effects can also have serious genetic consequences influencing the long-term sustainability of the reintroduced population if they result in small effective population sizes and reduced genetic variability, particularly if dispersers differ genetically from non-dispersers (e.g. Dingemanse *et al.*, 2003; Bremner-Harrison *et al.*, 2004; Le Gouar *et al.*, 2012).

Managing dispersal issues within reintroductions hence requires consideration of all factors contributing to persistence of the species from the outset. Armstrong *et al.* (2013) discussed three primary strategies that can be used to manage the effects of dispersal on reintroduction success: (1) attempting to reduce dispersal using a variety of potential tools; (2) translocating more individuals to compensate for dispersal; and (3) selecting reintroduction sites less prone to dispersal. We discuss options for 1 and 2 in Box 1. However, these management tools and mitigation efforts generally assume (though rarely explicitly) that dispersal is not adaptive – that a population can successfully establish at the reintroduction site as long as dispersal can be managed or prevented. If dispersal is ongoing and/or occurs in response to habitat being unattractive from the organism's perspective, these management approaches are unlikely to be anything other than a temporary fix to an ongoing problem. In those cases, follow-up translocations would be necessary to compensate for individuals being lost to the population through dispersal, and this raises serious concerns for the sustainability of the reintroduction attempt.

We believe the third strategy – selecting appropriate sites for reintroduction – is the most effective, and we also suggest a fourth, whereby an integrated landscape approach is incorporated into reintroduction planning. Discussion of these two strategies forms the basis of this chapter. Finally, we discuss balancing short-term establishment priorities with the need to create genetically sustainable populations.

Selecting appropriate sites for the target species

We believe the most effective tool to minimise the negative effects of dispersal on reintroduction success, at least in the short to medium term, is selecting suitable sites for reintroduction attempts. Decision making around appropriate site selection should involve: assessing characteristics of the species itself, including dispersal propensity and consequences for survival should animals disperse from protected areas; and assessments of both the release site and the surrounding landscape, including connectivity, linkages, and invasive species management at the landscape scale.

Species-based characteristics

Dispersal capabilities can vary considerably between species. This can relate to the distance individuals are able to travel, or gaps in habitat they are able to cross. Such limitations can be either physiological or behavioural, and can also vary within a species, between individuals and at different life stages. Concomitantly, species vulnerability in unmanaged areas will also vary. In Australia and New Zealand, this most typically (although not always) means vulnerability to exotic mammalian predators (e.g. Powlesland *et al.*, 1999; Short and Turner, 2000; Moseby and O'Donnell, 2003; Richards and Short, 2003; Innes *et al.*, 2010). Given that greater dispersal propensity will result in greater exposure of reintroduced animals to unmanaged areas (and hence predators), there is an obvious interaction between these two traits in landscapes of varying connectivity (Table 6.1).

Box 6.1 Management tools to reduce or mitigate effects of dispersal

A range of tools have been employed in attempts to reduce dispersal behaviour in translocated individuals. Generally these tools are targeted at reducing immediate post-release dispersal, with less consideration of the potential for ongoing dispersal in the long term. The success of such tools varies considerably and many are used despite any clear evidence they are effective.

Holding individuals in captivity on-site before release (‘delayed release’) is often used to attempt to reduce post-release dispersal. Holding wild individuals in captivity should always be treated with caution (Richardson *et al.*, 2015a) and there is little evidence that it can act to reduce post-release dispersal. However, this method can have utility for captive-bred individuals. Holding a small number of individuals on-site for longer time periods while the majority are released can act as an anchor, particularly for social species, and proved an effective method to reduce initial post-release dispersal of captive-bred kaka (*Nestor meridionalis*) that were reintroduced to a mainland site (Smuts-Kennedy and Parker, 2013), although the long-term effects of ongoing dispersal at this site are as yet unknown.

Supplementary feeding is another tool that is used to encourage individuals to stay in a release area, by removing the need to disperse to search for a food source. One study demonstrated the potential effectiveness of this method in pygmy blue-tongue lizards (*Tiliqua adelaidensis*; (Ebrahimi and Bull, 2013), and another found it reduced dispersal of captive-bred brown teal (*Anas chlorotis*) after translocation (Rickett *et al.*, 2013). However, this technique is generally less useful in wild-to-wild translocations of birds.

Hihi (*Notiomystis cincta*) translocated to large mainland sites have been provided with supplementary food at the release site, in feeder stations identical to those they are accustomed to using at the source site, yet have still shown significant dispersal of several kilometres from the release site in some individuals (Richardson, 2009; Chapter 3). Bellbirds released into Hamilton city in 2010 were provided with supplementary food yet dispersed a mean of 14 km from the release site in the first 3 weeks (range 0.5–139 km, with the highest dispersal representing return to source site) (J. Innes, N. Fitzgerald, Landcare Research Hamilton and C. Ninnes, University of Waikato, *pers. comm.*).

Acoustic anchoring using playback of pre-recorded calls has been used in several kokako (*Callaeas wilsoni*) reintroductions, one North Island (NI) robin (*Petroica longipes*) and one whitehead (*Mohoua albicilla*) reintroduction, but although it does appear to attract individual birds on occasion, the evidence to date suggests this is not an effective technique for significantly reducing dispersal (Leuschner, 2007; Molles *et al.*, 2008; Bradley *et al.*, 2011; Bradley *et al.*, 2012).

Releasing a higher number of individuals at the outset can potentially mitigate effects of dispersal by compensating for the loss of individuals due to dispersal from the release site. This may be successful if dispersal only occurs in the initial stages. Multiple releases over multiple years may also be a successful approach in some specific situations, such as where releases are to a highly connected landscape with dispersers having high survival probabilities, but becoming geographically isolated.

Species vulnerable to exotic mammalian predators, which also possess high/medium dispersal abilities, will clearly be at greatest risk. Reintroductions of such species to release sites with high levels of connectivity to unmanaged areas have a high risk of failure (Parlato and Armstrong, 2013). It is becoming increasingly well recognised that reintroducing such species to mainland sites is challenging, and large areas subject to ongoing intensive predator control are often required (e.g. Basse and McLennan, 2003; Robertson and de Monchy, 2012). Conversely, the advent of fenced sites (Burns *et al.*, 2012; Innes *et al.*, 2015) provides a benefit to flightless or ground-based animals, such as Australian mammals or flightless birds such as kiwi (*Apteryx* spp.) and takahe (*Porphyrio hochstetteri*) in New Zealand. Because fences contain these animals, connectivity becomes less important and the management status of areas outside the fence becomes less relevant. However, there may be an inherent trade-off in that any dispersal to provide demographic and genetic exchange between local populations and ensure long-term sustainability may need to be actively managed (see ‘Integrated landscape management’ and Weeks *et al.*, 2015).

Species with higher levels of resistance to predation by exotic mammals are sometimes assumed to be less affected by dispersal following reintroduction, because dispersal is less likely to equate to mortality. Although often affected by predation but to a less critical degree than their more endangered counterparts, these are often the species that persist at mainland sites at low densities, and show rapid responses to predator control (e.g. tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*) and tomtit (*Petroica macrocephala*)). In this context, dispersal into the surrounding landscape (sometimes termed the ‘halo’ effect) can be perceived as positive both in terms of ecological restoration goals and social advocacy outcomes. However, where such species have been extirpated from sites and require reintroduction, recovery can be more challenging. Reintroductions of such species frequently fail as individuals will disperse widely becoming geographically isolated, or return to the source site (e.g. Clarke and Schedvin, 1997; Parker *et al.*, 2004; Miskelly and Powlesland, 2013). Predator-resistant species with lower dispersal propensity may also disperse and become geographically isolated where the reintroduction site is highly connected (Bennett *et al.*, 2012), or have higher probabilities of long-term reintroduction failure where release sites are small and isolated from other habitat fragments.

Making decisions on site selection for reintroduction can be assisted where prior information is available on species reintroduction success (e.g. Parlato and Armstrong, 2012; Parlato and Armstrong, 2013; see 'Site-based characteristics' below) and post-release dispersal behaviour elsewhere. However, frequently, managers are obliged to make decisions where little or no information about post-release dispersal behaviour is available. How should this uncertainty be dealt with? Information from similar species can provide a useful guide (e.g. Doerr *et al.*, 2011), but should be treated with caution. It may also be possible to make inferences from historical range and declines in fragmented areas, although again caution is needed. Species with high dispersal propensity are more likely to persist in small, fragmented areas than those with limited dispersal abilities, but interactions with other factors can make this complex.

Table 6.1 Interactions between connectivity, dispersal propensity and predator vulnerability following reintroduction

Species with a medium to high dispersal propensity will show similar behaviours across habitats regardless of connectivity; therefore, the effects of connectivity for these species are included in a single column.

Species characteristics	**Site characteristics**		
	Low connectivity	**Medium connectivity**	**High connectivity**
Low dispersal propensity **Predator resistant**[1] (e.g. Australian woodland birds)	Low probability of dispersal related failure, e.g. isolated mainland site or island. Small populations might require ongoing genetic management. Creation of corridors may facilitate expansion of population and enhance 'halo effect'. Management tools to reduce dispersal unlikely to be needed.	Medium probability of dispersal related failure, e.g. mainland fragments in close proximity to unmanaged fragments. Some individuals lost, but if $\lambda > 1$ and sufficient founders to ensure genetic viability, population may persist. Dispersal may facilitate expansion of population, enhance 'halo effect' and aid establishment of metapopulations if habitat available in matrix. Management tools to reduce dispersal may help.	Medium-high probability of dispersal related failure, e.g. mainland sanctuaries situated in unmanaged continuous habitat. Many individuals lost, but if $\lambda > 1$ and sufficient founders to ensure genetic viability, population may persist. Dispersal may facilitate expansion of population, enhance 'halo effect' and aid establishment of metapopulations if habitat available in matrix. Management tools to reduce dispersal may help.
Low dispersal propensity **Predator vulnerable**[2] (e.g. North Island saddleback (*Philesturnus rufusater*), some flightless species)	Low probability of dispersal related failure, e.g. isolated mainland site or island. Small populations might require ongoing genetic management. Creation of corridors to facilitate dispersal	Medium probability of dispersal related failure, e.g. mainland fragments in close proximity to unmanaged fragments. Some individuals lost, but if $\lambda > 1$ and sufficient founders to ensure genetic viability, population may persist. ISM in matrix would increase probability of	Medium-high probability of reintroduction failure due to dispersal, e.g. mainland sanctuaries situated in (unmanaged) continuous habitat. Many individuals lost, but if $\lambda > 1$ and sufficient founders to ensure genetic viability, population may persist.

	would require invasive species management (ISM). Management tools to reduce dispersal unlikely to be needed.	reintroduction success. Management tools to reduce dispersal may help.	ISM in matrix would increase probability of reintroduction success. Management tools to reduce dispersal may help.
High/medium dispersal propensity **Predator resistant**[1] (e.g. bellbird, tomtit)	Medium–high probability of dispersal related failure, dependent on gap-crossing ability – species with limited gap-crossing ability will have higher chance of reintroduction success at sites of lower connectivity. Many individuals lost, but if $\lambda > 1$ and sufficient founders to ensure genetic viability, population may persist. Dispersal may facilitate expansion of population, enhance ‘halo effect’ and aid establishment of metapopulations if habitat available in matrix. Creation of corridors may facilitate expansion of population and enhance ‘halo effect’. Risk of reintroduction failure from individuals becoming isolated or returning to source site. Individuals may become geographically isolated. In this scenario, multiple releases over multiple years may be required to establish a population, especially at large sites. Management tools to reduce dispersal may help.		
High/medium dispersal propensity **Predator vulnerable**[2] (e.g. North Island kokako, hihi, NI robin, kaka, Australian ground-based mammals)	Medium–high probability of dispersal related failure, dependent on gap-crossing ability – species with limited gap-crossing ability will have higher chance of reintroduction success at sites of lower connectivity. High probability of reintroduction failure where ISM limited in area. Large areas subject to ongoing predator control required for reintroduction success. Creation of corridors in association with ISM may aid long-term sustainability of populations by linking protected areas. Management tools to reduce dispersal may help.		

---

[1] Predator resistant: able to persist in absence of management of exotic mammalian predators

[2] Predator vulnerable: unable to persist in absence of management of exotic mammalian predators

We urge caution in applying information about ‘natural’ dispersal behaviour (e.g. natal dispersal patterns and seasonal movements) to post-translocation dispersal behaviour. Individuals that have been through the stress of a translocation (Dickens *et al.*, 2010; Parker *et al.*, 2012b) can behave quite differently, and often exhibit greater, or different, dispersal abilities, than is known for the species under normal conditions (Clarke and Schedvin, 1997; Oppel and Beaven, 2002; Parker *et al.*, 2004; Bennett *et al.*, 2012; Kemink and Kesler, 2013; but see Caron *et al.*, 2013; Stiles *et al.*, 2013). For example, juvenile North Island (NI) robins (*Petroica longipes*) are typically limited by forest gaps of > 100 m when dispersing from natal areas (Richard and Armstrong, 2010), but post-translocation the closely related Stewart Island robin (*Petroica australis rakiura*) has been known to cross gaps of 800 m over open water (Oppel and Beaven, 2002). Sex-biased natal dispersal is a common phenomenon across species (Greenwood, 1980; Dobson, 2013), but the majority of studies of post-release dispersal find no significant effect of sex that is consistent between species or studies. Social effects should also be considered, particularly during follow-up translocations where conspecifics are already present at the site (Mihoub *et al.*, 2011).

Site-based characteristics

Equally critical are the characteristics of the site being considered for reintroduction. We use the term ‘habitat requirements’ to describe the site characteristics needed by a species, but we are conscious that use of the term ‘habitat’ varies widely in the literature. As noted by Hall *et al.* (1997), although some authors (e.g. Jones, 2001) use ‘habitat’ to refer only to the physical characteristics of the environment, it is more correct for ‘habitat’ to include all components of the environment that affect an area’s suitability for a species, including interspecific and intraspecific competition and interactions with predators and parasites.

Ensuring habitat requirements are met is not always straightforward. For example, Sheean *et al.* (2012) reviewed 54 Australian reintroductions and found that, despite attempts to choose and manage appropriate reintroduction sites, lack of adequate predator control and ‘habitat suitability’ were the two most common factors implicated in the failure of reintroductions. Given that released individuals may disperse in search of habitat, monitoring dispersal, not just attempting to reduce it, can provide valuable insights. Bennett *et al.* (2012; 2013a; b) radio-tracked reintroduced brown treecreepers (*Climacteris picumnus*), a declining Australian woodland bird, and found that they preferentially settled in forest areas that had extensive leaf litter rather than woodland areas intended as reintroduction sites. This was an unexpected result given prior knowledge of the species’ habitat requirements, but it highlighted the need for further restoration of the ground layer in woodland areas to make it more suitable for the species. We suspect that such findings may be common in many species, with the current or relict habitat distributions of many species reflecting predation refuges rather than true habitat preference (e.g. takahe; Beauchamp and Worthy, 1988), and reintroduction provides a valuable opportunity to expand our knowledge of species habitat preferences.

Assuming all other habitat requirements are met for the species to be reintroduced, consideration should also be given to the site in the context of the surrounding landscape. Frequently, protected areas and sanctuaries are viewed in isolation from the matrix in which they occur, and we can fail to adequately take into account that animals will not always recognise these boundaries. Key to assessing site suitability is the level of connectivity to the surrounding landscape, and the interaction with the dispersal abilities of the species. In an assessment of 14 reintroductions of NI robin, Parlato and Armstrong (2013) demonstrated that high landscape connectivity was a key factor associated with low individual establishment probability, presumably because birds were more likely to disperse from more connected sites. Where data are available for previous species introductions, similar methods could be used to predict suitability of proposed reintroduction sites. Where few data are available for the proposed species, it may be possible to infer suitability using data from species of similar dispersal abilities.

Integrated landscape management

The strategies for managing dispersal in reintroductions outlined thus far are based on reducing dispersal away from reintroduction sites to help ensure establishment of a population. However, intentionally restricting dispersal can lead to long-term failure of reintroductions by preventing gene flow between populations, which can increase levels of inbreeding and hence decrease long-term genetic sustainability (Frankham *et al.*, 2002). The importance of considering the long-term sustainability of reintroduced populations is becomingly increasingly recognised in reintroduction planning, and in particular, the need to consider this in the early stages of planning (Jamieson and Lacy, 2012). Thus, we suggest that despite its inherent challenges, integrated landscape management should be considered as an additional strategy to manage the effects of dispersal on reintroduction success.

In integrated landscape management, dispersal might be accepted, rather than prevented, and the wider landscape beyond specific reintroduction sites would be managed, both to provide appropriate habitat and to control threats. For example, in the case of NI robin, higher connectivity had negative consequences primarily due to the lack of invasive species management outside of protected areas, and the vulnerability of NI robins to predation by exotic mammals (Powlesland *et al.*, 1999). In restoration planning generally, there is often limited management of threats beyond isolated patches or sanctuaries, with little or no management carried out in the intervening matrix – this despite it being a critical component of species and ecosystem management strategies in Australia and New Zealand (Glen *et al.*, 2013). Indeed, it is a characteristic of community-led sanctuaries that they are not planned in this way, and are bottom-up projects that are generally focused on their 'patch', rather than being a component of a national or regional landscape-based strategy.

Although it might be challenging to consider such large-scale management around reintroduction sites, particularly control of exotic predators, landscape-scale conservation is already becoming a dominant approach in Australia and New Zealand (Fitzsimons *et al.*, 2013). Increasingly, empirical data (Doerr *et al.*, 2010) and more realistic modelling approaches (Kadoya, 2008) may predict where and how reintroduction sites are likely to be functionally connected to other sites in the landscape, allowing targeting of integrated landscape management to the most relevant connections and other protected areas. New methods such as these, improved technologies for predator control, and increased collaboration between agencies and communities, would result in management at a greater landscape scale than seen previously, and could change the way we view connectivity in reintroduction planning. An integrated landscape approach viewing dispersal as a natural component of a species life history would result in greater outcomes for sustainable restoration at a scale beyond individual sites.

Balancing short-term establishment and long-term sustainability

Given that limited dispersal may be required for establishment of reintroduced populations, but dispersal may eventually be required for long-term sustainability of populations, there may be a need to stage multiple management approaches over time, or prioritise management based on consideration of the relative risks. For example, where effective management techniques are available, these could be employed initially to limit dispersal of the founder population, but integrated landscape management increased over time to allow adaptive dispersal of subsequent generations. Even if the immediate priority during reintroduction is management to limit dispersal, reintroduction managers will need to ask at the outset if their site has the potential to create a viable population in the long term. If that is not possible, integrated landscape management may eventually be essential.

If reintroduced populations are too small to support long-term viable populations, and natural dispersal and gene flow between populations at the broader landscape scale cannot be re-established, Jamieson and Lacy (2012) state that it will be necessary either to carry out ongoing genetic restocking from the source population, or work with other partners to create a ‘managed metapopulation’ with frequent transfers between sanctuaries (see also Weiser *et al.*, 2012; 2013). This reality needs to be aligned with the difficulties in adding new individuals to established populations due to density dependent (Armstrong *et al.*, 2005) or behavioural (Parker *et al.*, 2010; Mihoub *et al.*, 2011; Parker *et al.*, 2012a; Chapter 4) factors. We share the concerns raised by Jamieson and Lacy (2012) that many reintroduction projects to small isolated sanctuaries may not be fully cognisant of this need or may lack the resources to manage this in the long term, and suggest that, in some cases, reintroductions of such species to these sites may not always be the best use of limited resources. Instead, we advocate for a more strategic view to reintroduction planning that integrates landscape management and reserve design, with the long-term goals of establishing self-sustaining populations and providing safe opportunities for dispersal and gene flow to recreate natural metapopulations.

Conclusions

We have outlined briefly how dispersal can compromise reintroduction success but also be critical to long-term sustainability of reintroduced populations, and discussed how dispersal can better be managed in reintroduction and restoration planning. Tools to either manage or mitigate dispersal exist, but tend to be successful only in specific cases and do not offer a long-term solution to the overall issue. We advocate that dispersal behaviour needs greater consideration at the outset of reintroduction planning and, hence, in restoration planning more generally. We suggest that this occurs through improved consideration of the characteristics that may make the target species vulnerable to dispersal-induced reintroduction failure, and suggest these factors be considered in conjunction with specific characteristics of the proposed release site, without being limited to our perceived boundaries of the site, but including the wider landscape as may be available to the species both now and in the future. Restoration managers will also need to carefully consider priorities where conflicts arise between species where some may benefit from increased connectivity and others will not (Baguette *et al.*, 2013).We emphasise a greater need for reintroduction planning to incorporate a landscape dimension, and suggest that the integrated landscape approach promoted by Glen *et al.* (2013) could also be applied to reintroduction planning. Sustainable populations of reintroduced species on mainland Australia and New Zealand will in some cases require a shift in thinking from a focus on small, isolated sites to long-term planning at a scale of landscapes and metapopulations. Implicit in this are many challenges, including an urgent need for invasive species management at a larger scale than seen before. Ambitious concepts such as ‘predator-free New Zealand’ (McGlone *et al.*, 2014) would transform how we view the links between dispersal, connectivity and reintroduction in our landscapes. We need to ensure we take into account the potential for future change in reintroduction planning – both change via advances in management, as well as through the environmental changes that may be brought about in the future under climate change scenarios.

Acknowledgements

We thank Doug Armstrong, Phil Seddon and John Innes for their comments and feedback that improved the quality of this chapter.

CHAPTER 7

Synthesis and future directions

Dispersal in reintroduced populations - advances in knowledge and remaining gaps

My study aimed to investigate the role of internal state and the external environment in dispersal patterns of a reintroduced passerine. I aimed to investigate these factors at two important stages for reintroductions: post-release dispersal, and natal dispersal. I outline my findings below, directions for future research and specific implications for management of hihi. I then conclude by discussing the implications of this research for reintroduction biology more widely.

Internal state, individual variation and dispersal decisions: understanding covariation of traits

I investigated the role of internal state in both natal and post-release dispersal in my study species, the hihi *(Notiomystis cincta)*. I started by demonstrating measurable personality traits in hihi, and investigating the factors influencing these. In conjunction with a concurrent study, I found evidence for covariation of multiple traits, with complex relationships apparent between personality, the natal nutritional environment, life history traits, and plumage characteristics. Previous studies have found linkages between these traits, and in species with melanin-pigmented plumage these were linked to the pleiotropic effects of the gene regulating melanin pigmentation (Ducrest *et al.*, 2008). An increasing number of studies have begun to find covariation between carotenoid-based pigmentation and a range of other phenotypic traits. It is thought that plumage characteristics may act as a signal for phenotype, including personality traits. Male hihi are particularly colourful, with black, yellow and white plumage, and I suggest an avenue for further research could be investigating the role these plumage characteristics play in signalling phenotype.

I found evidence for multiple effects of personality, the natal nutritional environment, and inbreeding effects on post-release dispersal. The effects of personality were unclear, in that some traits typical of the proactive personality type were linked to increased dispersal, whereas others were linked to reduced dispersal. I found evidence that lower individual quality – as dictated by inbreeding coefficients, or the early natal nutritional environment – may act to reduce dispersal immediately after release. The consequences of, and interactions with survival, would be an important direction to assess the implications of this for reintroduction success.

I found evidence for an effect of personality on natal dispersal patterns in one (Maungatautari), but not the other (Tiritiri Matangi), of my study populations, potentially an outcome of using a different measure of personality in the former. I found no evidence for an effect of inbreeding coefficient, and ambiguous evidence for an effect of early natal condition on natal dispersal at Maungatautari, and this may have been restricted by the available data for this site.

External environmental effects on dispersal decisions

I investigated the role of both physical and conspecific effects on habitat selection in a reintroduced population, comparing the relative importance of these between natal and post-release dispersal. I found evidence that physical attributes of the environment including stream proximity play a role in habitat selection at both the natal and post-release dispersal stage. There was evidence that conspecific attraction plays a strong role in natal dispersal patterns, but not post-release dispersal.

Females made settlement decisions in the first few weeks after translocation, but it was not possible to what degree this reflected informed selection vs random selection of stressed individuals. This early settlement behaviour has significant implications at the population level, hence remains an important gap in our understanding. Males appear to explore for longer, although transmitter battery life restricted our ability to detect the end of this phase. Settlement decisions in males appeared largely driven by female presence.

A remaining knowledge gap is the degree to which internal state interacts with the external environment to drive dispersal decisions. Preferences for certain physical characteristics may vary between phenotypes, and it has been shown in other species that the degree of conspecific attraction varies between personality types (Cote and Clobert, 2007; Cote *et al.*, 2008). Further, the role of heritability was not investigated in my study, and remains a significant knowledge gap in my study species.

Implications for hihi reintroductions

My results have provided some guidance to future site selection for hihi reintroductions, with particular regard to the mainland. I have shown that hihi are capable of dispersing long distances (> 6 km) in the first few weeks post-release in continuous forest, and that some juveniles will disperse similar distances during natal dispersal movements. I also found hihi to be capable of crossing forest gaps of at least 100 m, and potentially further if aided by isolated trees or vegetation in the landscape. A subsequent translocation of hihi to Bushy Park occurred in 2013, unfortunately too late to allow post-release monitoring to be a part of this thesis. This reserve has relatively low connectivity, with a gap of approximately 300 m between the forest edge and adjacent forest patches. Intensive radio-tracking did not detect any hihi dispersal from the site (Hihi Recovery Group, unpubl. data). In conjunction with my results, this suggests that hihi are limited by forest gaps of somewhere between 100 and 300 m, suggesting perhaps slightly higher dispersal abilities than Australian woodland species that are limited by gaps of 80-100 m (Doerr *et al.*, 2011), and North Island robin that are limited by gaps of < 110 m (Richard and Armstrong, 2010). Post-release monitoring of hihi at future reintroduction sites is recommended to further enhance our knowledge and therefore ability to predict suitable sites. In addition, recovery planning will be aided by knowledge of the level of dispersal from a reserve a hihi population could sustain to persist long-term.

My results may also provide some guidance towards monitoring methodology of hihi, although this was not a main focus of this research. My finding that female hihi settle within the first few weeks of release is particularly valuable. Radio-tracking of female hihi after release would significantly aid subsequent breeding monitoring at large sites by narrowing down the search area to detect territories. The results of species distribution modelling (Chapter 4) are also of value, and incorporating subsequent data from Maungatautari (and other hihi sites) would further refine our knowledge of hihi habitat preference, thus potentially informing monitoring strategy. I found that, based upon available data, only about 20% of the habitat at Maungatautari is preferred hihi habitat, and focusing search effort in this area could significantly reduce labour costs of monitoring the Maungatautari population should this continue to be the case as the population establishes. However, habitat preferences may change or relax as the population grows. Continually feeding new presence data into the model is a relatively simple task, and could enable development of a stratified monitoring strategy, as well as inform carrying capacity estimates for proposed release areas in the future.

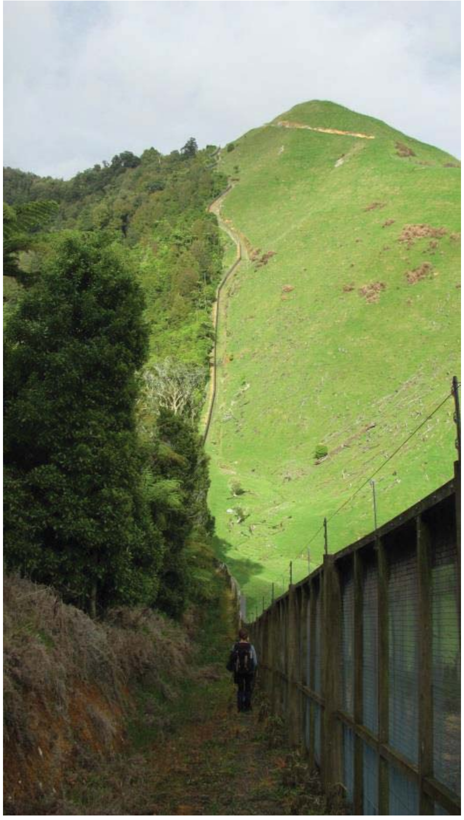
Implications for reintroduction biology

My results emphasise the importance of considering release strategies early in reintroduction planning. Adding individuals to the population (via reinforcement) in later years can be problematic for many reasons, and I show that a lack of conspecific attraction may reduce the likelihood that newly released individuals will integrate into the intended population. However, my study only looked at effects in the short-term, and did not investigate long-term genetic integration of these individuals. While first breeding attempts did not indicate significant integration with resident birds, the mating decisions of their offspring remain unknown. The intended outcomes of reinforcements can vary, and the degree to which integration of new individuals is an issue will depend on the desired outcomes (i.e. integration of new genetics vs simply bolstering numbers of individuals).

At reintroduction sites with significant dispersal potential, differential dispersal of different phenotypes has significant implications for reintroduction success. If dispersal equates to high mortality, the founder population will be primarily comprised of non-dispersers, and this may represent a small proportion of the genetic and phenotypic diversity translocated. Where non-dispersers are those in poorer condition, or with higher inbreeding coefficients, this again could be a mechanism for reintroduction failure. In addition, covariation among traits suggests that selection against dispersers is also likely to select against a variety of other traits. While this is purely speculative, I suggest it provides further impetus for the consideration of the effects of dispersal at sites with high landscape connectivity, and is again an avenue for further research.

My study provides a comparison between factors influencing natal and post-release dispersal patterns. I found both similarities and differences. Phenotypic traits that have been demonstrated to influence natal dispersal in other species (including this study) have now been shown to also influence post-release dispersal. I found similar physical characteristics of the environment influenced natal and post-release dispersal at the settlement phase, but to different degrees. A critical difference was the effect of conspecific attraction, which strongly drove settlement choices in natal dispersers, but had no demonstrable effect in post-release dispersers. Hence knowledge about natal dispersal may partially inform post-release dispersal, but should be treated with caution.

Finally, I conclude my thesis by discussing how an awareness of dispersal can inform reintroduction planning, and by default, restoration planning more generally. In conjunction with my results from other aspects of this study, I emphasise the importance of careful site selection prior to reintroduction, with consideration of the potential effects of dispersal. Good knowledge of the target species is essential to this, in particular understanding dispersal abilities, habitat preferences, and in reinforcements, the potential effects of conspecific presence. Understanding the degree to which post-release habitat selection is informed will further aid our understanding of these issues. Critically, I suggest incorporating an integrated landscape management approach into reintroduction planning. In practice, in the New Zealand context this translates to restoration on a much larger scale than has traditionally been the case, with an urgent need for improvements in introduced mammalian predator control methodology at mainland sites.



Appendix A Breeding season report to Hihi Recovery Group for hihi at Maungatautari, 2010/11 and 2011/12.

Prepared by Kate Richardson, March 2012

Abstract

Hihi were first reintroduced to Maungatautari Ecological Island (3400 ha) in 2009, with top-up translocations occurring in 2010 and 2011. Monitoring to date has included feeder monitoring by volunteers, a four-week contract survey in February 2010, and my PhD research in the 2010/11 and 2011/12 breeding seasons. My PhD research at Maungatautari has focused on compiling a natal dispersal dataset, by locating breeding territories across the mountain, identifying breeding adults by leg band combinations, and banding mountain-bred hihi at the end of each season.

A minimum of 42 adults (18 females and 24 males) were identified breeding in 2010/11, through a combination of the above field work, and genotyping juveniles bred that season. In 2011/12, a minimum of 71 adults were identified breeding (25 females and 46 males), indicating an increasing male-bias to the population. To date, 30 juveniles have been banded from the 2010/11 season, and 26 from the 2011/12 season. Indications are that less juveniles were produced in 2011/12 than in 2010/11, despite the higher number of breeding females. This may be related to the cold/wet spring in 2011 as a number of early nests were known to fail, or the high level of male harassment at nests that was observed.

2012/13 will be the final field season for my PhD, with territories to be located, but no banding of juveniles will be carried out. Future research and monitoring is strongly recommended to continue to monitor the status of this important population.

Introduction

Hihi were reintroduced to Maungatautari Ecological Island (3400 ha) in 2009 (79 birds), with top-up translocations occurring in 2010 (37 birds) and 2011 (39 birds). Six supplementary feeders have been set up close to the release site in the Southern Enclosure, but no artificial nest boxes have been provided as the site is mature forest considered to have sufficient natural nest cavities.

Monitoring to date has included feeder monitoring by volunteers, a four-week contract survey in February 2010, and PhD research in the 2010/11 and 2011/12 breeding seasons. This report summarises known breeding activity in the latter two seasons from this PhD research.

Methods

The aim of the PhD research is to identify all (or close to) breeding territories, and either identify the adults via leg band combinations, or if unbanded to catch and band them. At the end of each season an attempt was made to catch and band as many of the juveniles as possible.

Territories were identified by walking all pre-existing monitoring lines, and the gaps between them where necessary. This work was carried out from November 2010 to February 2011, and September 2011 to March 2012. Territories were generally identified by listening for the distinctive male territorial call. Nests were frequently found during the identification of the adult birds, although this was not the primary aim of the research and intensive nest monitoring could not be carried out.

Juveniles were caught and banded either at the supplementary feeders, or by mistnetting with call playback.

Results

2010/11

16 females were known to be alive at the beginning of the 2010/11 breeding season, with results from genotyping of juveniles showing at least another two females were breeding (Table 1). 12 were located on territories, with the remaining 6 breeding in an unknown location.

18 males were identified on territories during the season. Another six males were known to be alive, two of which were probably on active territories that were not found (VM-BO and WB-VM) (Table 1).

A total of 30 hihi produced this season have been banded to date (11 females and 19 males) (Table 1). Of these 20 survived to the 2011/12 season (7 females and 13 males).

Table A1 Number of known adults and juveniles banded in 2010/11 and 2011/12

Season	Males	Females	Minimum breeding	Juveniles banded
2010/11	24	18	42	30
2011/12	46	25	71	26

2011/12

24 females were known to be alive at the beginning of the 2011/12 breeding season (Table 1), with results from genotyping of juveniles pending. All were located on territories. It is assumed that there is at least one female breeding in an unknown location (with the male WB-VM).

36 males were identified holding territories; 24 of these were identified as active where

the female was observed. The remaining 12 were subjected to intensive monitoring to determine if a female was present, or sight fledglings, and while it cannot be confirmed that no female was present I consider it highly unlikely. All of these 12 are either located very close to active territories, were active the previous season but the female has been confirmed breeding elsewhere this season, or the male abandoned the territory mid-season to float.

Another 10 males were sighted during the season, either as probable floaters (9) or at feeders and suspected to be breeding in an unknown location (WB-VM) (Table 1).

As of March 2012 26 juveniles had been banded, with an estimated 30-35 in total on the mountain. During the course of field work it was noted that there were a number of apparent renests or first clutch failures, and two of the three late nests were confirmed to fail. A large degree of harassment of nests by males was also noted, with harassment continuing while females were feeding chicks in the nest. The early failures may be linked to the cold/wet spring and summer.

Natural nests

15 nests have been found at Maungatautari since field work commenced. 10 of these have been in pukatea, the remaining in tawa (3), mahoe (1) or rimu (1). The majority are 6-15 m high. One in a pukatea was found 2 m from the ground (SE T4), and another at ground level in a pukatea (Alberts 3-4). The ground level nest was found in January 2012 and was monitored once or twice weekly as it was possible to reach into the nest. One of four eggs hatched, and the chick either died or was abandoned at 2 ½ to 3 weeks of age.

Supplementary feeders

Feeder usage appears to peak at the beginning of breeding season (Sept/Oct) and again after fledging first clutches (January). This sometimes coincides with gaps in natural food supply but not always. Usage often seems to increase after rainfall. Almost all translocated birds are known to use feeders. Of the mountain-bred birds, generally only those breeding in southern/south-west part of mountain use the feeders.

Recommendations

- Field work will continue as part of this PhD into the 2012/13 season, with territories continuing to be mapped. However no banding of juveniles will occur.
- Future research into the status of this population is recommended - in particular more intensive monitoring of nest success would be of benefit.
- Banding of mountain-bred birds should continue, particularly where birds use supplementary feeders.

- Monitoring methods for this population should be trialled in 2012/13 to establish a framework for future surveys of this population.

Acknowledgements
Many thanks to Lydia Doerr and Scott Freeman for assistance with field work throughout the season. Thanks to all at MEIT for helping in countless ways – in particular Paul Quinn and Rod Millar for going above and beyond to help with the logistics of getting around the mountain. A big thank you to all of the MEIT pest team – James Matthews, Will Telford, Ben Pattinson-Yorke, Johnny Broughton, Neil Omundsen – for passing on their many hihi sightings over the season. The landowners who granted us access to the fence across their land – Albert and Elwyn Andree-Wiltens, Bill Garland, John and Penny Scott. John Polstra for providing Lydia and I with ATV training and certification. Everyone who helped in the field over the season - Melissa Murton, Lisa Stuart, John Ewen, Patricia Brekke, Leila Walker, Will Crowther, Gemma Green, Mark Lammas. Massey University, Zoological Society of London and the Hihi Recovery Group for supporting this research.

Territory locations at Maungatautari Ecological Island, 2010-2012

Territory	**2010/11 male**	**2010/11 female**	**2011/12 male**	**2011/12 female**	**Nest**	**Comments**
SE L10	VM-VR	YR-RM	VM-VR	YR-RM	Mahoe	
SE J13	N/A	N/A	RW-GM	GG-GM	Rimu	
SE L16	J-HM	YM-RY or JM-BV?	NY-GM	RR-GM	Tawa	
SE C7	N/A	N/A	HM-WJ	VM-(B)R	Pukatea	
SE E1	O(R)-VM	VM-(B)R	O(R)-VM	None?		
SE E11	HM-WJ	YM-RY or JM-BV?	NW-GM	None?		NW-GM seen calling here occasionally during 11/12
SE H3	RN-YM	None?	NW-GM	None?		
SE R2/T4	VM-RV	YM-RB	VM-RV	YM-RB	Pukatea nr R2 (10/11, first clutch), pukatea near T4 (11/12, first clutch)	
SE I7	RR-YM	J-HM	RR-YM	?		Female seen at beginning of 11/12, but not seen again, nor sign of fledglings
SE M12			M-HJ	None?		Male calling here frequently at beginning of season, close to edge of L10 territory
WFB 0-1	N/A	N/A	WB-GM	OW-GM	Suspected to be in large pukatea near culvert	
WFB 2-3	BB-YM	?	BB-YM	BW-GM		
WFB 4	?	?	GR-RM	J-HM	Tawa	Not known if active in 10/11. Area explored but possibly too late in season? GR-RM not found on territory elsewhere in 10/11. J-HM was breeding elsewhere.
WFB 5-6	?	?	BG-YM	?		Likely no female
SCB 2-3	JN-HM	HM-JO	OO-GM	HM-JO		GO-VM and RV-JM also present at times in 10/11, and GO-VM fathered all offspring.
TRB 4	GO-VM	HM-GJ	GO-VM	HM-GJ		
Quad 17	N/A	N/A	YN-GM	OY-GM	Pukatea	
WAB 1	N/A	N/A	OG-WM	GR-GM	Pukatea	
TAF 2	?	?	NV-HM	?		
TAH 12 area			GM-HW	WM-ON		Seen in January with 2 fledglings
SYF 10	N/A	N/A	WM-RW	?		Male seen and identified by two independent pest team members early in 11/12 season. No further hihi activity after October 2011.
BND 2-3	JM-BH	WN-RM	JM-BH	WN-RM		
BND/Weta	N/A	N/A	WY-GM			Likely no female, close to BND 2-3
BNB 1	N/A	N/A	WR-WM			Calling occasionally in this area
Mangaohoi	?	?	VM-BO	RN-GM		
Mangaohoi	N/A	N/A	GM-OW	OY-WM		
Bob 14	N/A	N/A	WM-NY	WM-OW	Tawa	GN-RM also present at end of season, no sign of either original adult.
Sub A	HH-JM and GN-RM	??-RM (most likely YO-RM)	N/A	N/A		
Alberts 3-4	YH-VM	GY-VM	YH-VM	GY-VM	Pukatea ground level nest	
Alberts 8-9	WW-YM	Unbanded	WW-YM	Unbanded	Pukatea	
Alberts/MP	VM-GV	?	VM-GV	Unbanded	Pukatea	
MPN 2-3	N/A	N/A	YY-GM	Unbanded		Male and female identified on territory early in season, but no further activity after November 2011. YY-GM seen frequently at Alberts 8-9 (tolerated by resident male) and at Alberts/MPD (after disappearance of resident male)
MPF 4-AG	N/A	N/A	WO-GM,	?		Not identified as territory, but two males often in area. In between two active territories, but far enough that could potentially be a third territory here.
TPB 16	N/A	N/A	WW-WM	HR-WM		
OTB 1	YR-YM	?	YR-YM	?		No female or sign of fledgings/juveniles either year
HIB 12	YY-YM	?	YY-YM	?		No female or sign of fledgings/juveniles either year
NE N20	N/A	N/A	YW-GM	WM-VY	Pukatea	

Individuals known alive at beginning of season, but not found on territory

Bird	Season	Male/female	Comments
YG-RM	2010/11	Male	Not seen again after October 2010
VM-BO	2010/11	Male	Seen in Mangaohoi area at end of season, and located on territory at Mangaohoi 8-9 in 2011/12
WB-VM	2010/11 and 2011/12	Male	Known to breed with unbanded female in 2010/11 (from genotyping of juveniles) and sighted at feeders both seasons. Not sighted any other location, ever.
VJ-M	2010/11	Male	Extra-pair father of SCB juvenile, never sighted
RG-YM	2010/11	Male	Frequently seen on E1 territory with O®-VM and VM-(B)R, never sighted elsewhere
RW-YM	2010/11	Male	Frequently seen on territories around southern enclosure, likely floater
YO-RM	2010/11	Female	Probably the Sub A female, but not confirmed
YG-VM	2010/11	Female	Frequent feeder user previous season, seen October 2011 but not again
VM-RH	2010/11	Female	Seen at feeders late in season
M-HV	2010/11	Female	Frequent feeder user, not seen again after October 2011. Seen near Quad 17 territory in September 2011
HG-JM	2010/11	Female	Seen at feeders mid-season
JM-BV	2010/11	Female	Frequent feeder user at times during season, always observed to head south after feeder visits. Most likely breeding in southern enclosure.
YM-RY	2010/11	Female	Frequent feeder user at times during season, always observed to head south after feeder visits, and seen feeding chicks near Feeder 5. Most likely breeding in southern enclosure. Died at end of 10/11 season (sighted with wing injury).
OG-GM	2011/12	Male	Seen repeatedly near Alberts 3-4, sometimes calling in Alberts/Mangakara area. Probable floater.
GW-GM	2011/12	Male	Seen repeatedly near Alberts 3-4, sometimes calling in Alberts/Mangakara and MPN area. Probable floater.
WM-WH	2011/12	Male	Probable floater.
BW-WM	2011/12	Male	Seen at feeders early in season. Probable floater.
OO-WM	2011/12	Male	Seen at feeders during season. Probable floater.
VO-WM	2011/12	Male	Seen at feeders during season. Probable floater.
RN-YM	2011/12	Male	Using feeders heavily at beginning of season, not seen again nor identified on same territory as previous year.
GN-RM	2011/12	Male	Seen at feeders and on other territories in Mangaohoi region. Seen at Bob 14 multiple times after resident male disappeared.
HH-JM	2011/12	Male	Seen in Mangaohoi region at beginning of season.

Appendix B Breeding season summary to Hihi Recovery Group for hihi at Maungatautari, 2012/13.

Prepared by Kate Richardson and Lydia Doerr, March 2013

Estimates of population size

- **67 known adult hihi as of September 2012 (61 banded, 6 unbanded)**
- 30 females (8 translocated, 6 from 2009/10 or 2010/11, and 16 from 2011/12).
- 23 of these were located on territories during the season, with the remaining 7 narrowed down early in the season and not found again/disappeared.
- 9 females used feeders at some point throughout the season.

- 37 males (16 translocated, 10 from 2009/10 or 2010/11, and 11 from 2011/12
- 34 of these were located calling on territory. The remaining 3 are known from sightings at feeders.
- 21 males used feeders at some point throughout the season

- Distance sampling survey carried out in October 2012 with 16 volunteers taking part across the week. A total of 53 500 m transects were laid out and/or walked across the mountain over the course of the week.

Breeding season monitoring and supplementary feeder use

- 17 nests were monitored intensively in 2012/13 as part of a BSc (Hons) project (Lydia Doerr). The majority of these were located in cavities in large pukatea.
- Breeding commenced approx. one month later than in previous seasons, with most first clutches fledging late December/first three weeks of January, and the last second clutches fledging in the last week of March.
- 12 of these were females in their second year or older – 7 used feeders to varying degrees, 5 did not
- 5 of these were first year females – 1 used feeders, the remaining 4 did not

- Feeder using females produced on average 3.4 young (total 27 from 8 females), non-feeder using females produced on average 2.0 (total 18 from 9 females).

Appendix C Record of female survival and recruitment in hihi at Maungatautari Ecological Island, 2009/10 to 2012/13, and estimates of λ (population growth rate).

	2009/10 (9)	**2010/11 (>19)**	**2011/12 (>24)**	**2012/13 (>29)**
	Founders (9)	**Founders (13)**	**Founders/locally bred (16)**	**Founders/locally bred (13)**
	YG-VM	YG-VM	WN-RM	WN-RM
	WN-RM	WN-RM	VM-R	VM-R
	VM-OO	VM-R	YR-RM	GY-VM
	VM-R	YR-RM	GY-VM	HM-JO
	YR-RM	GY-VM	M-HV	OY-WM
	GY-VM	YO-RM	HM-JO	WM-ON
	VV-VM	VM-RH	HM-GJ	WM-OW
	RG-VM	M-HV	J-HM	YM-RB
	YO-RM	HG-JM	HR-WM	Alb/MPD
		HM-JO	WM-WY	RR-GM
		JM-BV	OY-WM	OW-GM
		HM-GJ	WM-ON	RN-GM
		J-HM	WM-OW	OY-GM
			WM-VY	
		Locally-bred recruits (>6)	YM-RB	**New locally-bred recruits (>16)**
		YM-RB	Unbanded #1	BO-OM
		YM-RY		WO-OM
		Unbanded #1	**New locally-bred recruits (>8)**	BG-OM
		Unbanded #2	Alb/MPD	BR-OM
		Unbanded #3	RR-GM	NO-OM
		Unbanded #4	BW-GM	NN-GM
			GG-GM	GW-OM
			OW-GM	OW-OM
			RN-GM	OO-OM
			GR-GM	OY-OM
			OY-GM	ON-OM
				MKF unb
				TAL unb
				Mangaohoi unb
				Quad 17 unb
				AGB unb
Feeder users				
Founders	9	13	6	4
Locally-bred		2	4	5

Saf		
2009/10->2010/11	6/9	0.67
2010/11->2011/12	10/19	0.53
2011/12->2012/13	13/24	0.54
Rf		
2010/11	6 from 9	0.67
2011/12	8 from 19	0.42
2012/13	16 from 24	0.67
λ max		
2010/11	**1.34**	
2011/12	**0.95**	
2012/13	**1.21**	

Saf = Adult female survival

Rf = Number of females recruited to population per adult female.

λ max = Estimated rate of annual population growth.

References

Aguillon, S. & Duckworth, R. 2015. Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. *Behavioral Ecology and Sociobiology,* 69, 625-633.

Anthony, L. L. & Blumstein, D. T. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N e. *Biological Conservation,* 95, 303-315.

Armstrong, D. P., Davidson, R. S., Perrott, J. K., Roygard, J. & Buchanan, L. 2005. Density-dependent population growth in a reintroduced population of North Island saddlebacks. *Journal of Animal Ecology,* 74, 160-170.

Armstrong, D. P., McArthur, N., Govella, S., Morgan, K., Johnston, R., Gorman, N., Pike, R. & Richard, Y. 2013. Using radio-tracking data to predict post-release establishment in reintroductions to habitat fragments. *Biological Conservation,* 168, 152-160.

Armstrong, D. P. & Seddon, P. J. 2008. Directions in reintroduction biology. *Trends in Ecology & Evolution,* 23, 20-5.

Backström, T., Heynen, M., Brännäs, E., Nilsson, J. & Magnhagen, C. 2015. Dominance and stress signalling of carotenoid pigmentation in Arctic charr (*Salvelinus alpinus*): lateralization effects? *Physiology & Behavior,* 138, 52-57.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M. & Turlure, C. 2013. Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews,* 88, 310-26.

Balbontín, J., Møller, A. P., Hermosell, I. G., Marzal, A., Reviriego, M. & Lope, F. 2009. Geographic patterns of natal dispersal in barn swallows *Hirundo rustica* from Denmark and Spain. *Behavioral Ecology and Sociobiology,* 63, 1197-1205.

Barker, R. J. & Link, W. A. 2015. Truth, models, model sets, AIC, and multimodel inference: A Bayesian perspective. *The Journal of Wildlife Management,* 79, 730-738.

Basse, B. & McLennan, J. 2003. Protected areas for kiwi in mainland forests of New Zealand: how large should they be? *New Zealand Journal of Ecology,* 27, 95-105.

Beauchamp, A. J. & Worthy, T. H. 1988. Decline in distribution of the takahe *Porphyrio* (= *Notornis*) *mantelli*: a re-examination. *Journal of the Royal Society of New Zealand,* 18, 103-118.

Bellingham, M., Jack, S., Makan, T., Sumich, J. & de Poorter, M. 2009. *Ark in the Park Restoration Plan*. Auckland, New Zealand: Royal Forest and Bird Protection Society.

Belthoff, J. R. & Dufty, A. M. 1998. Corticosterone, body condition and locomotor activity: a model for dispersal in screech-owls. *Animal Behaviour,* 55, 405-415.

Bennett, V. A., Doerr, V. A., Doerr, E. D., Manning, A. D., Lindenmayer, D. B. & Yoon, H. J. 2012. Habitat selection and post-release movement of reintroduced brown treecreeper individuals in restored temperate woodland. *PLoS One,* 7, e50612.

Bennett, V. A., Doerr, V. A., Doerr, E. D., Manning, A. D., Lindenmayer, D. B. & Yoon, H. J. 2013a. Habitat selection and behaviour of a reintroduced passerine: linking experimental restoration, behaviour and habitat ecology. *PLoS One,* 8, e54539.

Bennett, V. A., Doerr, V. A. J., Doerr, E. D., Manning, A. D., Lindenmayer, D. B. & Yoon, H.-J. 2013b. Causes of reintroduction failure of the brown treecreeper: Implications for ecosystem restoration. *Austral Ecology,* 38, 700-712.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution,* 23, 361-8.

Blas, J., Bortolotti, G. R., Tella, J. L., Baos, R. & Marchant, T. A. 2007. Stress response during development predicts fitness in a wild, long lived vertebrate. *Proceedings of the National Academy of Sciences,* 104, 8880-4.

Bleyhl, B., Sipko, T., Trepet, S., Bragina, E., Leitão, P. J., Radeloff, V. C. & Kuemmerle, T. 2015. Mapping seasonal European bison habitat in the Caucasus Mountains to identify potential reintroduction sites. *Biological Conservation,* 191**,** 83-92.

Blount, J. D., Metcalfe, N. B., Arnold, K. E., Surai, P. F., Devevey, G. L. & Monaghan, P. 2003. Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. *Proceedings of the Royal Society of London B: Biological Sciences,* 270**,** 1691-1696.

Blumstein, D. T., Patton, M. L. & Saltzman, W. 2006. Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol Lett,* 2**,** 29-32.

Bradley, D. W., Molles, L. E., Valderrama, S. V., King, S. & Waas, J. R. 2012. Factors affecting post-release dispersal, mortality, and territory settlement of endangered kokako translocated from two distinct song neighborhoods. *Biological Conservation,* 147**,** 79-86.

Bradley, D. W., Ninnes, C. E., Valderrama, S. V. & Waas, J. R. 2011. Does 'acoustic anchoring' reduce post-translocation dispersal of North Island robins? *Wildlife Research,* 38**,** 69-76.

Brekke, P., Cassey, P., Ariani, C. & Ewen, J. G. 2013. Evolution of extreme-mating behaviour: patterns of extrapair paternity in a species with forced extrapair copulation. *Behavioral Ecology and Sociobiology,* 67**,** 963-972.

Brekke, P., Dawson, D. A., Horsburgh, G. J. & Ewen, J. G. 2009. Characterization of microsatellite loci in the hihi *Notiomystis cincta* (Notiomystidae, Aves). *Molecular Ecology,* 9**,** 1255-1258.

Brekke, P., Ewen, J. G., Clucas, G. & Santure, A. W. 2015. Determinants of male floating behaviour and floater reproduction in a threatened population of the hihi *(Notiomystis cincta)*. *Evolutionary Applications***,** Early View.

Brekke, P., Wang, J., Bennett, P. M., Cassey, P., Dawson, D. A., Horsburgh, G. J. & Ewen, J. G. 2011. Postcopulatory mechanisms of inbreeding avoidance in the island endemic hihi (*Notiomystis cincta*). *Behavioral Ecology*.

Bremner-Harrison, S., Prodohl, P. A. & Elwood, R. W. 2004. Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox *(Vulpes velox)*. *Animal Conservation,* 7**,** 313-320.

Burns, B., Innes, J. & Day, T. 2012. The use and potential of pest-proof fencing for ecosystem restoration and fauna conservation in New Zealand. *In:* Somers, M. J. & Hayward, M. (eds.) *Fencing for Conservation.* Springer New York.

Burtt, H. E. & Giltz, M. L. 1973. Personality as a variable in the behavior of birds. *The Ohio Journal of Science,* 73**,** 65-73.

Cain, B., Wandera, A. B., Shawcross, S. G., Edwin Harris, W., Stevens ‐ Wood, B., Kemp, S. J., Okita ‐ Ouma, B. & Watts, P. C. 2014. Sex-biased inbreeding effects on reproductive success and home range size of the critically endangered black rhinoceros. *Conservation Biology,* 28**,** 594-603.

Calvete, C. & Estrada, R. 2004. Short-term survival and dispersal of translocated European wild rabbits. Improving the release protocol. *Biological Conservation,* 120**,** 507-516.

Carere, C., Drent, P. J., Koolhaas, J. M. & Groothuis, T. G. G. 2005. Epigenetic effects on personality traits: early food provisioning and sibling competition. *Behaviour,* 142**,** 1329-1355.

Carere, C. & Maestripieri, D. 2013. *Animal Personalities: Behavior, Physiology and Evolution.* U.S.A., University of Chicago Press.

Caron, S., Ballouard, J.-M., Lepeigneul, O. & Bonnet, X. 2013. Experimental translocation (re-inforcement) of the Hermann's tortoise, Var, France. *In:* Soorae, P. (ed.) *Global Reintroduction Perspectives 2013: further case studies from around the globe.* IUCN/SSC Re-introduction Specialist Group, Gland, Switzerland, and Environment Agency-Abu Dhabi, Abu Dhabi.

Castro, I., Minot, E., Fordham, R. & Birkhead, T. 1996. Polygynandry, face ‐ to ‐ face copulation and sperm competition in the Hihi *Notiomystis cincta* (Aves: Meliphagidae). *Ibis,* 138**,** 765-771.

Chauvenet, A., Ewen, J., Armstrong, D., Coulson, T., Blackburn, T., Adams, L., Walker, L. & Pettorelli, N. 2012. Does supplemental feeding affect the viability of translocated populations? The example of the hihi. *Animal Conservation,* 15**,** 337-350.

Clarke, M. F. & Schedvin, N. 1997. An experimental study of the translocation of noisy miners *Manorina melanocephala* and difficulties associated with dispersal. *Biological Conservation,* 80**,** 161-167.

Clobert, J., Baguette, M., Benton, T. G. & Bullock, J. M. 2012. *Dispersal Ecology and Evolution.* Oxford, U.K., Oxford University Press.

Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S. & Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters,* 12**,** 197-209.

Cockrem, J. F. 2007. Stress, corticosterone responses and avian personalities. *Journal of Ornithology,* 148**,** 169-178.

Cote, J. & Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society of London B: Biological Sciences,* 274**,** 383-90.

Cote, J. & Clobert, J. 2012. Dispersal syndromes in the common lizard: personality traits, information use, and context-dependent dispersal decisions. *In:* Clobert, J., Baguette, M., Benton, T. G. & Bullock, J. M. (eds.) *Dispersal Ecology and Evolution.* Oxford, U.K.: Oxford University Press.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. 2010a. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 365**,** 4065-76.

Cote, J., Dreiss, A. & Clobert, J. 2008. Social personality trait and fitness. *Proceedings of the Royal Society of London B: Biological Sciences,* 275**,** 2851-2858.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. 2010b. Personality traits and dispersal tendency in the invasive mosquitofish *(Gambusia affinis)*. *Proceedings of the Royal Society of London B: Biological Sciences,* 277**,** 1571-9.

Crnokrak, P. & Roff, D. A. 1999. Inbreeding depression in the wild. *Heredity,* 83**,** 260-270.

Cruz-Angón, A., Sillett, T. S. & Greenberg, R. 2008. An experimental study of habitat selection by birds in a coffee plantation. *Ecology,* 89**,** 921-927.

Danchin, É., Giraldeau, L.-A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. *Science,* 305**,** 487-491.

Daniels, S. J. & Walters, J. R. 2000. Inbreeding depression and its effects on natal dispersal in red-cockaded woodpeckers. *The Condor,* 102**,** 482-491.

del Mar Delgado, M., Penteriani, V., Revilla, E. & Nams, V. O. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology,* 79**,** 620-32.

Dickens, M. J., Delehanty, D. J. & Michael Romero, L. 2010. Stress: An inevitable component of animal translocation. *Biological Conservation,* 143**,** 1329-1341.

Dingemanse, N. J. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology,* 15**,** 1023-1030.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits *(Parus major)*. *Proceedings of the Royal Society of London B: Biological Sciences,* 270**,** 741-7.

Dingemanse, N. J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour,* 142**,** 1159-1184.

Dobson, F. S. 2013. The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution. *Animal Behaviour,* 85**,** 299-304.

Doerr, V., Doerr, E. & Davies, M. 2010. *Does structural connectivity facilitate dispersal of native species in Australia's fragmented terrestrial landscapes*. Canberra, Australia: Collaboration for Environmental Evidence, CSIRO Sustainable Ecosystems.

Doerr, V. A., Doerr, E. D. & Davies, M. J. 2011. Dispersal behaviour of Brown Treecreepers predicts functional connectivity for several other woodland birds. *Emu,* 111**,** 71-83.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour,* 66**,** 973-988.

Dorazio, R. M. 2015. Bayesian data analysis in population ecology: motivations, methods, and benefits. *Population Ecology***,** 1-14.

Duckworth, R. A. 2009. Maternal effects and range expansion: a key factor in a dynamic process? *Philosophical Transactions of the Royal Society B: Biological Sciences,* 364**,** 1075-86.

Duckworth, R. A. & Badyaev, A. V. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences,* 104**,** 15017-22.

Ducrest, A.-L., Keller, L. & Roulin, A. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution,* 23**,** 502-510.

Ebrahimi, M. & Bull, C. M. 2013. Determining the success of varying short-term confinement time during simulated translocations of the endangered pygmy bluetongue lizard *(Tiliqua adelaidensis)*. *Amphibia-Reptilia,* 34**,** 31-39.

Eikenaar, C., Komdeur, J. & Richardson, D. S. 2008. Natal dispersal patterns are not associated with inbreeding avoidance in the Seychelles warbler. *Journal of Evolutionary Biology,* 21**,** 1106-16.

Eikenaar, C., Richardson, D. S., Brouwer, L. & Komdeur, J. 2007. Sex biased natal dispersal in a closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*. *Journal of Avian Biology,* 39**,** 73-80.

Ewen, J. G., Adams, L. & Renwick, R. 2013a. New Zealand Species Recovery Groups and their role in evidence ‐ based conservation. *Journal of Applied Ecology,* 50**,** 281-285.

Ewen, J. G., Armstrong, D. & Lambert, D. M. 1999. Floater males gain reproductive success through extrapair fertilizations in the stitchbird. *Animal Behaviour,* 58**,** 321-328.

Ewen, J. G., Armstrong, D. P., Empson, R., Jack, S., Makan, T., McInnes, K., Parker, K. A., Richardson, K. & Alley, M. 2012. Parasite management in translocations: lessons from a threatened New Zealand bird. *Oryx,* 46**,** 446-456.

Ewen, J. G., Parker, K. A., Richardson, K., Armstrong, D. & Smuts-Kennedy, C. 2011. Translocation of hihi *Notiomystis cincta* to Maungatautari, a mainland reserve protected by a predator-exclusion fence, Waikato, New Zealand. *Conservation Evidence,* 8**,** 58-65.

Ewen, J. G., Renwick, R., Adams, L., Armstrong, D. P. & Parker, K. A. 2013b. 1980-2012: 32 years of re-introduction efforts of the hihi (stitchbird) in New Zealand. *In:* Soorae, P. S. (ed.) *Global Re-introduction Perspectives: 2013. Further case studies from around the globe.* Gland, Switzerland: IUCN/SSC Re-introduction Specialist Group and Environment Agency-Abu Dhabi.

Ewen, J. G., Thorogood, R., Brekke, P., Cassey, P., Karadas, F. & Armstrong, D. P. 2009. Maternally invested carotenoids compensate costly ectoparasitism in the hihi. *Proceedings of the National Academy of Sciences,* 106**,** 12798-802.

Ewen, J. G., Thorogood, R., Karadas, F. & Cassey, P. 2008. Condition dependence of nestling mouth colour and the effect of supplementing carotenoids on parental behaviour in the hihi *(Notiomystis cincta)*. *Oecologia,* 157**,** 361-368.

Ewen, J. G., Thorogood, R., Karadas, F., Pappas, A. C. & Surai, P. F. 2006. Influences of carotenoid supplementation on the integrated antioxidant system of a free living endangered passerine, the hihi *(Notiomystis cincta)*. *Comparative Biochemistry and Physiology,* 143**,** 149-54.

Exnerova, A., Svadova, K. H., Fucikova, E., Drent, P. & Stys, P. 2010. Personality matters: individual variation in reactions of naive bird predators to aposematic prey. *Proceedings of the Royal Society of London B: Biological Sciences,* 277**,** 723-8.

Fargallo, J. A., Velando, A., López-Rull, I., Gañán, N., Lifshitz, N., Wakamatsu, K. & Torres, R. 2014. Sex-specific phenotypic integration: endocrine profiles, coloration, and behavior in fledgling boobies. *Behavioral Ecology,* 25**,** 76-87.

Fitzpatrick, S. & Price, P. 1997. Magpies' tails: damage as an indicator of quality. *Behavioral Ecology and Sociobiology,* 40**,** 209-212.

Fitzsimons, J., Pulsford, I. & Wescott, G. 2013. *Linking Australia's landscapes: Lessons and opportunities from large-scale conservation networks.* Australia, CSIRO Publishing.

Forsman, J. T., Hjernquist, M. B. & Gustafsson, L. 2009. Experimental evidence for the use of density based interspecific social information in forest birds. *Ecography,* 32**,** 539-545.

Forsman, J. T., Hjernquist, M. B., Taipale, J. & Gustafsson, L. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Behavioral Ecology,* 19**,** 539-545.

Frair, J. L., Merrill, E. H., Allen, J. R. & Boyce, M. S. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management,* 71**,** 541-554.

Frankham, R., Briscoe, D. A. & Ballou, J. D. 2002. *Introduction to Conservation Genetics.* Cambridge, U.K., Cambridge University Press.

Fustec, J., Lode, T., Le Jacques, D. & Cormier, J. P. 2001. Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. *Freshwater Biology,* 46**,** 1361-1371.

Garamszegi, L. Z., Eens, M., Török, J. & Tregenza, T. 2008. Birds reveal their personality when singing. *PLoS One,* 3**,** e2647-e2647.

Garten, C. T. 1977. Relationships between exploratory behaviour and genic heterozygosity in the oldfield mouse. *Animal Behaviour,* 25**,** 328-332.

Glen, A. S., Pech, R. P. & Byrom, A. E. 2013. Connectivity and invasive species management: towards an integrated landscape approach. *Biological Invasions,* 15**,** 2127-2138.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour,* 28**,** 1140-1162.

Grether, G. F., Levi, A., Antaky, C. & Shier, D. M. 2014. Communal roosting sites are potential ecological traps: experimental evidence in a Neotropical harvestman. *Behavioral Ecology and Sociobiology,* 68**,** 1629-1638.

Griffith, B., Scott, J. M., Carpenter, J. W. & Reed, C. 1989. Translocation as a species conservation tool: status and strategy. *Science,* 245**,** 477-480.

Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews,* 29**,** 137-150.

Groothuis, T. G. G. & Maestripieri, D. 2013. Parental influences on offspring personality traits in oviparous and placental vertebrates. *In:* Carere, C. & Maestripieri, D. (eds.) *Animal Personalities: Behavior, Physiology and Evolution* U.S.A.: University of Chicago Press.

Grunst, M. L., Grunst, A. S., Parker, C. E., Romero, L. M. & Rotenberry, J. T. 2014. Pigment-specific relationships between feather corticosterone concentrations and sexual coloration. *Behavioral Ecology*.

Guisan, A. & Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters,* 8**,** 993-1009.

Hall, L. S., Krausman, P. R. & Morrison, M. L. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin***,** 173-182.

Hanski, I. 1999. *Metapopulation Ecology.* Oxford University Press.

Hardouin, L. A., Legagneux, P., Hingrat, Y. & Robert, A. 2015. Sex-specific dispersal responses to inbreeding and kinship. *Animal Behaviour,* 105**,** 1-10.

Harrison, M. L., Green, D. J. & Krannitz, P. G. 2009. Conspecifics influence the settlement decisions of male Brewer's sparrows at the northern edge of their range. *The Condor,* 111**,** 722-729.

Hedrick, A. V. & Kortet, R. 2012. Sex differences in the repeatability of boldness over metamorphosis. *Behavioral Ecology and Sociobiology,* 66**,** 407-412.

Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L. & Arnold, K. E. 2010. Personality in captivity reflects personality in the wild. *Animal Behaviour,* 79**,** 835-843.

Hirzel, A. H., Hausser, J., Chessel, D. & Perrin, N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology,* 83**,** 2027-2036.

Hooten, M. B. & Hobbs, N. T. 2014. A guide to Bayesian model selection for ecologists. *Ecological Monographs,* 85**,** 3-28.

Innes, J., Burns, B., Sanders, A. & Hayward, M. W. 2015. The impact of private sanctuary networks on reintroduction programs. *In:* Armstrong, D. P., Hayward, M. W., Moro, D. & Seddon, P. J. (eds.) *Advances in Reintroduction Biology of Australian and New Zealand Fauna.* Australia: CSIRO Publishing.

Innes, J., Kelly, D., Overton, J., Gillies, C., Sullivan, J. & Ladley, J. 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology,* 34**,** 86-114.

IUCN. 2013. *Notiomystis cincta. The IUCN Red List of Threatened Species. Version 2015.2.* Available: www.iucnredlist.org.

IUCN/SSC. 2013. *Guidelines for reintroduction and other conservation translocations*. Gland, Switzerland: IUCN Species Survival Commission.

Jamieson, I. G. & Lacy, R. C. 2012. Managing genetic issues in reintroduction biology. *In:* Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (eds.) *Reintroduction Biology: Integrating Science and Management.* Chichester: Blackwell Publishing.

Johnson, A. M. & Fuller, R. C. 2014. The meaning of melanin, carotenoid, and pterin pigments in the bluefin killifish, *Lucania goodei*. *Behavioral Ecology*.

Johnson, E. J. 2002. The role of carotenoids in human health. *Nutrition in Clinical Care,* 5**,** 56-65.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *The Auk,* 118**,** 557-562.

Jones, K. A. & Godin, J. G. 2010. Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proceedings of the Royal Society of London B: Biological Sciences,* 277**,** 625-32.

Kadoya, T. 2008. Assessing functional connectivity using empirical data. *Population Ecology,* 51**,** 5-15.

Kasumovic, M. M. 2013. The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype. *Animal Behaviour,* 85**,** 1049-1059.

Keller, L. F. & Waller, D. M. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution,* 17**,** 230-241.

Kemink, K. M. & Kesler, D. C. 2013. Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Animal Conservation,* 16**,** 449-457.

Kluen, E., Kuhn, S., Kempenaers, B. & Brommer, J. E. 2012. A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. *Animal Behaviour,* 84**,** 279-287.

Koenig, W. D., Stanback, M. T., Hooge, P. N. & Mumme, R. L. 1991. Distress calls in the acorn woodpecker. *Condor***,** 637-643.

Krause, E. T., Honarmand, M., Wetzel, J. & Naguib, M. 2009. Early fasting is long lasting: differences in early nutritional conditions reappear under stressful conditions in adult female zebra finches. *PLoS One,* 4**,** e5015-e5015.

Kurvers, R. H., van Oers, K., Nolet, B. A., Jonker, R. M., van Wieren, S. E., Prins, H. H. & Ydenberg, R. C. 2010. Personality predicts the use of social information. *Ecology Letters,* 13**,** 829-37.

Le Gouar, P., Mihoub, J.-B. & Sarrazin, F. 2012. Dispersal and habitat selection: behavioural and spatial constraints for animal translocations. *In:* Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (eds.) *Reintroduction Biology: Integrating Science and Management.* Chichester: Blackwell Publishing.

Leuschner, N. 2007. *Ecology and behaviour of the whitehead (Mohoua albicilla) in its translocated ranges in New Zealand.* Unpublished MSc thesis, University of Auckland.

Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution,* 14**,** 343-348.

Link, W. A. & Barker, R. J. 2010. *Bayesian inference: with ecological applications.* Academic Press.

Lunn, D. J., Thomas, A., Best, N. & Spiegelhalter, D. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing,* 10**,** 325-337.

Makan, T., Castro, I., Robertson, A. W., Joy, M. K. & Low, M. 2014. Habitat complexity and management intensity positively influence fledging success in the endangered hihi (*Notiomystis cincta*). *New Zealand Journal of Ecology***,** 53-63.

Martin, C. A., Alonso, J. C., Alonso, J. A., Palacin, C., Magana, M. & Martin, B. 2008. Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation. *Journal of Animal Ecology,* 77**,** 326-34.

Massot, M. & Clobert, J. 2000. Processes at the origin of similarities in dispersal behaviour among siblings. *Journal of Evolutionary Biology,* 13**,** 707-719.

Mateos-Gonzalez, F. & Senar, J. C. 2012. Melanin-based trait predicts individual exploratory behaviour in siskins, *Carduelis spinus*. *Animal Behaviour,* 83**,** 229-232.

Matthysen, E. 2012. Multicausality of dispersal: a review. *In:* Clobert, J., Baguette, M., Benton, T. G. & Bullock, J. M. (eds.) *Dispersal Ecology and Evolution.* Oxford, U.K.: Oxford University Press.

Mayor, S. J., Schneider, D. C., Schaefer, J. A. & Mahoney, S. P. 2009. Habitat selection at multiple scales. *Ecoscience,* 16**,** 238-247.

McGlone, M., Bourdot, G., Byrom, A., Clout, M., Goldson, S. & Nelson, W. 2014. Challenges for pest management in New Zealand. *Royal Society of New Zealand "Emerging Issues".*

McQueen, J. C., Smuts-Kennedy, C., Collier, K., Clarkson, B. D., Burns, B. & MacGibbon, R. 2004. *An Ecological Restoration Plan for Maungatautari, 2003-2004; Working Document.* Centre for Biodiversity and Ecology Research, Department of Biological Sciences, University of Waikato, Hamilton, New Zealand.

Merow, C., Smith, M. J. & Silander, J. A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography,* 36**,** 1058-1069.

Metcalfe, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution,* 16**,** 254-260.

Mihoub, J.-B., Le Gouar, P. & Sarrazin, F. 2009. Breeding habitat selection behaviors in heterogeneous environments: implications for modeling reintroduction. *Oikos,* 118**,** 663-674.

Mihoub, J. B., Robert, A., Le Gouar, P. & Sarrazin, F. 2011. Post-release dispersal in animal translocations: social attraction and the "vacuum effect". *PLoS One,* 6**,** e27453.

Miskelly, C. M. & Powlesland, R. G. 2013. Conservation translocations of New Zealand birds, 1863–2012. *Notornis,* 60**,** 3-28.

Moehrenschlager, A. & Macdonald, D. W. 2003. Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. *Animal Conservation,* 6**,** 199-206.

Molles, L. E., Calcott, A., Peters, D., Delamare, G., Hudson, J., Innes, J., Flux, I. & Waas, J. 2008. "Acoustic anchoring" and the successful translocation of North Island kokako *(Callaeas cinerea wilsoni)* to a New Zealand mainland management site within continuous forest. *Notornis,* 55**,** 57-68.

Moseby, K. E. & O'Donnell, E. 2003. Reintroduction of the greater bilby, *Macrotis lagotis* (Reid) (Marsupialia: Thylacomyidae), to northern South Australia: Survival, ecology and notes on reintroduction protocols. *Wildlife Research,* 30**,** 15-27.

Naguib, M., Kazek, A., Schaper, S. V., Van Oers, K. & Visser, M. E. 2010. Singing activity reveals personality traits in great tits. *Ethology,* 116**,** 763-769.

Nakagawa, S. & Freckleton, R. P. 2008. Missing inaction: the dangers of ignoring missing data. *Trends in Ecology & Evolution,* 23**,** 592-596.

Niemuth, N. D. 2003. Identifying landscapes for greater prairie chicken translocation using habitat models and GIS: a case study. *Wildlife Society Bulletin,* 31**,** 145-155.

Noguera, J. C., Metcalfe, N. B., Surai, P. F. & Monaghan, P. 2015. Are you what you eat? Micronutritional deficiencies during development influence adult personality-related traits. *Animal Behaviour,* 101**,** 129-140.

O'Riain, M. J., Jarvis, J. U. M. & Faulkes, C. G. 1996. A dispersive morph in the naked mole-rat. *Nature,* 380**,** 619-621.

Oppel, S. & Beaven, B. M. 2002. Stewart Island robins (*Petroica australis rakiura*) fly home after transfer to Ulva Island. *Notornis,* 49**,** 180-181.

Osborne, P. E. & Seddon, P. J. 2012. Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling. *In:* Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (eds.) *Reintroduction Biology: Integrating Science and Management.* Chichester: Blackwell Publishing.

Ostro, L. E. T., Silver, S. C., Koontz, F. W. & Young, T. P. 2000. Habitat selection by translocated black howler monkeys in Belize. *Animal Conservation,* 3**,** 175-181.

Parejo, D. & Aviles, J. M. 2011. Predation risk determines breeding territory choice in a Mediterranean cavity-nesting bird community. *Oecologia,* 165**,** 185-91.

Parejo, D., Danchin, É., Silva, N., White, J. F., Dreiss, A. N. & Avilés, J. M. 2008. Do great tits rely on inadvertent social information from blue tits? A habitat selection experiment. *Behavioral Ecology and Sociobiology,* 62**,** 1569-1579.

Parejo, D., White, J., Clobert, J., Dreiss, A. & Danchin, E. 2007. Blue tits use fledgling quantity and quality as public information in breeding site choice. *Ecology,* 88**,** 2373-2382.

Parker, K., A., Hughes, B., Thorogood, R. & Griffiths, R. 2004. Homing over 56 km by a North Island tomtit *(Petroica macrocephala toitoi)*. *Notornis,* 51**,** 238-239.

Parker, K. A., Anderson, M. J., Jenkins, P. F. & Brunton, D. H. 2012a. The effects of translocation ‐ induced isolation and fragmentation on the cultural evolution of bird song. *Ecology Letters,* 15**,** 778-785.

Parker, K. A., Dickens, M. J., Clarke, R. H. & Lovegrove, T. G. 2012b. The theory and practice of catching, holding, moving and releasing animals. *In:* Ewen, J. G., Armstrong, D. P., Parker, K. A. & Seddon, P. J. (eds.) *Reintroduction Biology: Integrating Science and Management.* Chichester: Blackwell Publishing.

Parker, K. A., Hauber, M. E. & Brunton, D. H. 2010. Contemporary cultural evolution of a conspecific recognition signal following serial translocations. *Evolution,* 64**,** 2431-2441.

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

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

Pascual, J. & Senar, J. C. 2014. Antipredator behavioural compensation of proactive personality trait in male Eurasian siskins. *Animal Behaviour,* 90**,** 297-303.

Pearce, J. & Lindenmayer, D. B. 1998. Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater *(Lichenostomus melanops cassidix)* in Southeastern Australia. *Restoration Ecology,* 6**,** 238-243.

Pearce, J. L., Burgman, M. A. & Franklin, D. C. 1994. Habitat selection by helmeted honeyeaters. *Wildlife Research,* 21**,** 53-63.

Perrone, M. 1980. Factors affecting the incidence of distress calls in passerines. *The Wilson Bulletin***,** 404-408.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J. & Stenseth, N. C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution,* 20**,** 503-510.

Phillips, S. J., Anderson, R. P. & Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* 190**,** 231-259.

Powlesland, R., Knegtmans, J. & Marshall, I. 1999. Costs and benefits of aerial 1080 possum control operations using carrot baits to North Island robins *(Petroica australis longipes)*, Pureora Forest Park. *New Zealand Journal of Ecology,* 23**,** 149-159.

Pryke, S. R. & Andersson, S. 2003. Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition. *Behavioral Ecology and Sociobiology,* 53**,** 393-401.

Pryke, S. R., Andersson, S., Lawes, M. J. & Piper, S. E. 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behavioral Ecology,* 13**,** 622-631.

Quinn, J. L., Cole, E. F., Patrick, S. C. & Sheldon, B. C. 2011. Scale and state dependence of the relationship between personality and dispersal in a great tit population. *Journal of Animal Ecology,* 80**,** 918-28.

Quinn, J. L. & Cresswell, W. 2005. Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour,* 142**,** 1377-1402.

R Development Core Team 2013. R: a language and environment for statistical computing. Vienna, Austria: R Foundation of Statistical Computing.

Richard, Y. & Armstrong, D. P. 2010. Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. *Journal of Applied Ecology,* 47**,** 603-610.

Richards, J. D. & Short, J. 2003. Reintroduction and establishment of the western barred bandicoot *Perameles bougainville* (Marsupialia: Peramelidae) at Shark Bay, Western Australia. *Biological Conservation,* 109**,** 181-195.

Richardson, K., Armstrong, D., Hauber, M. & Ewen, J. 2010. Sex-specific shifts in natal dispersal dynamics in a reintroduced hihi population. *Behaviour,* 147**,** 1517-1532.

Richardson, K. M. 2009. *Reintroducing hihi (Notiomystis cincta) to the New Zealand mainland.* Unpublished MSc thesis, Massey University.

Richardson, K. M., Castro, I. C., Brunton, D. H. & Armstrong, D. P. 2015a. Not so soft? Delayed release reduces long-term survival in a passerine reintroduction. *Oryx,* 49**,** 535-541.

Richardson, K. M., Doerr, V., Ebrahimi, M., Lovegrove, T. G. & Parker, K. A. 2015b. Considering dispersal in reintroduction and restoration planning. *In:* Armstrong, D. P., Hayward, M. W., Moro, D. & Seddon, P. J. (eds.) *Advances in Reintroduction Biology of Australian and New Zealand Fauna.* CSIRO Publishing.

Rickett, J., Dey, C. J., Stothart, J., O'Connor, C. M., Quinn, J. S. & Ji, W. 2013. The influence of supplemental feeding on survival, dispersal and competition in translocated Brown Teal, or Pateke *(Anas chlorotis)*. *Emu,* 113**,** 62-68.

Riddle, O. 1908. The genesis of fault-bars in feathers and the cause of alternation of light and dark fundamental bars. *The Biological Bulletin,* 14**,** 328-[370]-1.

Rittenhouse, C. D., Millspaugh, J. J., Hubbard, M. W., Sheriff, S. L. & Dijak, W. D. 2008. Resource selection by translocated three-toed box turtles in Missouri. *Journal of Wildlife Management,* 72**,** 268-275.

Robertson, H. A. & de Monchy, P. J. M. 2012. Varied success from the landscape-scale management of kiwi *Apteryx* spp. in five sanctuaries in New Zealand. *Bird Conservation International,* 22**,** 429-444.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics,* 38**,** 231-253.

Ronce, O. & Clobert, J. 2012. Dispersal syndromes. *In:* Clobert, J., Baguette, M., Benton, T. G. & Bullock, J. M. (eds.) *Dispersal Ecology and Evolution.* Oxford, U.K.: Oxford University Press.

Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews,* 79**,** 815-848.

Rowe, M., Pierson, K. L. & McGraw, K. J. 2015. Exploratory behavior is associated with plasma carotenoid accumulation in two congeneric species of waterfowl. *Behavioural Processes,* 115**,** 181-190.

Saino, N., Romano, M., Scandolara, C., Rubolini, D., Ambrosini, R., Caprioli, M., Costanzo, A. & Romano, A. 2014. Brownish, small and lousy barn swallows have greater natal dispersal propensity. *Animal Behaviour,* 87**,** 137-146.

Schuett, W. & Dall, S. R. X. 2009. Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour,* 77**,** 1041-1050.

Senar, J. C. & Escobar, D. 2002. Carotenoid derived plumage coloration in the siskin *Carduelis spinus* is related to foraging ability. *Avian Science,* 2**,** 19-24.

Serrano, D., Tella, J. L., Donázar, J. A. & Pomarol, M. 2003. Social and individual features affecting natal dispersal in the colonial lesser kestrel. *Ecology,* 84**,** 3044-3054.

Sheean, V. A., Manning, A. D. & Lindenmayer, D. B. 2012. An assessment of scientific approaches towards species relocations in Australia. *Austral Ecology,* 37**,** 204-215.

Short, J. & Turner, B. 2000. Reintroduction of the burrowing bettong *Bettongia lesueur* (Marsupialia: Potoroidae) to mainland Australia. *Biological Conservation,* 96**,** 185-196.

Sih, A. 2013. Frontiers on the interface between behavioral syndromes and social behavioral ecology. *In:* Carere, C. & Maestripieri, D. (eds.) *Animal Personalities: Behavior, Physiology and Evolution* U.S.A: University of Chicago Press.

Sih, A. & Bell, A. M. 2008. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior,* 38**,** 227-281.

Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. 2012. Ecological implications of behavioural syndromes. *Ecology Letters,* 15**,** 278-289.

Sinn, D. L., Cawthen, L., Jones, S. M., Pukk, C. & Jones, M. E. 2014. Boldness towards novelty and translocation success in captive-raised, orphaned Tasmanian devils. *Zoo Biology,* 33**,** 36-48.

Smith, B. R. & Blumstein, D. T. 2007. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology,* 19**,** 448-455.

Smuts-Kennedy, C. & Parker, K. A. 2013. Reconstructing avian biodiversity on Maungatautari. *Notornis,* 60**,** 93-106.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & Van Der Linde, A. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology),* 64**,** 583-639.

Spinola, R. M., Serfass, T. L. & Brooks, R. P. 2008. Survival and post-release movements of river otters translocated to western New York. *Northeastern Naturalist,* 15**,** 13-24.

Stamps, J. & Groothuis, T. G. 2010. The development of animal personality: relevance, concepts and perspectives. *Biological Reviews,* 85**,** 301-25.

Stamps, J. A. & Swaisgood, R. R. 2007. Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science*, 102**,** 392-409.

Stiles, S., Stiles, J., Godwin, J. C., Jenkins, C., Rush, E. M., Lock, B., Johnson, V. M., Wines, M. & Guyer, C. 2013. Repatriation of eastern indigo snakes to conservation lands in South Alabama, USA. *In:* Soorae, P. (ed.) *Global Re-introduction Perspectives: 2013. Further case studies from around the globe.* Gland, Switzerland: IUCN/SSC Re-introduction Specialist Group and Environment Agency-Abu Dhabi, Abu Dhabi.

Støen, O.-G., Pitlagano, M. L. & Moe, S. R. 2009. Same-site multiple releases of translocated white rhinoceroses *Ceratotherium simum* may increase the risk of unwanted dispersal. *Oryx,* 43**,** 580-585.

Taylor, S., Castro, I. & Griffiths, R. 2005. *Hihi/stitchbird (Notiomystis cincta) recovery plan 2004-09.* Wellington, New Zealand: Department of Conservation.

Thorogood, R., Kilner, R. M., Karadaş, F. & Ewen, J. G. 2008. Spectral mouth colour of nestlings changes with carotenoid availability. *Functional Ecology,* 22**,** 1044-1051.

Tracy, L. N., Wallis, G. P., Efford, M. G. & Jamieson, I. G. 2011. Preserving genetic diversity in threatened species reintroductions: how many individuals should be released? *Animal Conservation,* 14**,** 439-446.

Tschirren, B., Fitze, P. S. & Richner, H. 2007. Maternal modulation of natal dispersal in a passerine bird: an adaptive strategy to cope with parasitism? *The American Naturalist,* 169**,** 87-93.

Tweed, E. J., Foster, J. T., Woodworth, B. L., Oesterle, P., Kuehler, C., Lieberman, A. A., Powers, A. T., Whitaker, K., Monahan, W. B., Kellerman, J. & Telfer, T. 2003. Survival, dispersal, and home-range establishment of reintroduced captive-bred puaiohi, *Myadestes palmeri*. *Biological Conservation,* 111**,** 1-9.

van Oers, K., Drent, P. J., Dingemanse, N. J. & Kempenaers, B. 2008. Personality is associated with extrapair paternity in great tits, *Parus major*. *Animal Behaviour,* 76**,** 555-563.

van Oers, K. & Naguib, M. 2013. Avian Personality. *In:* Carere, C. & Maestripieri, D. (eds.) *Animal Personalities: Behavior, Physiology and Evolution* U.S.A.: University of Chicago Press.

Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M. & Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology,* 4**,** 535-538.

van Overveld, T., Careau, V., Adriaensen, F. & Matthysen, E. 2014. Seasonal-and sex-specific correlations between dispersal and exploratory behaviour in the great tit. *Oecologia,* 174**,** 109-120.

Verbeek, M. E. M., De Goede, P., Drent, P. J. & Wiepkema, P. R. 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour,* 136**,** 23-48.

Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour,* 48**,** 1113-1121.

Walker, L., Ewen, J., Brekke, P. & Kilner, R. 2014. Sexually selected dichromatism in the hihi *Notiomystis cincta*: multiple colours for multiple receivers. *Journal of Evolutionary Biology,* 27**,** 1522-1535.

Walker, L. K., Armstrong, D. P., Brekke, P., Chauvenet, A. L. M., Kilner, R. M. & Ewen, J. G. 2013a. Giving hihi a helping hand: assessment of alternative rearing diets in food supplemented populations of an endangered bird. *Animal Conservation,* 16**,** 538-545.

Walker, L. K., Stevens, M., Karadaş, F., Kilner, R. M. & Ewen, J. G. 2013b. A window on the past: male ornamental plumage reveals the quality of their early-life environment. *Proceedings of the Royal Society of London B: Biological Sciences,* 280**,** 20122852.

Wang, J. & Santure, A. W. 2009. Parentage and sibship inference from multilocus genotype data under polygamy. *Genetics,* 181**,** 1579-1594.

Ward, M. P. 2005. Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. *Oecologia,* 145**,** 650-7.

Weeks, A. R., Moro, D., Thavornkanlapachai, R., Taylor, H. R., White, N. E., Weiser, E. L. & Heinze, D. 2015. Conserving and enhancing genetic diversity in translocation programs. *In:* Armstrong, D. P., Hayward, M. W., Moro, D. & Seddon, P. J. (eds.) *Advances in Reintroduction Biology of Australian and New Zealand Fauna.* Australia: CSIRO Publishing.

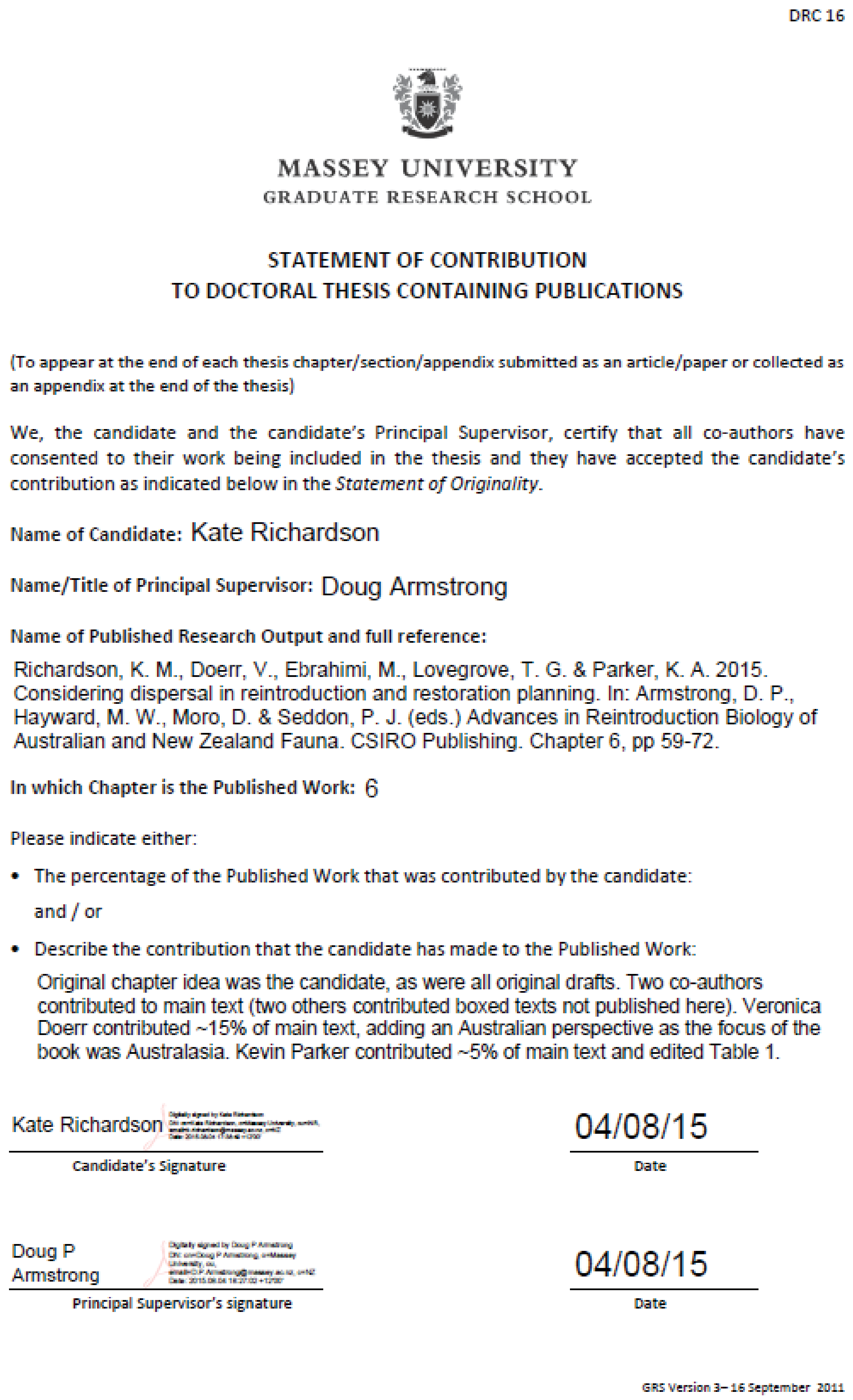
Weiser, E. L., Grueber, C. E. & Jamieson, I. G. 2012. AlleleRetain: a program to assess management options for conserving allelic diversity in small, isolated populations. *Molecular Ecology,* 12**,** 1161-1167.

Weiser, E. L., Grueber, C. E. & Jamieson, I. G. 2013. Simulating retention of rare alleles in small populations to assess management options for species with different life histories. *Conservation Biology,* 27**,** 335-344.

White, P. C. L., McClean, C. J. & Woodroffe, G. L. 2003. Factors affecting the success of an otter *(Lutra lutra)* reinforcement programme, as identified by post-translocation monitoring. *Biological Conservation,* 112**,** 363-371.

Wilson, D. & Paton, D. C. 2004. Habitat use by the southern emu-wren, *Stipiturus malachurus* (Aves : Maluridae) in South Australia, and evaluation of vegetation at a potential translocation site for *S. m. intermedius*. *Emu,* 104**,** 37-43.

Wolf, M., Van Doorn, G. S., Leimar, O. & Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature,* 447**,** 581-584.



DRC 16

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

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

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

Name of Candidate: Kate Richardson

Name/Title of Principal Supervisor: Doug Armstrong

Name of Published Research Output and full reference:

Richardson, K. M., Doerr, V., Ebrahimi, M., Lovegrove, T. G. & Parker, K. A. 2015. Considering dispersal in reintroduction and restoration planning. In: Armstrong, D. P., Hayward, M. W., Moro, D. & Seddon, P. J. (eds.) Advances in Reintroduction Biology of Australian and New Zealand Fauna. CSIRO Publishing. Chapter 6, pp 59-72.

In which Chapter is the Published Work: 6

Please indicate either:

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

  and / or

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

  Original chapter idea was the candidate, as were all original drafts. Two co-authors contributed to main text (two others contributed boxed texts not published here). Veronica Doerr contributed ~15% of main text, adding an Australian perspective as the focus of the book was Australasia. Kevin Parker contributed ~5% of main text and edited Table 1.

Kate Richardson
Candidate's Signature

04/08/15
Date

Doug P Armstrong
Principal Supervisor's signature

04/08/15
Date

GRS Version 3– 16 September 2011