The impacts of translocation on the cultural evolution of song in the North Island saddleback or tīeke (*Philesturnus rufusater*)

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Ka mahi ahau i te whare o te tīeke

(I am making a saddlebacks nest)

Photo: Martin Sanders

Ka whakarongo ake au
I te tangi a tōna waituitui
E rere runga rawa e
tui tui tuituia
Tuiā i runga
Tuiā i raro
Tuiā i roto
Tuiā i waho
Tui tui tuituia
Kua tū
Kua tau
Kua oti
Te whare tā tīeke
Tihei mauri ora

(*I am made peaceful*
by the harmonics of his binding song
Resonating up on high
Weaving, binding, stitching
Uniting what is above
with what is below
Connecting the internal
with the external
Weaving, Binding, stitching
It has been Erected,
It has been Bestowed,
It has been made complete
The sacred home of Tīeke
Indeed it is the vital essence of life abundant issuing forth)

Poem and translation by Zack Bishara

Abstract

The IUCN (1987) defines a translocation as a release of animals with the intention of establishing, re-establishing, or augmenting an existing population. The origins of translocation practise are very much in applied conservation management. However, translocations also provide other outputs. They provide a means by which the general public might connect and commit to conservation and they provide unique opportunities for scientific research because the age and source of founder populations are completely known. Geographical isolation plays a crucial role in speciation events. Thus studies of divergence of behavioural signals in isolated populations have been critical to understanding how barriers to gene flow develop. Bird song is a vital conspecific recognition signal (CRS) and many studies have demonstrated significant geographical variation in song with several hypotheses posed to explain this variation. However, a key problem in testing these hypotheses is an inability to measure the pace of song divergence. This is because the timing and source of founder events are rarely detected. Here I use the NI saddleback or tīeke (*Philesturnus rufusater*) isolated on a single island in 1964 but subsequently increased by translocation to 13 island populations, to show that significant geographical variation in song can develop in less than 50 years. Furthermore, my data shows a clear signal of serial population bottlenecks (up to 3 times) following translocation and supports both bottleneck and cultural mutation hypotheses in explaining this variation. Critically NI saddleback discriminate between songs from different islands and this discrimination might lead to an eventual reduction in effective population size. This illustrates the potential for human induced founder and isolating events, including conservation management, to be microevolutionary events and challenges us to consider the implications of conservation biology in an evolutionary context.

Preface

There is considerable geographical variation in communication signals between many populations of animals including humans and other primates, cetaceans, insects and amphibians. However, this variation is most evident in birds (Podos & Warren, 2007), particularly amongst the passerines which comprise almost half of all bird species (Fitzpatrick, 1988). Thus, geographical variation in bird song has attracted enormous research effort in documenting where it exists, how it might develop and why it is biologically significant (Podos & Warren, 2007). Bird song is of particular interest to evolutionary biologists and behavioural ecologists because it is a fundamental biological signal for defending resources, recognising conspecifics and choosing a mate (Catchpole & Slater, 1995; Podos & Warren, 2007). Furthermore, geographical isolation facilitates the development of behavioural barriers to gene flow between isolated populations of the same species (Darwin, 1871 ; West-Eberhard, 1983; Foster, 1999). Therefore, studies of divergence of behavioural signals, along with ecological factors and genetics, have been critical to understanding how barriers to gene flow develop (Grant & Grant, 1997; Slabbekoorn & Smith, 2002; Edwards et al., 2005; Phillimore et al., 2006; Price, 2008).

Several explanatory hypotheses have been proposed to explain geographical variation in bird song through the interaction of song learning mechanisms and isolation (Podos & Warren, 2007). The causal factors supporting these hypotheses tend to be either 1) short term or 2) long term. A critical short term factor is likely to be founder events, i.e. when dispersing individuals from an established population start a new population at a new location (Baker & Jenkins, 1987; Baker et al., 2003; Baker et al., 2006). The effect of this founder event will be relative to the size of the established population, the song diversity existing within it and the number of dispersers. If a small number of founders disperse from a very large established population that contains a great deal of song diversity there might be a bottleneck effect, i.e. the dispersing birds will only carry a small sample of the song diversity that is present in the established population to the new location. Conversely, if the established population is small or contains little song diversity, or if a large number of birds disperse, the effect of this bottleneck will be less apparent because the founders will carry much of the song diversity with them to the new location. This is analogous to the loss of genetic variation following founder events (Briskie & Mackintosh, 2004). In both cases the diversity of the founding population (the “neck” of the “bottle”) relative to the established population (the “bottle”) is critical in determining the song or genetic diversity of the new population, although the sex ratio and age composition of the founding population might also be important factors.

Long term effects that potentially generate geographical variation in bird song are more varied. Many bird species learn their songs from conspecifics (Catchpole & Slater, 1995; Podos & Warren, 2007; Price, 2008). However, learning errors can occur when songs are not accurately copied. This process of cultural mutation or drift provides a mechanism by which song diversity might change over time (Jenkins, 1977; Podos & Warren, 2007). This change might be neutral in large established populations but the effect is likely to be greater in small isolated populations. Genetic drift might also lead to song divergence in isolated populations (Podos & Warren, 2007). For example, syrinx mass is correlated with vocal frequencies and if genetic drift alters syrinx mass within a given population it is likely that frequency range will also shift (Podos et al., 2004). Selection pressures can also lead to geographical divergence in song. Cultural selection occurs when certain songs are favoured over others because they are more effective for communication (Podos & Warren, 2007). In several species cultural selection has been implicated as habitat dependent (Catchpole & Slater, 1995; Patten et al., 2004; Slabbekoorn, 2004) as low frequency slow songs are more effective in forested habitats while high frequency fast songs are favoured in open habitats (Catchpole & Slater, 1995). In Galapagos finches natural selection acts on bill morphology due to food availability and interspecific competition (Grant & Grant, 2008). This in turn constrains beak gape and vocal tract configurations during vocal production and as beak size increases trill rates and frequency bandwidths decrease (Podos, 2001; Podos & Nowicki, 2004; Huber & Podos, 2006). Sexual selection predicts that elaborate or complex songs, those that challenge developmental or performance capabilities and songs that enhance male-male communication will be favoured in some populations, particularly by females (Podos et al., 2004; Price, 2008). These sexually selected traits can vary widely between populations and might also result in geographic divergence in song (Podos & Warren, 2007).

An intimate knowledge of song development and population history is clearly invaluable in teasing apart the various mechanisms that can influence geographical variation in bird song. While the mechanisms of song development have been described for many species (Catchpole & Slater, 1995) population history is often difficult to discern. In continental populations varying levels of dispersal and immigration between populations, often over vast geographical distances, complicate resolution of population history. Isolated island populations offer valuable opportunities for research (Baker & Jenkins, 1987; Baker et al., 2006) but founder events are still rarely detected (Clegg et al., 2002; Baker et al., 2003; Brunton et al., 2008). In contrast, translocated populations of birds offer unique opportunities for studying evolutionary processes (Parker, 2008), such as the development of geographical in song, because detailed records are kept of the size, source and age of founding populations (Lovegrove, 1996; Hooson & Jamieson, 2003).

My study species, the North Island saddleback or tīeke Philesturnus rufusater, provides an ideal model system for studying the evolution of geographical variation in song. The NI saddleback is an ancient passerine in the family Callaeatidae (Holdaway et al., 2001). Anthropogenic factors reduced the NI saddleback to a single population of approximately 500 birds on Hen Island, New Zealand, by 1910. Although common on that island, the single population was vulnerable to extinction so a series of successful conservation translocations were initiated in 1964 (Lovegrove, 1996; Parker, 2008). Each translocation induced bottleneck was severe with an average of 43 birds (range = 20-146, N = 15) translocated from donor populations estimated at 500-1000 birds at the time of translocation. These bottlenecks were further accentuated by variable post-release survival of translocated birds (mean = 56%, range 41-79%, N = 5) (Parker & Laurence, 2008). There are currently 15 populations of NI saddleback, including the natural population on Hen Island, a single population on Coppermine Island established through natural dispersal from nearby (c. 150 m) Whatupuke Island (Newman, 1980) and 13 populations established through translocation (see Figure 1, Chapter 1). NI saddleback are weak fliers incapable of crossing water gaps > 250 m (Newman, 1980) and with the exception of Coppermine and Whatupuke Islands there is no natural dispersal between any of the populations. Furthermore, DNA analysis indicates that even the population on Coppermine was founded by a small number of founders (Lambert et al., 2005), suggesting that dispersal between the two islands is a rare event.

NI saddleback are a particularly vocal species with three main categories of calls; loud chatter songs that are given by both sexes, sexually dimorphic quiet calls and male rhythmical song (MRS) (Jenkins, 1977; Higgins et al., 2006). The evolution of MRS is the focus of the work presented in this thesis as it is used for territorial advertisement, defence and mate attraction (Jenkins, 1977). Critically, MRS is a culturally transmitted signal that young male NI saddlebacks learn from their contiguous neighbours when they acquire a territory (Jenkins, 1977). However, this process of learning MRS from neighbouring birds is not always accurate and changes in MRS can occur through learning errors, a process Jenkins (1977) referred to as cultural mutation.

Jenkins (1977) pioneering work identifying both the mode by which MRS is learnt and the evolution of new songs through cultural mutations was largely confined to a single population of NI saddlebacks on Cuvier Island. However, the processes Jenkins (1977) identified might also influence the evolution of NI saddleback song at a metapopulation level. In this thesis I exploit the detailed knowledge of NI saddleback population translocation history (essentially "forced" dispersal events; see Figure 1, Chapter 1) along with information on song learning mechanisms to address questions around the evolution of geographical variation in bird song. In particular I address how geographical variation in song might develop in NI saddleback and how this variation might manifest itself from both evolutionary and conservation biology perspectives. Furthermore, I predict that both the short term founder effects following initial translocation and subsequent population level cultural mutations provide a means by which geographical variation can develop between translocated island populations of NI saddleback.

Thesis outline

The primary aim of the thesis I present here is to use translocated populations of North Island (NI) saddleback or tīeke to investigate questions around the evolution of geographic variation in bird song. However, in describing the suitability of translocated systems for scientific research I also place translocation in a broader societal context. Therefore, while the cohesive theme of the thesis is based on translocated populations of NI saddlebacks each chapter is written as an independent scientific paper. This approach leads to inevitable repetition but this has been minimised where possible through reference to other chapters. The great majority of the work presented here is my own but four of the six chapters include input from others that warrants co-authorship. Their respective contributions are acknowledged below. The NI saddleback has generally been considered a subspecies (*Philesturnus carunculatus rufusater*) of the New Zealand saddleback but following work by Holdaway et al (2001) is increasingly cited as a full species (*P. rufusater*). I follow Holdaway et al (2001) throughout the thesis in referring to the NI saddleback as a full species, and add additional support to this conclusion in Chapter 5. The thesis structure is as follows:

Chapter One: This chapter uses translocated populations of NI saddlebacks as a case study to describe the multiple benefits that can accrue from translocations. The origins and motivation for modern translocations have their basis in applied conservation management and the process of creating new populations has obvious conservation outcomes. However, translocated systems also offer unique and invaluable research opportunities, particularly for evolutionary questions, because detailed records of the size, source and founding composition of translocated populations are usually available. The translocated populations of NI saddleback described in this chapter form the basis of subsequent investigation in this thesis. Finally, translocations provide a unique advocacy opportunity in that the general public can be involved in planning, implementation and post release monitoring. This aspect of the chapter might seem out of place in what is ostensibly a scientific thesis. However, it is not enough, for me at least, to only investigate purely scientific questions. As a field biologist I have a responsibility to contribute wherever possible to the conservation of biodiversity. Translocations achieve this by facilitating public participation in applied conservation and providing an outlet for communicating the scientific investigations that often accompany them. This chapter has been published as:

Parker, K.A. 2008. Translocations: Providing Outcomes for Wildlife, Resource Managers, Scientists and the Human Community. Restoration Ecology 16: 204-209.

Chapter Two: This key chapter demonstrates that significant geographic variation in song can rapidly develop through cultural evolution following conservation translocations. It is written in the concise form of a general science journal (e.g. Nature, Science, Current Biology, PNAs) and includes the following co-author contributions; I designed the sampling regime, conducted the field work, analysed the data and wrote the chapter with contributions from Marti J. Anderson, Peter F. Jenkins and Dianne H. Brunton. Marti J. Anderson (Massey University) provided significant guidance and input to the statistical analyses. Peter F. Jenkins collected the historical Cuvier data included in the analyses. Dianne H. Brunton conceptualised the project following the initial work of Peter F. Jenkins and also participated in field work.

Chapter Three: This chapter describes a translocation of NI saddleback from Tiritiri Matangi Island to Motuihe Island. This translocation has provided the outputs described in Chapter 1; it has created a new population of NI saddleback, there was significant community participation in all aspects of the translocation and it has subsequently been used for the playback experiments that are the subject of Chapter 4. I led the translocation, the post-release monitoring and wrote the chapter. My co-author, John Laurence, leads the restoration of Motuihe Island through the Motuihe Restoration Trust which planned, funded and facilitated the translocation. This chapter has been published as:

Parker, K.A. and J. Laurence, 2008. Translocation of North Island saddleback *Philesturnus rufusater* from Tiritiri Matangi Island to Motuihe Island, New Zealand. Conservation Evidence 5: 47-50.

Chapter Four: This chapter uses a playback experiment on the Motuihe population described in Chapter 3 to test the impacts of the divergence of song amongst translocated populations described in Chapter 2. I designed the experiments, carried them out, analysed the data and wrote the paper with input from my co-authors Mark E. Hauber (City University of New York) and Dianne H. Brunton. This chapter has been published as:

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

Chapter Five: This chapter assesses the role of vocalisations, morphology and mtDNA in defining the relationship between the NI saddleback and the closely related South Island (SI) saddleback (*Philesturnus carunculatus*). I collected all of the NI saddleback data used in the chapter, conducted all of the vocalisation and morphological analyses and wrote the chapter. Karen Ludwig (University of Otago) recorded the SI saddleback vocalisations. Ian J. Jamieson (University of Otago) and Tania King (University of Otago) collected the SI saddleback blood samples and conducted and interpreted the mtDNA analyses. These co-authors, along with Dianne H. Brunton, provided essential feedback whilst writing the chapter.

Chapter Six: This chapter draws general conclusions from the data presented in this thesis and speculates on the future role of song in isolated populations of translocated NI saddleback.

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As a child in the late 1970s and early 1980s I loved nature documentaries particularly the Wild South series by the now extinct Television New Zealand Natural History Unit. I was especially captivated by the programmes on the Chatham Island black robin (*Petroica traversi*) and the translocations used by the New Zealand Wildlife Service to bring them back from the brink of extinction. It was then that I decided that this was what I wanted to do when I grew up. I have been very fortunate to have been able to follow this dream and have subsequently been involved in 23 translocations of 7 species of birds. It gives me immense satisfaction to stand on a high promontory in the Hauraki Gulf Region and to look out at islands and headlands with populations of birds established by teams I either led or was a part of. What I did not realise was that in following this dream I would also embark on a scientific journey. One of the most influential people on this journey has been my primary thesis supervisor, Dianne Brunton. Her indefatigable energy, enthusiasm and patience are truly inspiring and her enduring faith in my ability to complete this thesis, even when I was unsure myself, truly essential. Thank you in so many ways. My good friend, colleague and mentor Tim Lovegrove has been an essential guide in sharing his immense knowledge of translocations, saddlebacks, natural history, culinary and gardening expertise along with providing me with occasional employment to help "keep the wolves at bay". I owe him a debt I doubt I can ever repay. I met Doug Armstrong in 1999 on my first translocation. He has become a scientific mentor whom I rely upon for tough but fair assessments of my work and I greatly value his opinion; kia ora e koro. There was a time, not so long ago, when statistical analysis carried a fair amount of trepidation for me, particularly when faced with almost 3000 songs from 15 islands…Marti Anderson has been my statistical saviour. She has helped me develop the skills required to tackle such a daunting data set and, more importantly, has been a great joy to work with. I never thought I could get so excited about complex multivariate data sets Marti! My good friends and colleagues John Ewen, Michael Anderson, Mark Hauber and Louis Ranjard have provided sage advice and counsel over the course of my research, and I hope that they will continue to do so into the future. Thanks guys, it is much appreciated. Peter Jenkins pioneering work in the 1970s laid down the foundation for this research and I have had many beneficial discussions with Peter, as well as obtaining historical saddleback recordings from him.

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