

The value of long-term ecological research: integrating knowledge for conservation of hihi on Tiritiri Matangi Island

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Abstract: In 1995 and 1996, release of 51 hihi (stitchbird, *Notiomystis cincta*) onto Tiritiri Matangi Island (wild caught on Hauturu, Little Barrier Island) marked the start of a research and ecological restoration success story. Although establishment of populations of hihi elsewhere in New Zealand has proven to be difficult, the population on Tiritiri Matangi Island has grown to c. 150 individuals and has become one of New Zealand's few detailed case-study species. Here we review the major contributions from over 15 years of ongoing research on this dynamic species at this spectacular study location to demonstrate how behavioural ecology, molecular ecology, parasitology, and applied population ecology can inform conservation management.

Keywords: stitchbird; *Notiomystis cincta*; long-term research; behavioural ecology; population modelling; parent-offspring conflict; mating systems; genetic diversity; effective population size; disease; conservation

Introduction

Ever since we became aware that introduced predators and habitat modification were likely responsible for the loss of our dawn chorus, New Zealand has been at the forefront of conservation practice, developing translocation and predator removal skills (Wilson, 2004). However, whilst many species respond positively to the pioneering tools of predator eradication and/or translocation to predator-free sites, this has not been the case for the hihi (stitchbird, *Notiomystis cincta*). Results of earlier translocation attempts (Fig. 1) suggested that, in addition to predator removal, supportive management was necessary for the survival of most reintroduced hihi. The ongoing management of hihi reintroduced to Tiritiri Matangi in 1995 has led to a breeding population of c.150 birds in 2010 (Armstrong & Ewen, this issue). This has provided a rare opportunity for long-term research and monitoring in collaboration with the New Zealand Department of Conservation and the Supporters of Tiritiri Matangi Island.

Despite recognition of a need for an interface between behavioural research, ecology and conservation (e.g. Clemmons & Buchholz 1997; Buchholz 2007), integration of these fields has been limited (Caro 2007; Angeloni et al. 2008). Here we review these research approaches with hihi on Tiritiri Matangi to demonstrate how long-term monitoring of this population has facilitated a diverse research programme that integrates behavioural ecology, genetics, parasitology, and applied population ecology. We show how combining these approaches has provided some solutions, and stimulated further questions regarding the conservation of hihi, sometimes in unexpected ways. We discuss how these research approaches can work together with conservation management.

Translocation history

Hihi were once found throughout the northern regions of New

Zealand but, by c.1890 (after European colonisation), they became restricted to one population (Hauturu, Little Barrier Island). Conservation efforts for hihi began with attempts at reintroduction to Hen, Cuvier, and Kapiti islands during the 1980s (reviewed in Taylor & Castro 2000b). Unfortunately, however, the Hen and Cuvier populations declined to extinction and the Kapiti population could be maintained only with additional birds from Hauturu until a change in management (food supplementation) resulted in increased abundance and a higher carrying capacity (Chauvenet et al. 2012). From these several translocation attempts to largely predator-free islands, it was clear that conservation of hihi could not rely solely on the removal of exotic predators. The next translocation attempt, to Mokoia Island (1994), marked the beginning of a new approach, with associated research becoming more hypothesis-driven (adaptive management, Armstrong et al. 2007; Ewen & Armstrong 2007). This tested the main alternative hypothesis for poor hihi survival: that a food shortage was key (Lovegrove 1985; Castro 1995; Rasch et al. 1996). However, this research showed that while reproductive success was greatly improved by providing supplementary food (Armstrong & Perrott 2000; Castro et al. 2003), the type of food (sugar water or complete food supplement) and distances of females to feeders were unimportant (Armstrong et al. 2007). Supplementary food also had no effect on the low survival of adults, which was more likely caused by high densities of disease-causing *Aspergillus fumigatus* spores (Perrott 2001) and ruru (morepork, *Ninox novaeseelandiae*), a predator of hihi (Armstrong et al. 2010; Low 2010). The remaining hihi were therefore removed from Mokoia in 2002.

The reintroduction of hihi to Tiritiri Matangi, with 38 birds in September 1995 and a further 13 birds the following August has been far more successful. This reintroduction was a group effort that involved scientists from Massey University and the University of Auckland in partnership with the Department of

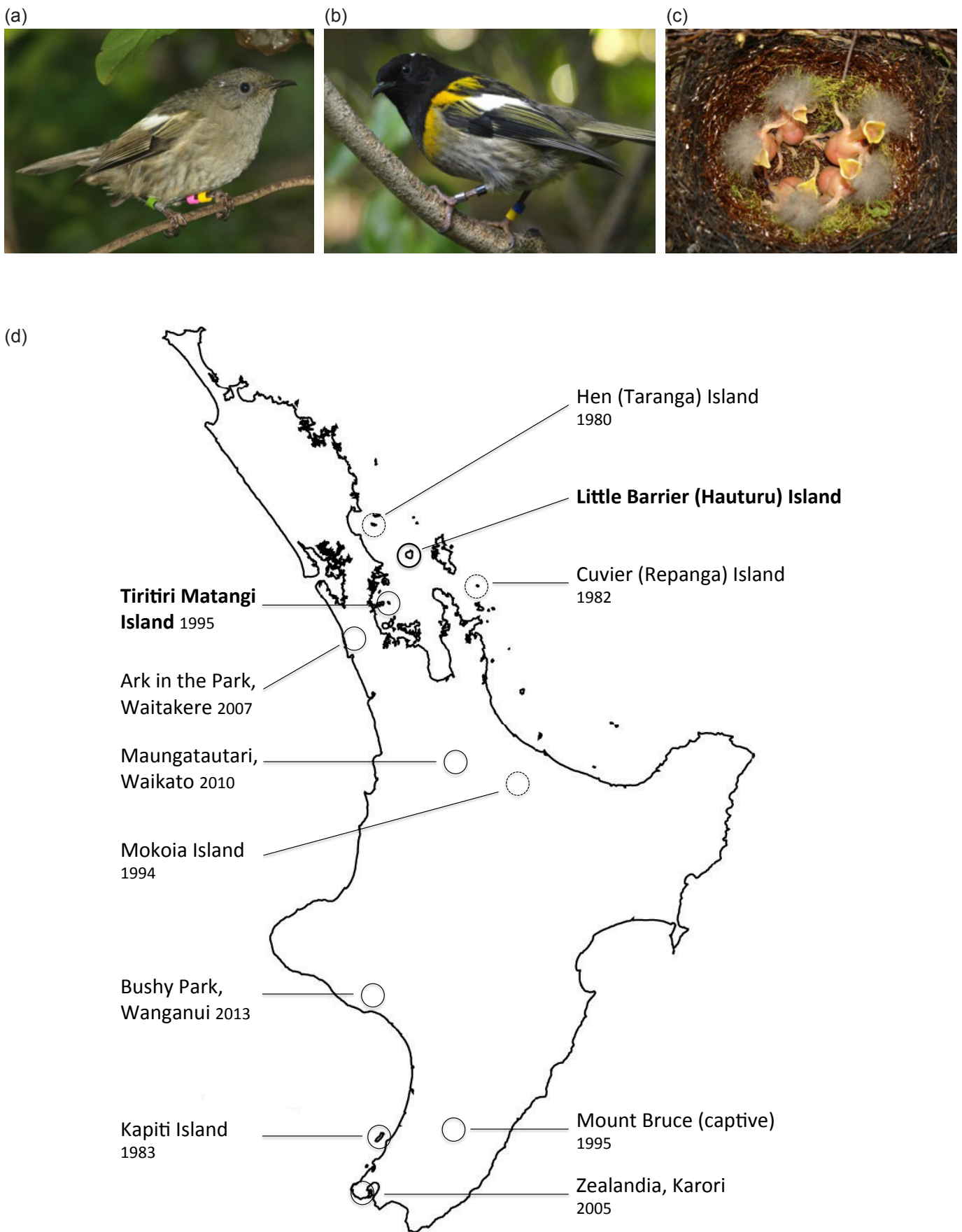


Figure 1. (a) Female (photo by Matt Gribble) (b) male (Matt Gribble) and (c) nestling (6 days old, Rose Thorogood) hihi *Notiomystis cincta*, and the (d) location and dates of first reintroduction attempts (failed sites, dashed circles). Tiritiri Matangi Island and the original source population (Little Barrier Island) for their reintroduction are shown in bold.

Conservation and the Supporters of Tiritiri Matangi, with help from Mel Galbraith and students from Glenfield College in Auckland, as well as countless volunteers. Although survival immediately after release was poor, especially in females (Armstrong et al. 2002), the long-term adult survival rate on Tiritiri Matangi has been high. The population has grown from four females in the first breeding season (1995/1996) to about 70 a decade later and has subsequently been held near this level by harvests of hihi from the island to establish populations elsewhere (Armstrong & Ewen, this issue). The supplementary feeding strategy developed on Mokoia was applied as part of the Tiritiri Matangi reintroduction. While we have never tried stopping supplementary feeding during the breeding season on Tiritiri Matangi, an on-off feeding experiment conducted in 1996 between breeding seasons (Armstrong & Ewen 2001) suggested that supplementary sugar water did improve survival in some months, and possibly at times when there is intense competition from bellbirds. This information was used as the basis for the decision to provide feeders year round. Management of the Tiritiri Matangi hihi population also relies on the provision of nest boxes which address the lack of natural cavities on the island and the management of ectoparasitic mites on nestlings in these boxes. Nest boxes are easily accessible and facilitate complete monitoring of breeding attempts, with all nestlings banded to allow individual identification (Taylor & Castro 2000a). These management features have greatly assisted our research programme, allowing detailed studies of individuals not usually possible with wild birds.

The behavioural ecology of hihi

Hihi are of great interest to behavioural ecologists because of their enigmatic behaviours. They are one of New Zealand's few sexually dimorphic and strikingly dichromatic passerines. The larger males are characterised by a black head with white, erectile ear tufts and a yellow shoulder badge, as well as piercing single, double and triple note territorial calls, whereas females are olive-brown and have more subtle vocalisations (see Higgins et al. 2001). The hihi mating system can vary from monogamy to polygynandry (Castro et al. 1996), but on Tiritiri Matangi is predominantly social monogamy with frequent extra-pair copulation attempts. These copulation attempts are often forced and, uniquely, face-to-face (see below), and they result in high levels of extra-pair paternity ($61 \pm 3\%$ of offspring within clutches, Brekke et al. 2012; Ewen et al. 1999). Dimorphism and the plasticity of behaviours hint at the different selective pressures this species has faced during its evolution, and lead us to ask why and how evolutionary conflict between and within the sexes, as well as among parents and offspring, might also impact on the success of our conservation actions.

(a) Implications of hihi mating strategies for conservation

Despite birds being used as models of monogamy and morality in religious teachings (Davies 1992), extra-pair matings are common in most avian species (Griffith et al. 2002). However, hihi are unusual in that these matings can be forced on the female by extra-pair males (Ewen et al. 2004; Low 2005b), with males using specific behaviours to overcome female resistance to mating (Low et al. 2005). Also unlike any other species documented, during mating, hihi not only copulate in the usual bird manner (i.e. the male mounts the female from behind while she stands), but can copulate face-to-face

(Anderson 1993; Castro et al. 1996). Building on Castro et al.'s (1996) pioneering work on the hihi mating system on Kapiti Island, much of our detailed understanding of the ecology of face-to-face copulation was gained through observation of the Tiritiri Matangi population. This understanding informed our ideas of their population dynamics.

Passerines, such as hihi, differ from many other animal groups in that males do not possess a penis. This has consequences for copulation efficiency; primarily because the lack of a penis makes it extremely difficult for a male to inseminate a female without her co-operation. Thus, it has been proposed that forced copulation should be anatomically impossible in passerines (Briskie & Montgomery 2001). Despite this, virtually all observed extra-pair copulations on Tiritiri Matangi involved male force and female resistance (Low 2005b) and yet extra-pair males appear to be quite successful at inseminating females (Ewen et al. 1999; Brekke et al. 2012). So how do male hihi manage to force females to copulate? The answer lies in their unique face-to-face copulation position and their timing of forced copulations. Male hihi have solved the problem of requiring female co-operation through a behavioural innovation; by flipping the female onto her back and lying facedown on top of her (illustrated in Castro et al. 1996). But face-to-face copulation raises the question of how the male orients his backwards-facing cloaca to allow sperm transfer (non-avian species with face-to-face sex solve this problem when the male gets an erection). To answer this, we measured the size and orientation of male cloacae at different times of the year. The breeding cloaca of male hihi turns out to be an excellent example of convergent evolution; male hihi store excess sperm behind the cloaca during the breeding season. This effectively rotates the cloaca forward so that it can function like an erect penis for sperm transfer (Low et al. 2005).

But how do males know when females are fertile and time their copulations accordingly? To answer this we took advantage of the supplementary feeding regime on Tiritiri Matangi and placed digital scales near these feeders to record the daily weight of all birds during a three-month period. Male interest in females coincided exactly with the significant weight gain of females prior to egg-laying; thus, male hihi appear to be able to assess female fertility based on changes in the female's body shape or flying ability (Low 2004). When a female is fertile, extra-pair males will leave their own partners (unpaired males can also be involved; Ewen et al. 1999) and encroach into the territory of the fertile female in an attempt to copulate with her. Spectacular chases end with the female being held to the ground. On Tiritiri Matangi these chases could involve up to seven extra-pair males, with the resident male attempting to keep them away from his mate (Low 2005b). Because of this, the resident male is forced to change his territorial defence from one which is centred on the nesting site (Ewen et al. 2004) to one which is flexible and centred on the location of the female (Low 2005a).

These interactions suggest that this mating strategy could be physically costly to both sexes. For example, females can be injured during forced copulation (Castro et al. 1996) and high levels of harassment by males interfere with their feeding and foraging during egg formation (Low 2008). During chick rearing, males may temporarily abandon their brood-feeding duties if a female in the local area is fertile (Low 2005b; Low et al. 2006). Fledglings may be subject to harassment from extra-pair males (Ewen and Armstrong 2002) because they resemble fertile females (Low 2004). Resident males also pay increased costs from this strategy. During their mate's

fertile period, the resident male loses almost as much weight in defending her from other males as he does during chick rearing (Low 2006). However, this strategy seems to be evolutionarily stable (Low 2005b), as these behaviours do not seem to have any negative consequences on population growth (Ewen et al. 2011, see below).

(b) Parents and their young – evolutionary conflict is mediated by carotenoids

Determining what enables successful breeding has long been a goal for hihi conservation (Rasch et al. 1996; Taylor et al. 2005), and behavioural ecology, more generally. Behavioural ecology views parents and their offspring in an evolutionary battle over investment (Krebs & Davies 1997). Parents have limited resources to allocate among members of their current brood and to future reproductive attempts; however offspring are selfish and prefer more care than parents are willing to give (Trivers 1974). How has evolution acted on parents and their young to ensure reproductive success? Our research on Tiritiri Matangi has aimed to tease apart the relationships among diet, health, and the behaviour of nestlings and their parents, to simultaneously address the needs of conservation and to test behavioural ecology theory (e.g. Ewen et al. 2006c; Ewen et al. 2008; Ewen et al. 2009; Thorogood et al. 2008; Thorogood et al. 2011).

Our focus is on the interaction between carotenoid biomolecules in the diet and the behavioural responses of parents and nestlings. Carotenoids are dietary components that animals cannot make themselves but which have two important physiological roles; as a contributor to the immune system (Costantini & Møller 2008), and by providing the pigments for yellow, orange and red coloured tissues (McGraw 2006). Therefore, carotenoids make a good candidate for assessing the importance of habitat quality and disease risk at an individual level. First, we manipulated carotenoids availability to adults during the breeding season. We hypothesised that carotenoids in the diet of adults and nestlings could be important for resistance to disease (see below), and furthermore, because carotenoids are the main constituent of egg yolk (Blount et al. 2000), that parents would be faced with a decision over how to allocate these resources among their nestlings and themselves. We found that mothers given feeders with carotenoid-supplemented sugar water invested these carotenoids into their egg yolks (Ewen et al. 2006c), and that adults supplemented during chick rearing also passed on these extra carotenoids to their young via feeding (Ewen et al. 2008). We next asked how carotenoids altered nestling behaviour, and whether variation in carotenoid levels shaped parents' responses.

When nestling birds are begging, one of the most striking aspects of their display is their wide open, brightly coloured mouth. However, compared with postural and vocal begging behaviours, this colouration has been largely overlooked (Kilner 2006). Due to technological advances in spectrophotometry, we can now study this colour objectively, and understand how mouth colouration relates to the environment and how it might signal information about nestlings to parents. By manipulating carotenoids, we provided clear experimental evidence for a long-standing yet inadequately-tested hypothesis that mouth colour is carotenoid-based (Thorogood et al. 2008). By supplementing nestlings independently from their parents, these carotenoid experiments also showed that parental responses to chick mouth colour depend on their own carotenoid environment (Thorogood et al. 2011).

Parents with more carotenoids may signal their health and

capabilities to their respective partners, encouraging them to invest more (see Hill & Montgomerie 1994). Or, they may hold on to these resources for a second breeding attempt, ignoring the demands of their current brood. Although hihi on Tiritiri Matangi often lay second clutches, the chicks have much poorer survival within the nest than those in first clutches. If second clutches do fledge, however, they are just as likely to survive to adulthood (Low et al. 2007a). Parents supplemented with carotenoids were more likely to lay a second clutch and to ignore their current brood's increased mouth colour. But parents unlikely to lay a second clutch (i.e. control parents) were encouraged to feed more if their nestlings showed more intense carotenoid-coloured mouths (Thorogood et al. 2011). Such flexibility in parental provisioning rules has not been demonstrated before, and is a major step forward in solving the puzzle of parent-offspring conflict (Kilner & Hinde, 2012).

The positive effects of carotenoids on nestling development, however, are not straightforward (e.g. Ewen et al. 2009) and may depend on variation in other components of their diet (Walker et al. 2013a). Therefore, understanding how carotenoids interact with the behaviour and productivity of wild birds like hihi remains limited by a lack of knowledge of natural carotenoid variability. Hihi are well-suited to providing the solution, and future work will continue to integrate manipulations of the environment with assessment of behavioural responses. We now have a much better understanding of the link between food and parental care, so future work will examine how environmental variation affects how hihi attract mates. What does the carotenoid-based yellow shoulder plumage of males signal to females (Ewen et al. 2006c), for example, and how does this tie in with variation in their carotenoid-environment (Walker et al. 2013b). Hihi on Tiritiri Matangi make a fantastic model system with which to solve these behavioural ecology puzzles.

Molecular ecology – genetic management and reintroduction

Has the evolution of the behaviours described above influenced the genetic diversity of the Tiritiri Matangi hihi? Genetic diversity is predicted to be low in hihi because the remnant population is restricted to a small offshore island and each translocation represents a population bottleneck (Brekke et al. 2011). Small populations like these are expected to experience an erosion of genetic diversity over time, because genetic drift occurs at a rate proportional to population size (Keller et al. 2011). The founding bottleneck in Tiritiri Matangi's hihi population was severe. Of the 51 individuals from Hauturu released onto Tiritiri Matangi in 1995 and 1996, only 12 males and four females contributed to the gene pool. To understand the impact of this reintroduction bottleneck on the genetic diversity of this small and isolated population in the long term, we have measured genetic variability at a large number of neutrally-inherited microsatellite loci.

First, we compared the genetic diversity of hihi from Hauturu and Tiritiri Matangi (Brekke et al. 2011). Most other New Zealand endemics that have been through similar reintroduction bottlenecks show low genetic diversity (Jamieson 2009). That is, they exhibit low variation at the level of individual genes (most often inferred from 'neutral markers', genes which are not under natural selection). A loss of genetic diversity is important because it can limit a species' ability to adapt to change (Keller et al. 2011). However, hihi on Tiritiri Matangi showed no decrease in genetic diversity when compared with the Hauturu source population, which itself

displayed higher genetic diversity than expected (Brekke et al. 2011). To explain this, we compared the effective population size (N_e), the number of individuals contributing to the gene pool, with the actual population size, known from our intensive biannual census counts. Our knowledge of the age of every hihi on Tiritiri allowed us to use new, more accurate methods to calculate an N_e of 111 for the 2006/2007 breeding season (Wang et al. 2010). In conjunction with the census population size (N_c) of 163, this gave an N_e/N_c ratio of 0.68 (Wang et al. 2010). This ratio is remarkably high for a bottlenecked population of an endangered species since meta-analyses give an average estimate of N_e/N_c of 0.1 (Frankham et al. 2002). For hihi, this means that reproductive variance is low; a large proportion of the population contributes their genes during each breeding season and this helps slow the loss of genetic diversity. Nevertheless, there has been a loss of alleles and significant population divergence (F_{ST}) when compared with the remnant population on Hauturu (Brekke et al. 2011). This is important because losing alleles that occur in low frequency in source populations may reduce a population's adaptive potential, making the reintroduced population less able to cope with a changing environment and stochastic events such as disease outbreaks (Frankham et al. 2002).

Second, we looked at the genetic implications of inbreeding in hihi. In a small and isolated population like that on Tiritiri Matangi, the chances of encountering and mating with relatives are much increased, leading to higher rates of inbreeding. This can have negative consequences as it leads to a reduction in allelic diversity of genes. Individuals are more likely to be homozygous for recessive deleterious alleles or they lose any advantage of heterozygosity (Jamieson 2009). One consequence of this may be hatching failure and developmental abnormalities (Briskie & Mackintosh 2004). On Tiritiri Matangi, there is an average (\pm S.E.) hatching failure of $24.8 \pm 2.7\%$ in hihi (Thorogood & Ewen, 2006) which is almost three times higher than most outbred populations (Koenig 1982; Briskie & Mackintosh 2004), and anomalies such as twinning have occurred (Thorogood & Ewen, 2006). When the inbreeding values of unhatched eggs from one breeding season were analysed, male embryos that failed to hatch were found to be much more inbred than females, suggesting that males are more susceptible to the impacts of inbreeding (Brekke et al. 2010).

However, the behavioural ecology of hihi may act to mitigate the prevalence of negative genetic consequences caused by reintroduction bottlenecks. Recent research has shown that the strategy of extra-pair matings can maintain the lower than expected variance in reproductive success identified with the N_e/N_c ratio (Castro et al. 2004; Wang et al. 2010; Brekke et al. 2011). Analysis of extra-pair paternity among Tiritiri Matangi's hihi revealed that although females chose closely-related social mates, when it came to fertilisation of extra-pair offspring, this occurred with less-related males than expected if mating were random with respect to relatedness (Brekke et al. 2012). Whether this is the result of behavioural strategy, post-copulatory control of fertilisations by females or genetic compatibility remains to be determined. However, care must still be taken that re-introduction bottlenecks do not lead to a decline in the long-term fitness and viability of the population. One potential solution that we are exploring is to adopt a programme of artificial gene-flow between populations (Brekke et al. 2011), as initiated in 2010.

Our genetic research has also highlighted the species' importance for conservation at the taxonomic level. Hihi

were originally classified by Du Bus (1839) as part of the Melaphagidae (of which the other two predominantly nectarivorous species in New Zealand, tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*), belong and with whom hihi compete for food (Craig 1985)). However, support for hihi as a honeyeater has long been questioned, even by Du Bus whose type description acknowledged unusual facial whiskers more typical of insect specialists. Research using molecular samples from Tiritiri Matangi hihi, amongst others, allowed Ewen et al. (2006a) to show that hihi are more closely aligned with New Zealand's wattlebirds (Callaeidae) than with honeyeaters. This was corroborated by an independent research group (Driskell et al. 2007) who suggested altering the classification to create an endemic bird family, the Notiomystidae for the hihi, of which they would be the sole representative. The results from these two studies clearly showed that hihi have had a long relationship with New Zealand and, as Driskell et al. (2007) pointed out, this adds heat to a biodiversity hotspot and raises the profile of hihi as a species that demands conservation intervention due to its evolutionary distinctiveness.

Parasitology and health – implications for conservation

The genetic diversity of hihi on Tiritiri Matangi may also have implications for their resistance to disease and pathogens. The health of hihi has not escaped the detailed attention of both managers and researchers on Tiritiri Matangi. This is understandable given the problems encountered in the Mokoia Island reintroduction and the fact that pathogens (both macroparasites and microparasites; Hudson et al. 2002) are increasingly cited as major threats in conservation (Daszak et al. 2000; Cleaveland et al. 2002; Tompkins & Poulin 2006). Pathogens in hihi across all populations and in captivity have received some attention (Alley et al. 1999; Cork et al. 1999; Alley & Twentymen 2004), with necropsies of recovered hihi carcasses (older than three weeks of age) currently numbering about 260 individuals collected since 1991 (Ewen et al. 2012).

One widespread pathogen affecting hihi is *Aspergillus fumigatus*, which is a common fungus in the environment. It is often linked to mortality both in captivity and the wild (24% of all necropsy reports; including individuals from Tiritiri Matangi; Ewen et al. in press) as it can cause the disease aspergillosis, giving rise to respiratory problems. Gross lesions form in the respiratory tract. These usually consist of large fungal granulomas in the lung or thoracic air sacs (Alley et al. 1999). In most species, this disease occurs in otherwise immuno-compromised individuals (Alley et al. 1999). Spore counts are higher in more disturbed habitats and may lead to increased exposure (Perrott 2001). The high spore counts on Mokoia Island were hypothesized to account for the low adult survival rate there (Armstrong & Perrott 2000; but see Low 2010 and Armstrong et al. 2010 for discussion of alternative hypotheses). Infection status is currently difficult to assess in living hihi, making detailed study of this pathogen at the host-population level difficult. During translocation, however, *A. fumigatus* is a primary target of preventative medication during quarantine (Ewen et al. 2012).

The intensive monitoring of hihi on Tiritiri Matangi means that observers are more likely to notice and record health problems. For example, a parasite that has had a measurable population-level impact is *Salmonella enterica* serotype Typhimurium DT195 (Ewen et al. 2007). In February 2006, an outbreak of this pathogen caused an estimated mortality of 26% of the adult hihi on Tiritiri Matangi (Ewen et al. 2007).

This strain of *Salmonella* had not been recorded previously in any wild or domestic bird species in New Zealand. Such a novel and highly virulent pathogen highlights the risks of some pathogens in wildlife conservation. Furthermore, the alternative host species that brought about contact with susceptible hihi remains unknown. Generalist pathogens that can spill into susceptible and novel alternative hosts require heightened caution in species conservation. The impact this salmonella strain can have means it remains a key pathogen screened during the quarantine phase of hihi translocations.

Hihi on Tiritiri Matangi have also provided the opportunity for detailed observation of two common health conditions in the species. The first, sub-lingual oral fistulas are lesions in the oral-cavity floor that become most noticeable when the bird's tongue protrudes through it. Protruding tongues can become extremely long, curling round beneath the mandible (Castro & Taylor 2001; Low et al. 2007a). This condition is rare in birds, being first described in hihi and subsequently in sooty terns (*Onychoprion fuscata*) breeding on Ascension Island (Reynolds et al. 2009). Low et al. (2007b) found that approximately 10% of adult hihi on Tiritiri Matangi had some form of sub-lingual lesions, but these were not present in nestlings.

The cause of the lesions remains unknown, but it appears that they have no negative impact on the birds except for sometimes changing a bird's foraging behaviour when its tongue protrudes. Affected birds have a higher dependence on supplementary feeders and perhaps this is the reason that the lesions are not fatal. A second condition is a progressive feather-losing dermatitis probably caused by ovoid burrowing mites identified as *Knemidocoptes* spp. (Low et al. 2007c). Males are more likely to suffer dermatitis than are females and the condition presents during the breeding season. Again, this affliction has no noticeable impact on survival or condition (latter measured only in females) (Low et al. 2007c).

Some parasites, however, do cause problems for hihi. During the first breeding season on Mokoia Island, bloodsucking mites (*Ornithonyssus bursa*) reached numbers sufficient to kill some hihi broods. Subsequently, nest boxes were cleaned and artificial nests were provided when mite infestations approached these levels, but it was estimated that broods not subject to intervention would have had a 29% (S.E. 9%) probability of being killed (Armstrong et al. 2007). Nests on Tiritiri Matangi have therefore also been similarly managed to prevent high levels of mite infestation. To test the effectiveness of this intensive management, we performed an experiment during the 2005/06 breeding season on Tiritiri Matangi. If nests were left untreated, the probability of fledging was reduced by 31% (S.E. 13%) (Ewen et al. 2009) and the experiment also showed that mites reduced the growth of nestlings. However, maternal investment of carotenoids into the yolks of the eggs was able to buffer nestlings from these negative effects. This research provides a rare example of how a healthy diet is important to cope with common parasites in wild bird populations.

Population ecology and experimental management

Perhaps the most important implication of our research programme is our ability to combine information and predict future population growth under different environmental and population scenarios. Despite the many fascinating complexities of hihi on Tiritiri Matangi, their population dynamics to date have been quite straight forward. Because females undertake most of the reproductive effort in hihi, it has

been reasonable to assume that females are the limiting sex, and therefore their population dynamics can be described by a simple female-only model. Also, we do not need to worry about immigration and emigration to and from the island, as there are no hihi in the surrounding area and emigration appears unlikely (no emigrants have ever been detected).

Population dynamics are therefore determined by four parameters: number of young fledged per female per year, juvenile survival probability (probability of surviving to the breeding season), probability of a surviving juvenile being female, and annual survival probability of adult females. In many populations these parameters are subject to complex age dependence, they may vary dramatically over time and space and among individuals, and are subject to density dependence which is often very difficult to model.

In contrast, the only important age effect in hihi is the difference in reproductive rate between first-year and older females (Armstrong et al. 2002; Armstrong et al. 2007; but see Low et al. 2007a for additional subtle differences among other age classes). Annual variation in survival is modest on Tiritiri Matangi (Armstrong & Ewen, this issue), and individual variation is also sufficiently subtle to be unimportant to population dynamics. We have not detected density dependence in survival, and very subtle density dependence in reproductive success was detected only after 12 years (Ewen et al. 2011). Given the growth of the population, the lack of density dependence is presumably because the number of sugar-water feeders has increased as the population grows.

Since 2005, we have taken an annual harvest of 50–80 hihi (mostly juveniles), except for 2006 and 2012 when translocations were delayed for a year due to the *Salmonella* outbreak. Harvest rates were designed to maintain the Tiritiri Matangi population at 70–80 females, based on predictions of a stochastic population model constructed from the following parameter estimates. Based on data collected from 1996–2004, we obtained estimates (and standard errors) for the population as follows: 2.27 (0.23) and 3.46 (0.21) fledglings per year for first-year and older females respectively, 0.43 (0.02) juvenile survival probability, 0.5 probability of a surviving juvenile being female, and 0.69 (0.03) annual adult survival probability. Combining these into a Leslie Matrix gave a finite rate of increase of 1.30 (0.06), meaning the population grows at about 30% per year once the ratio of first-year to older females stabilises. So far, these predictions have been quite reliable (Armstrong & Ewen, this issue), suggesting we have a reasonable understanding of the population's dynamics.

As a first step to incorporating our detailed knowledge of hihi behavioural ecology into our population model, we modelled the effects of sex-ratio biases and the implicit male harassment of females on the population dynamics of Tiritiri Matangi's hihi (Ewen et al. 2011). Interestingly, these models showed no evidence that a male-biased sex ratio reduced female survival or the number of fledglings produced per female. Our next step is to incorporate the results of our other experiments into this population model. It will be useful to model the effects of relaxing mite control and the provision of sugar water, for example, especially if the current demand for harvesting the population discontinues. There is also great potential to construct alternative population models to assess the sensitivity of predictions to changes in model assumptions and complexity. In particular, it will be important to incorporate the estimated inbreeding depression (see above) into the model to assess the effect on long-term projections.

Looking to the future

Behavioural ecologists have been criticised for working with endangered animals simply to tap into alternative funding sources, and that behavioural ecology rarely contributes to conservation (Caro 2007; but see Buchholz 2007). However, our research programme with hihi demonstrates that behavioural questions can help conservation management, and conservation of species can aid the answering of behavioural questions, meaning that here both approaches are vital and mutually beneficial. For example, from behavioural research, we know that carotenoid availability in the environment alters parents' responses to the carotenoid-mediated displays of their young, and also the success of those young at dealing with nest mite infestations, a direct conservation problem. Whilst carotenoid supplementation is unlikely to be the panacea for hihi translocations, it does highlight the importance of considering the environment on a finer, biochemical scale, and the next step will be integrating this information into management decisions. In-depth studies of hihi mating behaviours suggested that aggressive encounters between males and females may have impact on the growth of populations. However, later population modelling has shown this to be less than straightforward, and may possibly provide information for conservation management plans regarding sex ratios in future bird translocations.

Studying endangered species is also of importance for behavioural ecology. Too often, empirical tests of theoretical behaviour are limited to a few common species, to ease data collection and allow large sample sizes. However, this limits knowledge of the applicability of these theories, mostly to species in the Northern Hemisphere. Our research programme on hihi has improved scientific understanding of the interactions between the environment and life-history strategies from parent-offspring conflict theory to the role of extra-pair paternity in determining mating systems and female choice. We intend to continue this research programme in the future by further developing models for understanding population growth dynamics, as well as continuing with our attempts to disentangle the relationships among health, environment, and reproductive success.

Finally, Caro (2007) suggests seven steps towards better integration of behavioural research with conservation. Amongst these, he recommends that research should be used to raise species' profiles and capture the public's attention. We are fully committed to increasing hihi advocacy. Our research has received substantial media exposure (see www.hihiconservation.com/media) which improves recognition of the species nationally and internationally in both the academic and lay communities, and increases chances for attracting sponsorship and funding for hihi conservation initiatives. As hihi have been so closely monitored on Tiritiri Matangi since the population's inception, we have a valuable resource in this long-term dataset which we hope will continue to benefit hihi and their conservation, as well as fundamental and applied science in general.

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