Temporal changes in cultural diversity across a growing meta-population of North Island saddleback (tīeke; *Philesturnus rufusater*): effects of mixed versus single-source translocations

A thesis presented in partial fulfilment of the requirements for the degree of Masters of Science in Biology at Massey University, Auckland, New Zealand

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Dedicated to all the hard-working conservation scientists, environmentalists and park rangers around the world, and their ceaseless efforts to preserve this beautiful planet we call home.

Thesis Abstract

Songbirds, the largest Order of birds, have intrigued humans for centuries given their ability to learn and produce melodious song. However, humans have also caused irreparable damage to many oscine passerines via the introduction of invasive mammalian predators. This is most apparent in New Zealand, where its distinctive avifauna have been decimated by induced species. Historical conservation efforts have done well to preserve and increase the populations of many remaining indigenous species, but the consequences of these actions on the song diversity and overall song culture of our endemic songbirds are poorly understood. The North Island (NI) saddleback (tīeke; *Philesturnus rufusater*) is an endemic social passerine that provides an excellent study species to examine such consequences given its well-recorded conservation history. Recent conservation translocations of the NI saddleback have been conducted with emphasis on maximising song diversity of populations, however, no empirical evidence currently exists showcasing whether the management practices employed have had the desired outcome. Using historic recordings of Male Rhythmical Song (MRS) – a conspecific reignition signal responsible for distinctive NI saddleback song culture - in conjunction with new recordings of MRS from three culturally distinct populations with unique translocation histories, my thesis examines current and historic conservation management policies and their potential consequences for NI saddleback song culture.

I first examined whether a translocation strategy employed at Shakespear Regional park (which involved the simultaneous release of birds from two culturally distinct source populations) achieved the desired outcome of maximising cultural complexity in a new population. I found that first-generation males learned source population MRS types, but no male sang MRS from both source populations. Also, rapid innovation of MRS was identified at Shakespear, where many young males innovated their own MRS irrespective of

their proximity to an adult social tutor. There was evidence of culturally distinct song neighbourhoods forming one-year post-translocation, and although assortative pairing did occur, females did not exclusively pair with males from the same source population. This signifies that MRS is not solely sufficient enough to act as a pre-mating barrier between NI saddleback of different cultures. I then examined how song culture changes over a discrete timeframe in the Motuihe Island population of NI saddlebacks. I found that population-level song repertoire, cultural diversity, and song variability all increased dramatically in 11 years. The immense changes to Motuihe's song culture can be explained by the cultural bottleneck and cultural mutation hypotheses. My work indicates that consideration must be made on the future restoration initiatives of new sites if conservation translocations aim to conserve ancient dialects in NI saddleback. Finally, I examined how acoustic characteristics of MRS vary between populations and correlate with the translocation history of each population. My main finding was that populations that have undergone more serial translocations have lower song diversity, and drivers for the development of these distinct acoustic signatures are a result of cultural bottlenecks, cultural drift and cultural mutations in relation to each population's unique translocation history. Although I expected populations that were established from a multi-sourced founder group to have higher cultural complexity than serially translocated populations of a similar age, population bottleneck events experienced during my project inhibited this. This highlights the ongoing need for the control and eradication of introduced mammalian predators, not only to conserve NI saddleback culture, but the species as a whole.

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Permits and Ethics

North Island saddleback song recording at my three field sites (Shakespear Regional Park, Tāwharanui Regional Park and Motuihe Island) was undertaken with permission from Ngati Manuhiri iwi, the New Zealand Department of Conservation (78225-FAU), the Auckland Regional Council (NS 456), the New Zealand Defence Force, and Massey University Animal Ethics Committee (19/33).

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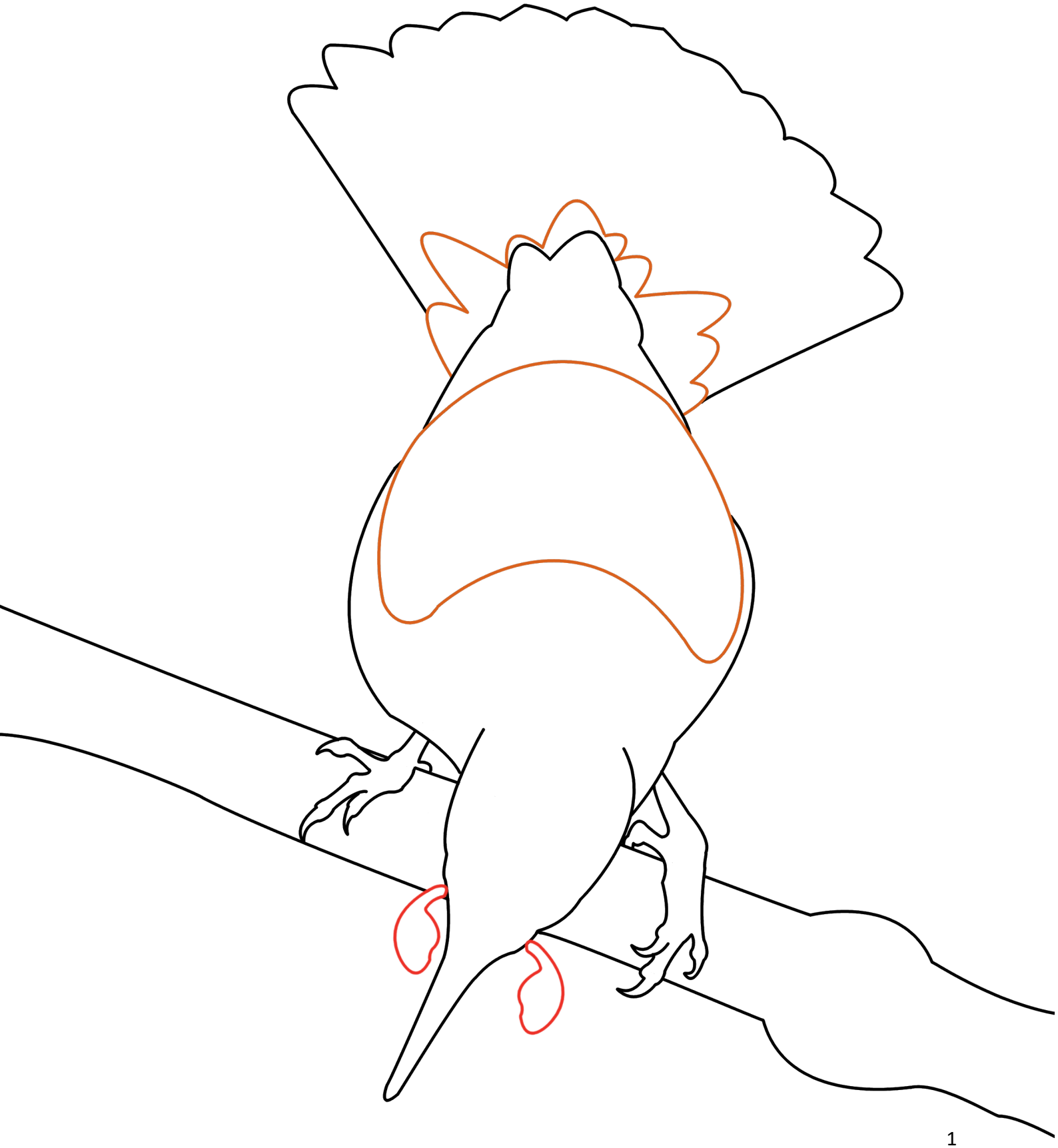
Chapter 1:
General Introduction



Humanity's far-reaching impact on nature has contributed to the decline of wildlife, loss of biodiversity, irreversible changes to climate and degradation of our planet's ecosystems. Unsurprisingly, our influence has altered the natural functions of a wide variety of these ecosystems, particularly those that have developed largely in isolation from the rest of the world. One such prevalent example are the ecosystems of New Zealand, with its distinctive biota that has evolved in remoteness since its founding landmass separated from Gondwanaland roughly 80 million years ago. An excellent illustration of the impacts that human population growth, habitat destruction, and the spread of introduced species can have on isolated species can be seen within the declining numbers of New Zealand's avifauna (Dowding & Murphy, 2001). Though pioneering conservation efforts of the last 100 years have done well to rescue many remnant species from extinction (see *Translocations* section), these early initiatives may have failed to preserve aspects of their culture (Parker, 2012).

1.1 Animal Culture

Like human culture, animal culture is a difficult phenomenon to define. Culture in non-human animals involves the process of cultural learning through socially transmitted behaviours (Nishida, 1987; Laland & Janik, 2006). These behaviours are shared by many members of a group and persist over generations (Nishida, 1987; Laland & Janik, 2006). Unlike genetic traits, novel cultural behaviours can be socially transmitted horizontally (within a generation), vertically (from parent to offspring) and obliquely (between generations) (Aplin, 2019; Garland et al., 2011). The formation of culture in animals is likely the result of several factors, but it has been widely accepted that the interplay between geographical and demographic features is an integral component to their formation (Aplin, 2019). These novel behaviours can be anything from innovative foraging techniques to

regionally distinct vocalisations. For examples, bottlenose dolphins (*Tursiops truncatus*) of Sharks Bay, Australia, use of marine sponges as foraging tools (Krutzen et al., 2005); humpback whale (*Megaptera novaeangliae*) song types have migrated east across the South Pacific (Garland et al., 2011); and multiple populations of chimpanzees (*Pan troglodytes*) across Africa have developed a variety of novel tool use and grooming techniques (Biro et al., 2003; Hopper et al., 2007; Whiten, 2005, 2011). The notion of culture in non-human animals had been observed as early as Darwin's work, but the actual term was developed by Japanese primatologists in the 1940s when they discovered socially transmitted food behaviours in macaques (*Macaca fuscata*) (Darwin, 1859; Galef, 1992; Nishida, 1987; Reznikova, 2012). Although social learning has been identified in a number of social species since then, the development of distinct cultures appears to be taxonomically restricted (Aplin, 2019; Heyes, 2012).

Culture exists predominantly within the cetacean and primate taxa (Laland & Janik, 2006; Whitehead et al., 2004; Whiten et al., 2017), but birds are known to exhibit an array of cultural traits, identified in multiple and diverse wild species (Aplin, 2019). The New Caledonian crow (*Corvus moneduloides*) for example, has shown the presence of local tool-type cultures similar to that of chimpanzees (Hunt & Gray, 2003). In passerines, great tits (*Parus major*) of Britain have developed new foraging behaviours that allows them to feed from milk bottles (Fisher & Hinde, 1949), and there are many studies showing that song culture can differ between populations of songbirds with the formation of local dialects (Catchpole & Slater, 2003; Podos & Warren, 2007; Slater, 2003). Following the latter example, the formations of geographic song dialects, or 'cultures', remains one of the most intriguing features of songbird ecology. As behavioural ecologist Michelle Hall so eloquently stated: "The melodious beauty and elaborate complexity of birdsong has long inspired poets, writers, and musicians – as well as behavioural ecologists." (Hall, 2013). Indeed, recent discoveries by behavioural ecologists has given light that variation, selection and inheritance – staple

terminology usually applied in a genetic context – are prevalent processes to birdsong dialect development (Aplin, 2019). With this in mind, endeavours to uncover the importance of cultural diversity have led researchers to speculate that the social transmission of birdsong in passerines may influence essential factors of genetic evolution (Aplin, 2019; Baker & Cunningham, 1985; Baptista, 1992; Ellers & Slabbekoorn, 2003; Parker et al., 2010; Slabbekoorn & Smith, 2002; Whitehead et al., 2004).

Ongoing research on the culture of birds ultimately emphasises the importance of preserving the cultural inheritance of birdsong. Song learning from conspecifics is an intrinsic aspect of songbird ecology, as song cultures can have important consequences on the survival and reproduction of individuals, and potentially contribute to speciation through their influence on mate choice (Baker & Cunningham, 1985; Baptista, 1992; Ellers & Slabbekoorn, 2003; Irwin, 2000; Parker et al., 2010, 2012; Slabbekoorn & Smith, 2002). In the context of conservation science, the impacts of conservation protocol on cultural processes is often overshadowed by the emphasis put on the persistence of the population and the preservation of genetic diversity (Griffith et al., 1989; Thorne, 2007; Jamieson & Lacy, 2012; Lambert et al., 2005; Taylor et al., 2008). This thesis investigates aspects of song culture in an endemic New Zealand passerine in relation to its conservation history. Using the North Island saddleback (tīeke; *Philesturnus rufusater*) as a model species, I aim to increase the understanding of the implications of conservation practices to New Zealand bird song and cultural diversity. It is my hope that the information provided by my thesis will help in the recovery of the North Island saddleback both in terms of their current population persistence, and in future conservation translocations to mainland New Zealand.

1.2 Study Species

1.2.1 Family

The New Zealand wattlebirds are ancient passerines thought to have arisen some 65 million years ago during the Tertiary period (Fleming, 1962; Kuschel, 1975). There are five species of endemic New Zealand wattlebirds that belong in the Callaeatidae family (Parker, 2013) and are represented by the three extant species - the North Island saddleback (*Philesturnus rufusater*), South Island saddleback (*Philesturnus carunculatus*) and North Island kokako (*Callaeas wilsoni*), and the two extinct species – the South Island kokako (*Callaeas cinereal*) and Huia (*Heteralocha acutirustris*) (Holdaway et al., 2001; Parker, 2013).

They are characterised by the presence of fleshy wattles, poor flight abilities, conspicuous foraging habits and inquisitive behaviours; the latter three of which likely developed largely in the absence of many mammalian ground predators (Jenkins, 1977; Lovegrove, 1992; Merton, 1975; Parker, 2011; Wilson, 2004). These attributes make Callaeatidae passerines extremely vulnerable to extinction in the presence of exotic mammalian predators (Hooson & Jamieson, 2003a; Lovegrove, 1996; Merton, 1973). So much so that species belonging to the Callaeatidae family have either been reduced to remnant populations or driven to extinction since the arrival of early European settlers (Heather & Robertson, 1996; Parker, 2011).

1.2.2 Species

The South Island and North Island saddlebacks have generally been considered subspecific since first being recorded in 1770 and 1772 respectively, by early European naturalists

(Heather & Robertson, 1996; Higgins et al., 2006; Hooson & Jamieson, 2003a; Merton, 1965; Oliver, 1955; Turbott, 1990; Williams, 1976) but have more recently been distinguished as two separate species (Helbig et al., 2002; Holdaway et al., 2001). This re-classification into full species status for North Island and South Island birds was further corroborated by Parker (2011), where he assessed the differences of vocalisations, morphology and mtDNA in defining the relationship between the two species (Parker, 2011). Although once a contentious topic, most are now in agreement that based on differences in plumage characteristics, morphology, mtDNA, vulnerability and vocalisations, the North and South Island saddlebacks are two separate species (Helbig et al., 2002; Higgins et al., 2006; Holdaway et al., 2001; Parker, 2011). As such, I will follow the new classification of the species as two distinct species as it has been recently adapted by the Department of Conservation (DOC).

1.2.3 Morphology

One commonly used Māori name for the saddleback is 'tīeke' and is thought to be an onomatopoeic reflection of their rapid chatter call (Guthrie, 2020; Merton, 1965; Richter-Gravier, 2019). In Māori folklore, 'tīeke' is synonymous for the North Island and South Island saddlebacks (Merton, 1965; Richter-Gravier, 2019) and for the remainder of this thesis I will refer to the North Island saddleback by its more traditional Māori name. Tīeke are medium sized (average length = 25cm) and appear sexually monomorphic in plumage; adult tīeke of both sexes have fleshy orange-red wattles, slate grey legs, glossy black plumage, a strip of gold across the mantle and a striking chestnut coloured 'saddle' extending between wing covers across the back, with similar colouring on the undertail coverts (Jenkins, 1977; Parker, 2013; Thorne, 2007) (Figure 1.1). In Māori legend, the tīeke received its distinctive band of colour running across its back from having its feathers singed by the heat of Maui's

hand (a demi-god in Māori lore), after his battle with the sun (Guthrie, 2020; Richter-Gravier, 2019). Indicators of sex result from morphometric measurements (Jenkins & Veitch, 1991). Males typically have longer bill length, larger wattle size, and a greater body mass (75 - 90g) than females (65 - 80g), though there is much overlap between sexes (Jenkins, 1977; Jenkins & Veitch, 1991). Therefore, the only reliable way of accurately determining the sex of the species through morphometric measurements is by measuring the length of the tarsus, where males have generally larger measurements (Jenkins & Veitch, 1991).

Figure 1.1: An adult North Island saddleback (tīeke; *Philesturnus rufusater*) (sex unknown) on Tiritiri Matangi. Photographed by Tommy Pedersen, October 2016.

1.2.4 Vocalisations

The tīeke produce three distinct vocalisations: two innate calls and one socially learned song type (Jenkins, 1977; Parker et al., 2012). The "chatter" call is a loud, powerful repetition of syllables produced by both the male and female throughout the year (Azar et al., 2013;

Jenkins, 1977). It has consistent physical acoustic structure, though it can vary in length (Jenkins, 1977). It is an innate vocalisation and is predominantly used as an alarm call when the bird is startled (Parker, 2011). The "quiet" calls are short, flute-like vocalisations (Jenkins, 1977). They are sexually dimorphic and are primarily used in pair-bonding behaviours and during foraging (Jenkins, 1977; Parker, 2011). The "Male Rhythmical Song" (MRS) vocalisations are exclusively sung by adult, site-attached male tīeke (Jenkins, 1977). They are usually composed of a few high-pitched pure-toned introductory notes, followed by a repeated phrase (Jenkins, 1977). MRS is used as a part of a behavioural display to establish and maintain territorial boundaries, and for mate attraction (Jenkins, 1977; Parker et al., 2012). Males can have between one to four MRS types in their repertoire, with an average of 1.8 ± 0.7 (Jenkins, 1977; Parker et al. 2012). MRS type sharing is common between individuals of the same population, where an average of 20 MRS types exists per population and males will typically share MRS types with their contiguous, territorial neighbouring males (Jenkins, 1977; Parker 2011). That being said, MRS type sharing *between* populations is very uncommon in the species (Parker et al., 2012). This vocalisation type is a socially learned song; young male tīeke learn MRS from their contiguous neighbours once they settle on a territory (Jenkins, 1977). Since MRS is a culturally transmitted signal, it is subject to change through learning errors (Jenkins, 1977; Parker et al., 2012). As such the evolution of MRS is the focus of the work presented here, as it is responsible for the formation of new regional dialects (Parker, 2008; Parker et al., 2010, 2012).

1.2.5 Diet & Habitat

The tīeke is a diurnal, forest-dwelling, non-migratory, endemic passerine of New Zealand (Heather & Robertson, 1996; Jenkins, 1977; Parker, 2011, 2013). They are a socially and sexually monogamous, long-lived species of songbird capable of living for 20 years in the

wild (Brouwer & Griffith, 2019; Hooson & Jamieson, 2003b; Taylor et al., 2008). Being omnivorous, tīeke primarily forage in pairs on the forest floor looking for various invertebrates throughout detritus material, but will also feed on fruit and nectar from a variety of plant species when available (Atkinson, 1966; Atkinson & Campbell, 1966; Blackburn, 1964, 1966, 1967; Merton, 1966; Pierre, 2000). Once tīeke have formed a monogamous pair, the pairing is usually permanent after the pair fledges their first brood (Lovegrove; 1980). Similarly, tīeke are site faithful and once acquiring a territory will often stay sedentary within the same territory for their entire lifespan (Armstrong et al., 2005; Jenkins, 1977). However, territory boundaries of tīeke are known to change with time, population-density, and habitat quality (Armstrong, 2005; Blackburn, 1964; O'Callaghan, 1980). Territory size is heavily influenced by population-density, and the flexibility in their feeding ecology allows the tīeke to occupy a diverse assortment of territorial habitat (Armstrong et al., 2005; Atkinson & Campbell, 1966; Taylor et al., 2005). The robust and flexible nature of tīeke territories lends to the tolerability of relatively small territories (0.4-ha), which in turn allows for high population-densities within small, isolated populations (Lovegrove, 1996; Lovegrove & O'Callaghan, 1982).

1.2.6 Breeding Behaviour

The breeding behaviour of the tīeke is also influenced by population-density (Armstrong et al., 2005; Hoyle, 1993). As such the timing of the breeding season tends to vary annually and by location (Hooson & Jamieson, 2003a; Thorne, 2007). In low-density settings, tīeke will exhibit high reproductive rates (up to four clutches of four eggs) through an extended breeding season (August-May), resulting in rapid population expansion (Armstrong et al. 2005; Craig, 1994; Hooson & Jamieson, 2003a). In high-density settings, reproductive rates are relatively low and tīeke will only attempt one clutch with one to two eggs during a

condensed breeding season (October – January) (Blackburn, 1966; Hooson & Jamieson, 2003a). When breeding, tīeke will typically nest in cavities close to the forest floor but are capable of nesting in a variety of protected sites (Armstrong et al., 2002; Blackburn, 1966; Heather & Robertson, 1996; Hooson & Jamieson, 2003a; Parker, 2013). They roost in cavities year-round and have been known to both roost and nest in predator-exclusion boxes if erected for use (Armstrong et al., 2002; Blackburn, 1966; Lovegrove, 1992, 1996; Stamp, Brunton & Walter, 2002). Nests are constructed out of detritus material, usually out of large strips of lacebark (*Hoheria populnea*) and dead leaves, with a kanuka bark (*Kunzea ericoides*), feather and/or grass lining (Blackburn, 1966). The female tīeke is responsible for choosing the nesting site and building the nests (Blackburn, 1966). Both parents feed nestlings and fledglings, but the female tīeke exclusively incubate the eggs for 18-20 days and brood young nestlings for roughly 27 days before fledging (Blackburn, 1966; Lovegrove, 1980; Hooson & Jamieson, 2003a; Thorn, 2007). Once fledged, the survivability of young adult tīeke is influenced by population-density, where low population-density settings promote survivability (Armstrong et al., 2005). Tīeke become sexually mature after their first year, where they will then disperse from their natal territories to establish their own territory and/or find a mate (Armstrong et al., 2005; Taylor et al., 2005).

1.2.7 Dispersal

Like all Callaeatidae, the tīeke are weak fliers; their rounded wings do not allow for prolonged flight and consequently tīeke are rarely airborne for more than 50m at a time, and incapable of flying distances greater than 200m (Merton, 1975; Newman, 1980; Parker 2011). This results in a dependency on translocations to establish new populations, as dispersal from source populations is limited (Parker, 2011). Current populations of tīeke were all derived from a single, small source population (N ≈ 500 individuals from Hen Island) (Figure 1)

(Lovegrove, 1996; Parker et al., 2012). Given the tīeke's weak flying capabilities and isolated populations, geneflow between populations is minimal (Newman, 1980; Taylor et al., 2008), and a genetic analysis of nine populations found that, generally, serial bottleneck translocations resulted in a loss, or significant alteration in the levels of genetic variation between source and translocated populations (Lambert et al., 2005).

1.2.8 Status, Distribution & Translocation History

Tīeke were once numerous across the North Island of New Zealand, but by the 1890s were reduced to a small, remnant population of roughly 500 individuals isolated on an offshore island known as Hen Island (Hooson & Jamieson, 2003b; Lovegrove, 1996; Merton, 1965; Parker, 2013; Williams, 1976). Their decline in numbers was largely due to their vulnerability to introduced predators as a result of the tīeke's conspicuous behaviour, nest and roost locations, and poor flying abilities (Hooson & Jamieson, 2003b; Lovegrove, 1996; Merton, 1965). Efforts towards their recovery began in the 1920s, but early translocation attempts ultimately failed (Lovegrove, 1996). The first successful translocation wasn't realised until 1964, when a population of tīeke was established on Whatupuke Island (Lovegrove, 1996). Since then, many conservation translocations of tīeke were conducted, each bringing with it a better understanding of the conditions that the species' needed to proliferate (Armstrong & Craig, 1995; Hooson & Jamieson, 2003b; Lovegrove, 1992; Merton, 1965; Thorn, 2007). However, the historic return of tīeke to the mainland was not realised until the advent of mainland "sanctuaries" – carefully selected areas of land on the mainland where predator-proof fencing can be erected to keep predators out, and the restoration and rehabilitation of native biota is conducted by various trusts, government organizations and private enterprises (Hooson & Jamieson, 2003b; Innes et al., 2012, 2012; Maitland, 2011; Saunders & Norton,

2001). All subsequent translocations to the mainland in unfenced areas have been unsuccessful (Sullivan, 2006).

By in large, the conservation history of the tīeke is a success story. The species has grown from a relic few (500) to over 7000 individuals in the last 60 years (Merton, 1965; Parker, 2013). Currently, populations of tīeke exist on 18 offshore islands and 6 mainland sanctuaries (Figure 1.2 & 1.3) (Hooson & Jamieson, 2003b; Lovegrove, 1996). The success story of the tīeke from a conservation perspective has bolstered its International Union for Conservation of Nature (IUCN) conservation status to Near Threatened (Parker, 2013), and DOC's assessment under the New Zealand Threat Classification System (NZTCS) to Recovering (Robertson et al., 2012). The ongoing improvements and success of conservation management strategies surrounding the tīeke suggest that the species will continue to grow, prosper, and eventually make its return to its native mainland ranges following the removal of exotic pests.

1.3 Translocations

Translocations are conservation procedures that involve the deliberate movement and release of wildlife (Miskelly & Powlesland, 2013). They are used to establish, re-establish or augment a population in the wild (Armstrong & McLean, 1995; Griffith et al., 1989). Translocations remain as one of the success stories of New Zealand conservation since its implementation by Sir Richard Henry in the late 1800s (Miskelly & Powlesland, 2013). This pioneering approach of conservation management has played an integral role in the recovery and preservation of some of New Zealand's most threatened avifauna (Saunders & Norton, 2001). Indeed, passerines such as the black robin (kakaruia; *Petroica traversi*), the stitchbird (hihi; *Notiomystis cincta*) and the South Island saddleback (tīeke) owe their existence to the

pioneering approaches of conservation management developed in the late 1800s (Butler & Merton, 1992; Hooson & Jamieson, 2003a; Merton 1975; Miskelly & Powlesland, 2013).

The governing body currently responsible for the conservation of New Zealand's biota is the Department of Conservation (DOC). DOC has been chiefly responsible for the development and regulation of environmental legislation across New Zealand since 1987 (Salmon, 2013). Prior to DOC, many other conservation bodies had been in operation since the 1890s (e.g. the New Zealand Wildlife Service c. 1945) and were largely responsible for the development of many pioneering methods for early conservation management practices (Salmon, 2013). As the use of translocations grows in New Zealand, guidelines have been developed by DOC to cover a broad range of topics concerning translocations (Armstrong & McLean, 1995; Parker, 2008). These guidelines encompass the current trends and ideas of conservation science, including site selection, public perception, translocation justifications and founder group details, all in hopes to aid in the success of future translocations (Miskelly & Powlesland, 2013; Parker, 2008; Saunders, 1995; Thorn 2007). When a translocation is conducted, detailed records are often kept about the source, size and age of the founder events (Lovegrove, 1996; Parker, 2008; Parker et al., 2012). Consequently, the management practices, and translocation history of newly established populations are absolutely known. This scenario presents a unique opportunity for conservation scientists to 1) evaluate both long- and short-term implications of creating isolated populations; 2) identify potential adherent effects of previous conservation management strategies; and 3) critically evaluate conservation management goals moving forward (Lambert et al., 2005; Parker, 2008; Parker et al., 2010, 2012).

With the primary objective of early translocations being to establish a population of animals in the wild, initial conservation translocations commonly measured their success on the self-sustainment of newly created populations (Griffith et al., 1989; Thorne, 2007). Later focus

shifted to the potential impacts of translocations on genetic diversity, and though this is an obvious concern, it has been well studied (Jamieson & Lacy, 2012; Lambert et al., 2005; Taylor et al., 2008). However, a seemingly less obvious concern lies within the impacts of these conservation practices on cultural and social processes, and as such has largely gone overlooked until recently (Parker, 2011; Parker et al., 2012). Historically, species translocations were often single-sourced, linear and serial in nature (Figure 1.), meaning that a new population would be established from a small subset of an existing population, hence undergoing multiple bottlenecks (Hooson & Jamieson, 2003b; Lambert et al., 2005; Lovegrove, 1996; Taylor et al., 2005). This subsampling resulted in early translocated populations suffering a loss of not only genetic diversity, but also elements of their culture during the translocation process (Baker & Jenkins, 1987; Lambert et al., 2005; Parker et al., 2010).

A growing number of studies on animal culture have given way to evidence that emphasises the importance of preserving socially transmitted song cultures in passerines (Aplin, 2019), and as such, most recent translocations have encompassed procedures to maximise song diversity in species like the tīeke (Parker et al., 2012). However, no empirical evidence currently exists showcasing whether the management practices employed have had the desired outcome. These well-documented and varied translocation strategies employed at different sanctuaries to establish populations of tīeke provided us with an excellent opportunity to examine the current and historic conservation management policies and their potential consequences on tīeke song culture.

Figure 1.2: The geographic location of each population of tīeke on the North Island, New Zealand. Populations marked in black circles indicate currently existing populations, and populations marked in grey x's are populations that failed.

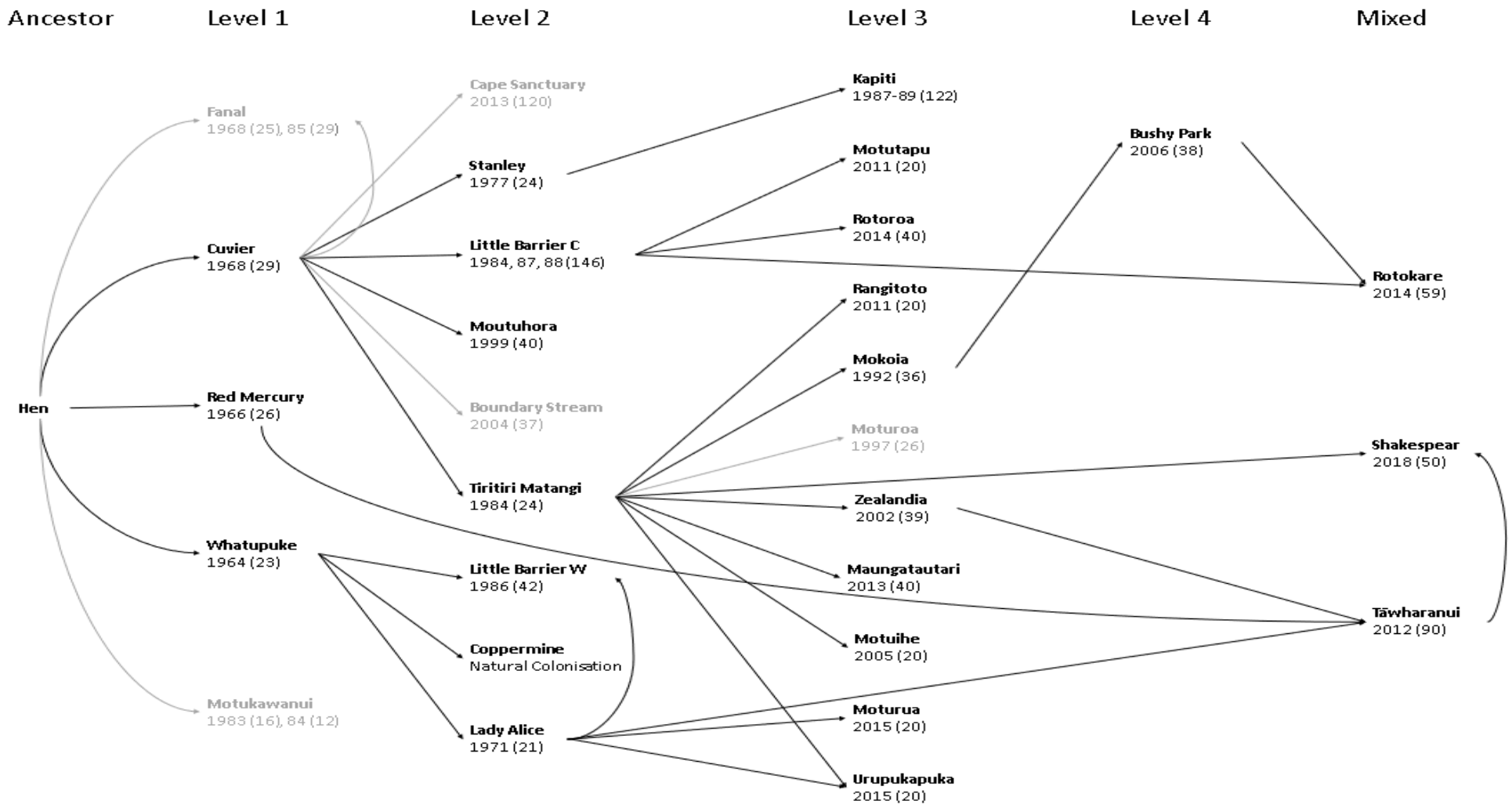


Figure 1.3: The translocation history of the tīeke updated from Parker et al. (2012). This shows the location of translocation, source population, years of translocations, and the number of individuals translocated in brackets. The arrows indicate the source of founding population and the translocation level refers to the amount of serial bottlenecks the population has experienced. Colonies in black are successful translocations and currently existing populations. Colonies in grey are failed populations.

1.4 Foundational Research

Parker (2011) set out to quantify any potential effects that serial bottleneck translocations may have had on socially learned tīeke song by recording male MRS from 14 different translocated populations between 2004 and 2008. Parker et al. (2012) manually segmented MRS phrases from the recordings and categorically sorted them into specific MRS types. He found an average of 20 MRS types per population (range 7 - 40, N = 300 recordings) (Parker, 2011). By comparing the quantity of MRS types shared between populations, Parker et al. (2012) empirically demonstrated that culturally distinct tīeke populations form due to rapid changes in their culture. He speculated that founder effects, bottleneck effects and cultural mutations may drive this phenomenon (Parker et al., 2012). Though geographic variation in bird song is a naturally occurring process (Podos & Warren, 2007), the rate that was seen in tīeke raised concerns about human-induced allopatric speciation (Parker et al., 2012). To address this question, a series of playback experiments were conducted on a population of tīeke on Motuihe Island to quantify whether the process of change in MRS between populations had any functional significance as a communication signal for individual tīeke populations (Parker et al., 2010). Fundamentally, Parker et al. (2010) investigated early signs of population divergence by testing whether the tīeke from Motuihe responded differently to conspecific signals from increasingly culturally distant populations via serial translocations. Tīeke were tested with playbacks of familiar MRS of the island and unfamiliar MRS from Hen and Cuvier islands and their responses were quantified. Parker et al. (2010) found that tīeke responded significantly faster to the playback of Motuihe MRS than to playback of MRS from other populations. The study concluded that the delayed response observed when tīeke heard MRS from Hen and Cuvier indicated that discriminatory behaviours to unfamiliar song developed rapidly (< 25 years) (Parker et al., 2010).

These early investigations into the impacts of translocations on tīeke culture by Parker (2011) acted as the foundation for my research. I expanded on Parker's (2011) historical dataset by adding updated recordings of Motuihe, and recordings of two new populations: Tāwharanui and Shakespear. Using my recent and Parker's (2011) historic recordings, I explored the impacts that modern conservation translocations had on tīeke song culture. Shakespear, Motuihe, and Tāwharanui were chosen study-sites for they all have varied, unique, and well-documented translocation histories (Figure 1.3). This allowed for a multifaceted assessment of their song cultures in relation to their translocation history: 1) the Shakespear population allowed me to investigate what happened to tīeke song culture one-year post-translocation; 2) the Motuihe population allowed me to investigate how tīeke song culture changed over a discrete timeframe; and 3) the Tāwharanui population allowed me to investigate what happened to tīeke song culture when birds from culturally distinct populations were simultaneously reintroduced into the same area.

1.5 Study Sites

1.5.1 Shakespear

The study-site at Shakespear Regional Park is a combination of 377-ha of land owned by the Auckland Regional Council (ARC), and 130-ha of land owned by the New Zealand Defence Force (NZDF) (Auckland Regional Council, 2010) (Figure 1.4). Both lands are enclosed by a pest-proof fence, but land owned by the NZDF is not open for public access. Since much of the conservation practices are the same on both lands (B. Harrison pers. comm., 2019), and tīeke exist in both areas, I will refer to the entire 507-ha area enclosed by the pest-proof fencing as "Shakespear". Shakespear is located 50km northeast of Auckland City at the eastern tip of the Whangaparaoa Peninsula (Figure 1.2 & 1.7). It is composed of

approximately 270-ha of mixed growth, native vegetation, 30-ha of beach and 207-ha of active grazing paddocks dispersed throughout the park for sheep (*Ovis aries*) and cattle (*Bos taurus*) (Auckland Regional Council, 2010) (Figure 1.4). The land was originally occupied by a local hapū known as Ngāti Kahu, who sold it to the Crown in 1853 (Auckland Regional Council, 1991). The area is named after the Shakespear family, who have been connected to the land since the late 1800s and was primarily used as farmland during this time (Auckland Regional Council, 1991). The 130-ha currently owned by the NZDF was originally purchased from the Shakespear family shortly after the outbreak of World War II (WWII) due to its strategic importance in the protection of Auckland ports (Auckland Regional Council, 1991). Major military infrastructures were erected at the north western tip as a part of the costal defence network (Auckland Regional Council, 1991). After WWII, the New Zealand Army (now the NZDF) retained the property and continue to use it to this day as a training facility and firing range (Auckland Regional Council, 1991). The Shakespear family continued to occupy the remaining property until 1967, where it was sold to the Auckland Regional Authority (now ARC) (Auckland Regional Council, 1991). This land was developed into a regional park and is open for public use, and as such is considered an open sanctuary.

In 2011, a 1.7km coast to coast pest-proof fence was completed, and a multi-species mammalian pest eradication followed soon thereafter which successfully eliminated all targeted species except mice (*Mus musculus*) (Auckland Regional Council, 2010, 2018). Shakespear's pest-proof fence is open at its coastal ends during low tides, and therefore is susceptible to mammalian incursions, so rangers maintain extensive poisoned bait stations and trapping lines throughout ARC and NZDF land (B. Harrison pers. comm., 2019). Many of the forests on ARC land are a result of intensive replanting efforts by the local community group (known as the 'Shakespear Open Sanctuary Society' - SOSSI). Shakespear is home to a variety of endemic species including little spotted kiwi (kiwi pukupuku; *Apteryx owenii*), New Zealand bellbirds (korimako; *Anthornis melanura*) and most recently a translocated group of

40 stitchbirds (hihi) (K. Parker, pers. comm., 2019). The recently established population of tīeke at Shakespear are composed of individually colour-banded adults translocated from Tiritiri Matangi (N = 40) and Tāwharanui (N = 10), and their first-generation unbanded progeny (N = 25) (Figure 1.3). The timing of this recent translocation gave me the rare opportunity to examine how tīeke song types change over one generation.

Figure 1.4: The study site of Shakespear, which includes Shakespear Regional park and NZDF land. Grassy areas are light green and are used as paddocks for grazing cattle and sheep. Darker green areas are forested land. The urban township of Army Bay can be seen west (left in the image) of Shakespear.

1.5.2 Motuihe Island

Motuihe Island is a 179-ha recreation reserve located 19km east of Auckland City in the Hauraki Gulf (Figure 1.2, 1.5 & 1.7). The island has a long and varied history of human habitation and as such has gone through a diverse amount of modifications. For hundreds of years the island was occupied by various Māori hapū including the Maru iwi, Te Arawa and Ngati Paoa (Motuihe Trust, 2019). As such, Motuihe has a long history of Māori settlement, where notable battles were fought on the island's headland when different tribes

contested for ownership (Motuihe Trust, 2019). The island was purchased by William Fairburn in 1839 and farming on the island began shortly thereafter (Motuihe Trust, 2019). When the small-pox virus reached New Zealand shores in 1872, Motuihe was designated as a human quarantine station and facilities were built to care for the infected (Motuihe Trust, 2019). This was later developed into an animal quarantine station in 1892 (Motuihe Trust, 2019). During World War I (WWI), Motuihe was developed into an internment camp where prisoners of war were detained (Motuihe Trust, 2019). Following the war, the island was again repurposed into a quarantine station with the arrival of the Spanish influenza in 1918 (Motuihe Trust, 2019). With the outbreak of WWII, Motuihe saw yet another transition of use when it was to be incorporated into New Zealand's costal defence network (Motuihe Trust, 2019). Buildings were converted and added to form a naval training base, which continued in operation until 1963 (Motuihe Trust, 2019). Afterwards, Motuihe Island saw a return to farming practices until its acquisition by DOC in 1987, where ecological restoration initiatives followed soon thereafter (Motuihe Trust, 2019). In 1993 and 1995, poison bait drops were administered to eradicate Norway rats (*Rattus norvegicus*) and mice from the island (Motuihe Trust, 2019; Parker & Laurence, 2008). Restoration of Motuihe was further intensified with the establishment of the community led Motuihe Island Restoration Trust in 2000 (Motuihe Trust, 2019; Parker & Laurence, 2008; Parker, 2011). A subsequent eradication operation involving poison bait drops, poisoned bait stations, traps, and specialist hunters and dogs (*Canis familiaris*) was conducted to eliminate all rabbits (*Oryctolagus cuniculus*) and cats (F*elis catus*) on the island. The operation was a success and Motuihe was declared pest-free in 2004 (Motuihe Trust, 2019; Parker & Laurence, 2008). Shortly thereafter, species endemic to New Zealand who were at risk of going extinct were reintroduced to the island via translocation (Motuihe Trust, 2019; Parker & Laurence, 2008). Many of the island's forests are a result of intensive replanting efforts made by conservation volunteers and make for suitable habitat for a variety of New Zealand fauna including tuatara (*Sphenodon punctatu*)

and Red-crowned parakeets (kākāriki; *Cyanoramphus novaezelandiae*) (Ortiz-Catedral & Brunton, 2010).

Motuihe island is now jointly managed and controlled by DOC and the Motuihe Trust and is considered a recreation reserve open to the public (Motuihe Trust, 2019). Consequently, incursions of rats (*Rattus rattus & R. norvegicus*) have been known to occur at Motuihe Island as a result of the frequent island visits by boaters. Therefore, extensive poisoned bait stations, camera traps and trap lines are maintained by DOC and the Trust to rapidly eliminate any intruding pests. In 2005, a population of tīeke was successfully established on Motuihe Island from a single-sourced translocation of 20 birds from Tiritiri Matangi (Figure 1.3). Three years later the entire population's song repertoire was recorded and analysed by Parker (2011). This provided me with the opportunity to examine how song types of this passerine population have changed over a finite period of time, after I re-recorded the population's song repertoire in 2019.

Figure 1.5: The study site of Motuihe Island, taken in 2017. Intensive revegetation can be seen across the island, with mature coastal forests located primarily on the western side of the island. Remnant grazing paddocks can be seen at the centre-most point of the island, and to the north tip, which is used for camping.

1.5.3 Tāwharanui

Tāwharanui Regional Park is a 558-ha mainland, open wildlife sanctuary located 75km northeast of Auckland City, at the eastern tip of the Tokatū Peninsula (Figure 1.2, 1.6 & 1.7) (Auckland Regional Council, 2010). It is composed of approximately 254-ha of native, mixed growth forests and wetlands, 50-ha of beach and 254-ha of active grazing paddocks dispersed throughout the park for sheep and cattle. Tāwharanui has a rich and colourful history of Māori occupation spanning hundreds of years (Murdoch, 2008). Although many hapū contested the land for its obvious strategic location and rich natural resources, the primary residents of Tāwharanui were the Ngāti Raupō belonging to the Te Kawerau people (Murdoch, 2008). Māori occupation of Tāwharanui continued until shortly after the Musket Wars when many were exiled from the surrounding area, only to return in the 1830s to find large parts of their ancestral land now owned by European timber traders without their knowledge or consent (Murdoch, 2008). Tāwharanui was officially sold to Antonio Martin in 1877 and subsequently converted to farmland and timber mill (Murdoch, 2008). Although Tāwharanui changed ownership a handful of times after this, the land-use remained largely the same until 1973, when it was purchased by the Auckland Regional Authority (now ARC) and converted into a regional reserve (Murdoch, 2008).

Early years as a remote nature reserve saw work done to preserve remnant forests, reduce pastureland, and plant native flora (Murdoch, 2008). Many of the forests at the park are a result of intensive replanting efforts by the local community group (known as the 'Tāwharanui Open Sanctuary Society' - TOSSI) and make for suitable habitat for many New Zealand biota. Intensive replanting began in 2005 and thus the only old growth forest in the park (known as the Ecology Bush) is located at the park's centre (Murdoch, 2008). In 2004, a 2.7km coast to coast pest-proof fence was completed, turning Tāwharanui into a 'mainland island', though the fence is open at its coastal ends during low tide (Auckland Regional

Council, 2010; Day & MacGibbon, 2007). A multi-species mammalian pest eradication followed soon thereafter and was largely successful, though mice and rabbits persisted within the park and incursions of cats, rats (*R. rattus & R. norvegicus*), stoats (*Mustela erminea*) and common brushtail possums (*Trichosurus vulpecula*) are known to occur (Maitland, 2011). A monthly culling of rabbits is carried out to keep population densities as low as possible (M. Maitland & M. Puckett pers. comm, 2019), and mice remain in high densities at the park (Goldwater et al., 2012). Poisoned bait stations and extensive trap lines are maintained by the park's rangers in the event that an incursion does occur (Maitland, 2011), and occasionally specialist hunters and dogs are brought in to exterminate some larger, evasive mammals (M. Puckett pers. comm., 2019). Tāwharanui has seen many indigenous species reintroduced to its land, including the South Island takahē (*Porphyrio hochstetteri*) and North Island brown kiwi (*Apteryx mantelli*) (M. Puckett pers. comm., 2019). To maximise song diversity, the group composition of tīeke selected to be reintroduced into Tāwharanui Regional Park was composed of birds from three culturally distinct island populations (Figure 1.3). By using the population at Tāwharanui, I examined how the cultural evolution of the species was affected by simultaneously reintroducing culturally divergent populations into the same area.

Figure 1.6: The study site of Tāwharanui Regional Park. Grassy areas are light green and are used as paddocks for grazing cattle and sheep. Darker green areas are forested land.

1.6 Aims & Objectives

The well-documented and varied translocation history of the tīeke makes this social passerine a model species to investigate long- and short-terms consequences of conservation practices. Each study-site was used to explore a separate set of questions pertaining to tīeke song culture, and as such provided me with a convenient method for structuring my data chapters. Due to the structure of this thesis, with each data chapter structured as a manuscript in preparation for journal submission, there is some overlap between chapters. Here I have used the tīeke and three of its unique, isolated populations as an illustrative example of conservation practices and their influence on animal culture.

Chapter 2: Shakespear - novel and ancestral song types within a newly established translocated population

I explain the unique conservation translocation employed at Shakespear as a method of maximizing the cultural complexity of the population. I then explore the potential cultural changes to the tīeke population at Shakespear as a result of this conservation strategy.

Objectives:

1. Test whether males with established territories share fewer MRS types with males whose territories are more physically distant.
2. Determine whether assortative pairing occurs between culturally distinct populations of tīeke.
3. Investigate the song dialect of first-generation males in relation to their contiguous neighbours.

Chapter 3: Motuihe - rapid cultural evolution within a single-sourced population

In this chapter I investigate how a completely isolated, single-sourced, serially translocated population's song culture changes with time. Specifically, I provide a quantitative analysis of any rates of change and/or increase in song types within the population.

Objectives:

1. Assess the changes to the population-level song repertoire over a period of 11 years.
2. Compare the song diversity between the 2008 and 2019 populations.
3. Identify any changes to song variability over a period of 11 years.

Chapter 4: Tāwharanui - the effects of varied conservation translocations and cultural bottlenecks on cultural diversity

Here I summarise my findings on the cultural complexity of tīeke in relation to different conservation management strategies. I then provide an empirical comparison of tīeke culture between 17 isolated study-sites using historic and recent audio recordings of tīeke song.

Objectives:

1. Identify the cultural complexities of historic and recently recorded tīeke populations in relation to the ancestral dialect of Hen Island.
2. Determine whether mixing culturally distinct populations affects the cultural complexity of tīeke.

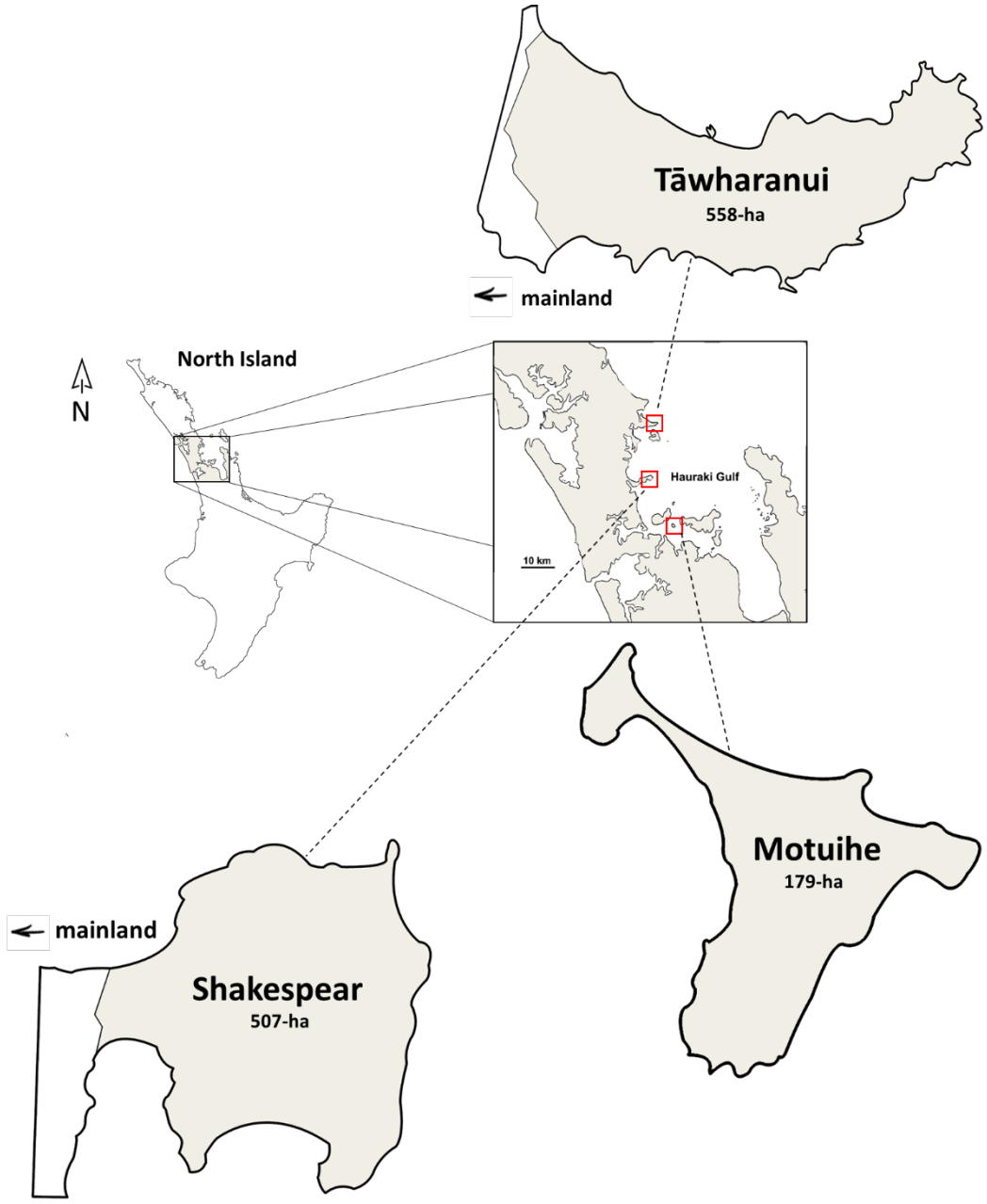


Figure 1.7: Location of the study-sites Tāwharanui, Shakespear and Motuihe Island, in the Hauraki Gulf of the North Island, New Zealand.

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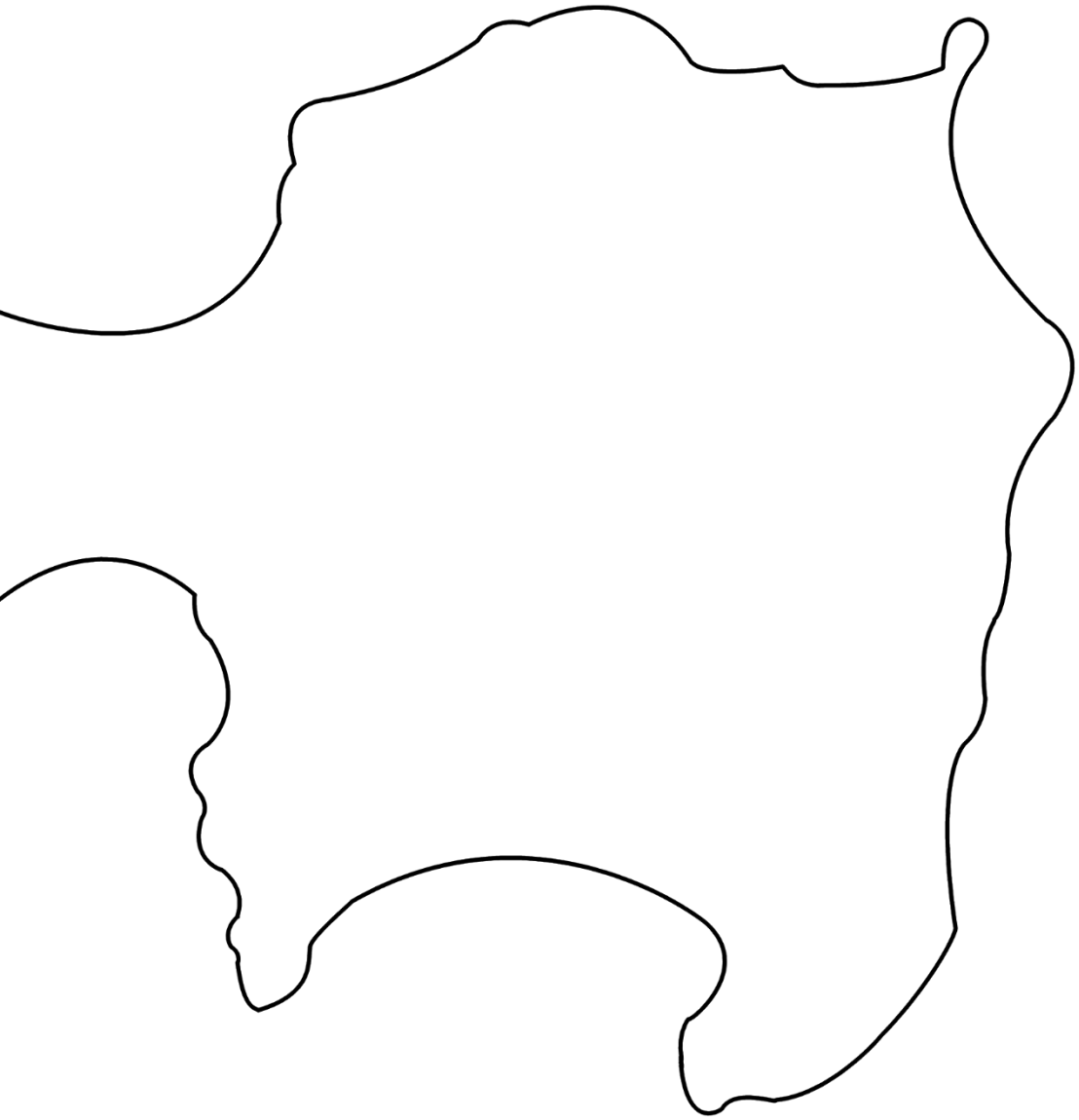
Chapter 2:

Shakespear - novel and ancestral song types within a newly established translocated population



2.1 Introduction

Vocalisations that are socially learned and are susceptible to song learning errors or "cultural mutations" (Dawkins, 1976; Jenkins, 1977; Lynch, 1996). These errors play a significant role in the cultural evolution through horizontal (within a generation), vertical (from parent to offspring) and oblique (between generations) cultural transmission (Aplin, 2019; Garland et al., 2011). Cultural evolution theory proposes that changes in bird song culture may contribute to speciation over time due to its role in assortative mating within populations and its potential to restrict gene flow among populations (Baker & Cunningham, 1985; Baptista, 1992; Ellers & Slabbekoorn, 2003; Parker et al., 2010, 2012; Slabbekoorn & Smith, 2002). In isolated populations such as island and translocated populations, the accumulation of these cultural mutations combined with the random loss of song variants over time may lead to culturally distinct populations.

Research on the tīeke (North Island saddleback; *Philesturnus rufusater*) by Jenkins (1977) and Parker et al. (2012) empirically demonstrated this process and reported rapid cultural changes to Male Rhythmical Song (MRS) resulting in the formation of culturally distinct tīeke populations (Parker et al., 2012). Adult male tīeke use MRS – a socially learned vocalisation susceptible to learning errors - as a part of a behavioural display to establish and maintain territorial boundaries and for mate attraction (Jenkins, 1977; Parker et al., 2012). In tīeke, this process results in populations that can be distinguished by their MRS types (Parker et al., 2012). Early translocations of the species were primarily focused on tīeke survivability and population persistence as a marker for success (Griffith et al., 1989; Merton, 1965; Taylor et al., 2005), however more recent conservation translocations have seen a shift in focus to the preservation of genetic and cultural diversity (Angeloni et al., 2008; Anthony & Blumstein, 2000; Armstrong & Craig, 1995; Gedir et al., 2013; Parker, 2008; Parker & Laurence, 2008; Thorne, 2007).

The presence of culture - particularly song culture – in birds has been identified in many wild, free-living species. For example, red-capped robins (*Petroica goodenovii*), western gerygones (*Gerygone fusca*) and singing honeyeaters (*Lichenostomus virescens*) of Western Australia all showed distinctive differences in song culture between mainland and offshore populations (Baker et al., 2006), and introduced yellowhammers (*Emberiza citronella*) of New Zealand have preserved ancient dialects that are now extinct in their native home ranges of Britain (Pipek et al., 2018). The mechanisms that drive the formation of song dialects are likely multifaceted, but the interplay between time, environmental and demographic features is widely accepted as an integral component to their formation (Aplin, 2019; Lachlan et al., 2013). It is apparent that geographically unique song cultures form naturally in the wild (Podos & Warren, 2007), however, concerns around the formation of unique tīeke culture arise from the rate by which they are forming (Parker et al., 2010, 2012; Parker & Laurence, 2008) – a potential undesirable by-product of early conservation translocations. Parker et al. (2012) speculated that founder effects coupled with cultural mutations may have led to the rapid changes detected in tīeke song culture. Further, he speculated that these rapid changes could potentially contribute to population divergence and lead to human induced, allopatric speciation (Lachlan & Servedio, 2004; Parker et al., 2010, 2012; Slabbekoorn & Smith, 2002); something that conservation scientists want to avoid. With the long-term goal of reintroducing tīeke to the mainland post-exotic-predator eradication (Armstrong & Davidson, 2006), a significant concern for conservation scientists is whether or not tīeke from culturally distinct populations will interbreed, or if they remain in their culturally distinct groups, with MRS acting as a pre-mating barrier and thus limiting genetic mixing (Parker et al., 2010).

Historically, species translocations were often single-sourced, linear and serial in nature (Figure 1.3), meaning that a new population would be established from a small subset of an existing population, hence undergoing multiple bottlenecks (Hooson & Jamieson, 2003;

Lambert et al., 2005; Lovegrove, 1996; Taylor et al., 2005) (Figure 1.3). This subsampling results in the loss of not only genetic diversity (Lambert et al., 2005), but also some MRS types during the translocation process, thus creating greater cultural differences between populations. One approach to prevent rapid changes in tīeke song culture (and thus slow potential population divergence in new populations) is to preserve cultural complexity in new populations (Parker, 2011; Parker et al., 2012). Thus, modern conservation translocation procedures have incorporated the consideration of the composition of the founder population used to establish new populations. Indeed, the founder populations of recent tīeke translocations have been composed of a mix of tīeke, multi-sourced from culturally distinct populations, each with its own unique translocation history. The range of single and multi-sourced translocations undertaken of tīeke provide the opportunity to empirically examine the effects of cultural evolution on song diversity in free-living animals.

The decisions to follow new conservation management strategies to maximise song diversity (Angeloni et al., 2008; Anthony & Blumstein, 2000; Parker et al., 2012; Parker & Laurence, 2008) resulted in the Shakespear founder population being composed of birds from two culturally distinct populations (K. Parker pers. comm., 2019). An even sex ratio of 40 tīeke were selected from Tiritiri Matangi Island – an offshore island population established in 1984 by 24 tīeke from Cuvier (Figure 1.2, 1.3 & 1.7) (Hooson & Jamieson, 2003). Another even sex ration of 10 tīeke were selected from Tāwharanui Regional Park (K. Parker pers. comm., 2019) – a mainland sanctuary population established in 2012 by 90 tīeke; 30 from Mokoia Island, 30 from Red Mercury Island and 30 from Lady Alice Island (Figure 1.2, 1.3 & 1.7) (see *Tāwharanui* chapter). The 50 tīeke selected from Tiritiri Matangi and Tāwharanui were all uniquely colour-banded and released in Shakespear in 2018. The Shakespear tīeke founder population provided a unique opportunity to study how tīeke culture is affected by simultaneously reintroducing two culturally different populations into the same isolated area one-year post-translocation. In 2019, I mapped tīeke territories and digitally recorded male

tīeke MRS from the population at Shakespear to investigate how MRS song types have changed over one generation, and identify whether tīeke from separate populations and cultures recognize and ultimately pair with one another when introduced to the same area.

In this chapter I explore the potential cultural changes to the tīeke population at Shakespear as a result of the unique conservation translocation employed to establish the population. This is important to fundamentally understand whether mixing cultural distinct source populations into a founder group has any functional significance to a new population from a cultural conservation perspective. To do so I tested whether males with established territories shared fewer MRS types with males whose territories were more physically distant. I also determined whether assortative pairing occurred between the two cultural distinct source population of tīeke at Shakespear. Lastly, I investigated the amount and types of MRS of Shakespear's first-generation males in relation to their contiguous neighbours. This chapter, in addition with the other chapters in my thesis, adds to the current knowledge of tīeke culture within the context of conservation translocations.

For this study I predicted that:

1. Given the function of MRS, males with established territories will share fewer MRS types with males whose territories are more physically distant.
2. Assortative pairing based on source populations will occur, with MRS acting as a pre-mating barrier.
3. Territorial first-generation males will innovate MRS if they do not have a contiguous, adult social tutor to learn from on a neighbouring territory.

4. If a first-generation male's contiguous neighbours were from Tāwharanui *and* Tiritiri Matangi, the focal male will produce Tāwharanui *and* Tiritiri Matangi MRS types.

2.2 Methods

2.2.1 Study-site & Population

The study-site at Shakespear is a combination of 377-ha of land owned by the Auckland Regional Council (ARC) known as Shakespear Regional Park, and 130-ha of land owned by the New Zealand Defence Force (NZDF) (Auckland Regional Council, 2010). Both lands are enclosed by a pest-proof fence, but unlike the regional park, land owned by the NZDF is not open for public access. Since much of the conservation practices are the same on both lands (B. Harrison pers. comm., 2019), and tīeke exist in both areas, I will refer to the entire 507-ha area enclosed by the pest-proof fencing as "Shakespear". Shakespear is located 50km northeast of Auckland City at the eastern tip of the Whangaparaoa Peninsula (Figure 1.7). It is composed of approximately 270-ha of mixed growth, native vegetation, 30-ha of beach and 207-ha of active grazing paddocks dispersed throughout the park for sheep (*Ovis aries*) and cattle (*Bos taurus*) (Figure 2.1a) (Auckland Regional Council, 2010). In 2011, a 1.7 km coast to coast pest-proof fence was completed, and a multi-species mammalian pest eradication followed soon thereafter which successfully eliminated all targeted species except mice (*Mus musculus*) (Auckland Regional Council, 2010, 2018). Shakespear's pest-proof fence is open at its coastal ends during low tides, and therefore is susceptible to mammalian incursions, so rangers maintain extensive poisoned bait stations and trapping lines throughout ARC and NZDF land (B. Harrison pers. comm., 2019). Many of the forests on ARC land are a result of intensive replanting efforts by the local community group (known as the 'Shakespear Open Sanctuary Society' - SOSSI) and make for suitable habitat for tīeke

once properly established (Atkinson & Campbell, 1966; Jenkins, 1977; Parker & Laurence, 2008). Replanting on ARC land began in 1972 and therefore areas that were replanted first have matured and are well established (Nature Space, 2012). An example of such a forest would be 'Waterfall Gully', located on the western side of the park. NZDF land has largely gone unmodified post-WWII (B. Harrison pers. comm., 2019) and mature coastal forests can be found on the north-eastern most side of the military land. Tīeke predominantly exist in these more mature forested areas, however they have successfully dispersed to forest patches throughout Shakespear. Post-translocation surveys indicated an initial survival rate of 74% and that the population had increased to 57 tīeke after the first breeding season (Parker, 2018, 2019).

2.2.2 Field Methods

The ARC land of the park was initially explored July 22nd, 2019 by two researchers to consult with park rangers on tīeke sightings and to become familiar with the park. A list of all bird colour-banded combinations and a map of all sighted individuals was obtained prior to the field season so that tīeke could be easily identified and a general idea of where they were located was known (see *Appendices*). Intensive sound recording fieldwork at Shakespear commenced on October 29th, 2019 and lasted till November 27th, 2019. Recordings of MRS were taken by 1-4 trained field ecologists all using Marantz PMD661MKII Handheld Solid-State Recorders, Sennheiser MKE 600 Shotgun microphones and Rycote Softy wind guards mounted on Rycote pistol grips. Raw recordings were in .WAV format with a sample rate of 48 kHz, and 24-bit sampling precision. The raw files were backed up on external hard drives and Massey University cloud drives and given a unique file name which included the name of the recorder, date of recording, and area of recording for future use. Recordings of tīeke did not occur on days with rain or high wind. Initially only ARC land was available to

be sampled and researchers systematically covered the area irrespective of the number of male tīeke present. Later in the season, emphasis was put on individual male tīeke with the fewest MRS recordings, or areas where undetected tīeke had been previously sighted on surveys. Researchers would spend between six to ten hours in a designated section of the park, spanning from shortly after sunrise till 1130 and/or 1300 till shortly before sunset. Hiking trails and predator trap lines were used to travel through native bush in search of tīeke in addition to off-trail trekking in order to get to areas where tīeke had been previously seen or heard. Once a tīeke was located, researchers identified the individual by its colour-bands (individuals without bands were assumed to be first-generation birds), noted its location via GPS coordinates (Garmin Ltd, 1996-2020), and estimated territory boundaries on a map of the park. The GPS coordinates and territory sketches were used in Google Earth (Google LLC, 2020) at the end of each day to plot and adjust territory boundaries of each pair of birds (Figure 2.1). The territories could be visualized while in the field on an iPhone 6s (Apple Inc, 2020) and the Google Earth (Google LLC, 2020) app to give a general idea of where each bird could be found, and which birds had not been sampled. Researchers would follow the focal male anywhere between 10 – 60 minutes depending on how frequently the focal bird was singing or how often that area had been sampled previously. The final 12 days of recording at Shakespear were spent on NZDF land and a similar approach to recording tīeke was taken. On the first day on NZDF land, I walked around the land with a Garmin GPS (Garmin Ltd, 1996-2020) and plotted points where birds were sighted, with primary focus on areas around the firing ranges as this was the only day live round shooting was not taking place.

2.2.3 Territory Mapping

Each territory was plotted on Google Earth (Google LLC, 2020) by transcribing GPS points taken in the field into .KML polygon shapes (Figure 2.1). The shapes of the territories were confirmed by comparing them to territory boundary sketches made in the field. Midpoints of each territory were calculated by using Earth Point (Earth Point, 2020) a polygon area and midpoint calculation tool for Google Earth. A physical distance matrix was then created in Microsoft Excel (Microsoft Corporation, 2002) by measuring the Euclidian distances between each midpoint of each territory. Physical distance measurements between midpoints of territories was conducted in Google Earth.

a.

b.

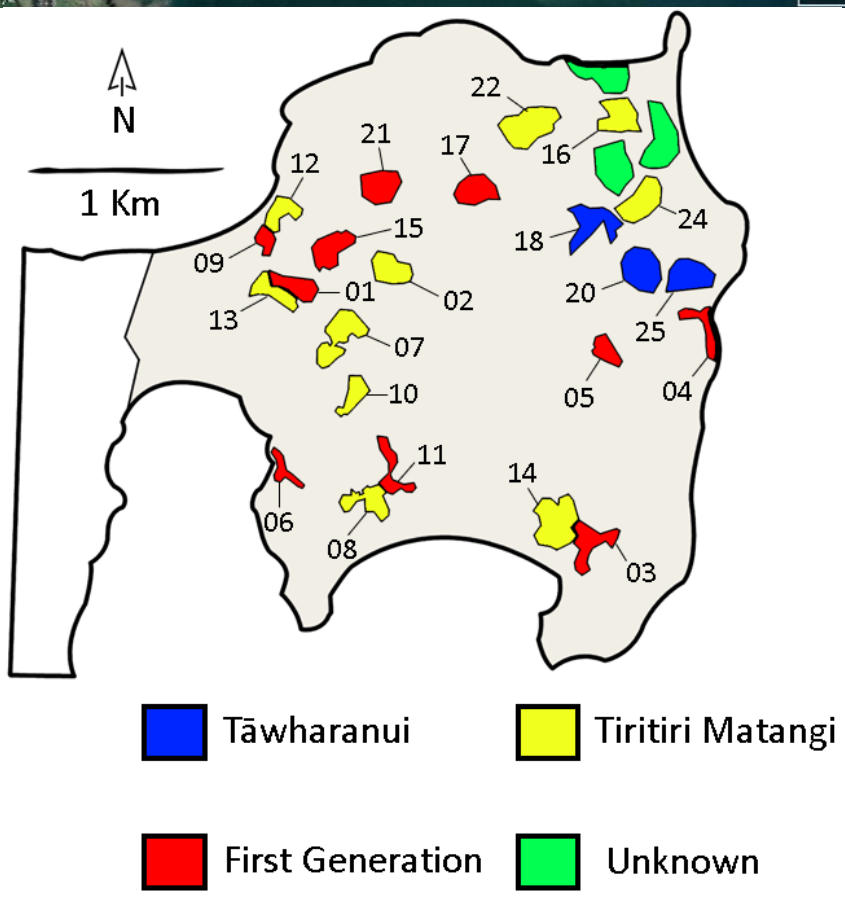


Figure 2.1: a) 2019 images of the study site Shakespear with territory boundaries of male tīeke. **b)** A simplified, rendered map of Shakespear. Yellow territories are males from Tiritiri Matangi, blue territories are males from Tāwharanui, red territories are unbanded first-generation males, and green territories are unidentified tīeke. Disassortative mate pairings occurred in territories 02, 18, 20 and 25. Territory 08 had no female partner. Territories 16 and 24 had female partners that could not be identified.

2.2.4 Song Analysis

Tīeke MRS types are easy to distinguish from one another both visually (from digitally rendered spectrograms) and aurally (Figure 2.2) and as such this remains the most widely accepted method of categorising bird song type (Parker, 2011). I did all the song analysis and segmentation so as to standardise selection criteria across all populations and remove any differences due to the observer. The Shakespear raw recordings of tīeke from 2019 were first inspected in Raven 1.6 (Cornell Lab of Ornithology, Ithaca, NY, USA). High quality tīeke vocalisations were then cut out of the raw recording and new .WAV files (sample size=24 bits, pad size=1.1 seconds) were created for each track. Each track was given a unique, annotated filename which included the type of vocalisations (chatter, MRS, or quiet call), recordist, date, and location of the recording. Tracks which included MRS were subsequently uploaded to KOE (Fukuzawa et al., 2020; Webb, 2020) (FFT=512, overlap=50%) and the single most repeated phrase within the MRS was manually segmented to be analysed as a representative of the entire MRS following the method outlined by Parker et al. (2012) (Figure 2.2). These segmented MRSs were sorted by duration and compared using KOE and the features "Unit table" and "Exemplars". These tools allow researchers to bulk label, and visually and aurally inspect and compare all spectrograms and song type classifications in an automatically generated reference page based on specific selections. Song types were then assigned to each MRS based on audio and visual similarities (matching). MRS matchings were generally conservative, but allowances were made for individual variation present between birds within Shakespear i.e. small variations in tempo, pitch, or the number of repeated syllables within a phrase (Figure 2.8). A single experienced bird song researcher was asked to replicate MRS type matching on a subset of Shakespear song (containing 200 MRSs and 19 different MRS types) following the same method of classification using the same KOE program. MRS types were compared between the bird song researcher and my originally categorised phrases to check for agreement.

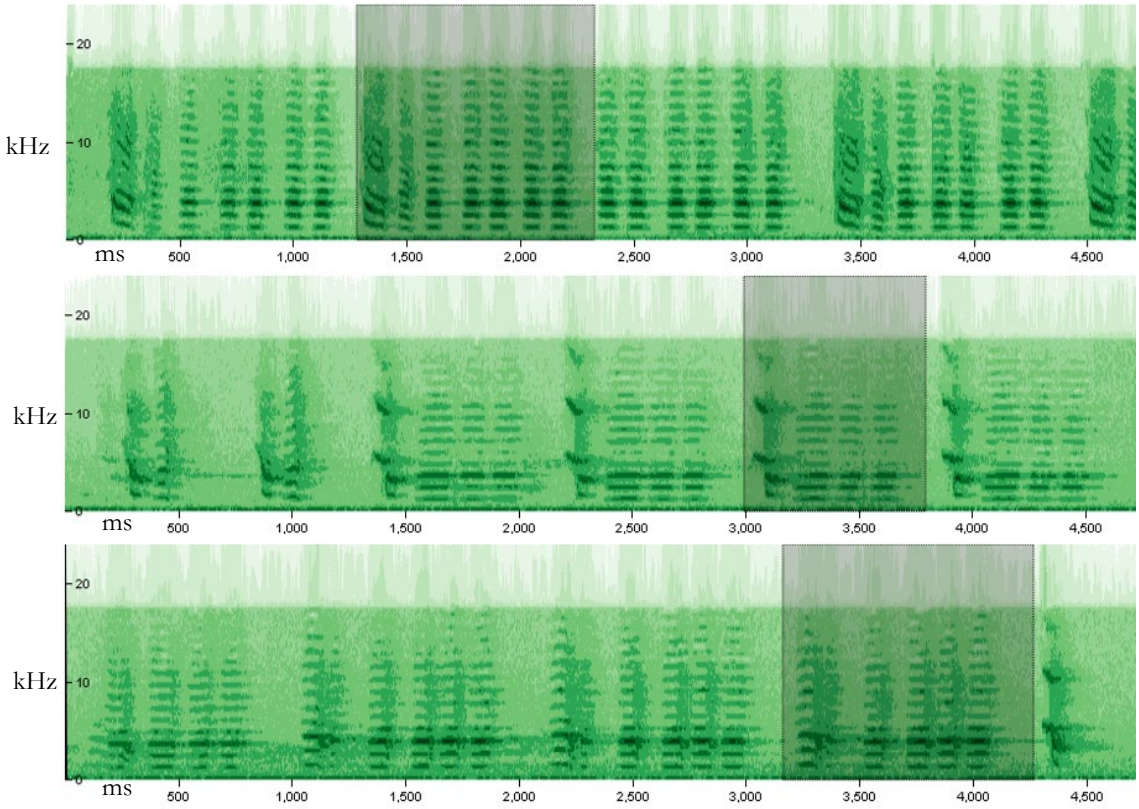


Figure 2.2: Spectrograms showing MRS of three different MRS types sung by three different males (top to bottom: Territory 05, 11 & 01) at Shakespear. The grey rectangle indicates the single phrase selected to represent the song type and to be measured for spectral analysis

2.2.5 Spectral Analysis

A spectral analysis was conducted in KOE (Fukuzawa et al., 2020; Webb, 2020) on each phrase selected. 223 features were exported to Microsoft Excel (Microsoft Corporation, 2002) and the mean, median, standard error and standard deviation were then calculated for each feature for each phrase. All multivariate analyses were run using the PRIMER v7.0.17 computer program (Quest Research Limited, 2015) with the PERMANOVA+ add-on package (Anderson et al., 2008). Linear Discriminant Analyses (LDA) were run on the dataset to highlight the features that were best at discriminating differences between MRS types within Shakespear (see *Appendices*). These "within-population" features were checked

for skewness by running a draftman plot for each MRS type. It was determined that none of the within-population features needed to be transformed prior to further analysis.

Each MRS type was then separately analysed and checked for extreme outliers, resulting in two tracks being removed from all further analysis. This was done by first normalising the within-population features each MRS type, then forming a Euclidian-Distance resemblance matrix for each separate MRS type, then running a non-metric multi-dimensional scaling (nMDS) ordination plot to check for normal clustering within each MRS type.

Once extreme outliers were removed, an nMDS was run comparing every phrase with one another using the within-population features, allowing for a visualisation of the spectral similarities of MRS types in relation to one another in non-dimensional acoustic space. This was achieved by normalising the highlighted within-population features, then creating a Euclidian-Distance resemblance matrix prior to running an nMDS.

2.2.6 Song & Statistical Analysis

A table was created in Microsoft Excel (Microsoft Corporation, 2002) by plotting the number of MRS types sang for each individual. This table was used to visualise how many MRS types were sung by each individual, which individuals sang which MRS types, what location each MRS type came from (i.e. Tāwharanui, Tiritiri Matangi, or first-generation) as well as which MRS types were the most/least popular in the park (see *Appendices*). A duplicate dataset was created and standardised to be used in subsequent multivariate analysis.

The proportion of MRS types sung were categorically sorted as a function of the age of the singing male (first-generation, or greater than first-generation) and a one-way ANOVA with 95% confidence intervals was run in Microsoft Excel on the dataset (see *Appendices*). This

allowed us to test if there were any significant differences in the number of MRS types sung with respect to male tīeke age (Figure 2.3a). A similar one-way ANOVA with 95% confidence intervals was also run on MRS types categorically sorted as a function of the location of the singer (Tāwharanui, Tiritiri Matangi, or first-generation) which allowed us to identify if there were any significant differences in the number of MRS types sung in relation to the lineage of the singing male (see *Appendices*) (Figure 2.3b).

The standardised data was used to create a Bray-Curtis resemblance matrix which provided similarity scores indicating how many MRS types were shared between individuals. The data was not square root transformed prior to forming a resemblance matrix as no skewness was detected within the dataset. A dendrogram was created which visualized the relationships between each individual based on their song repertoire, and an nMDS was created which plotted each individual as a function of their MRS repertoire in non-metric space. Bray-Curtis similarity scores were also compared to physical distance scores of each male and were categorically sorted into five groups discriminated by distance. A one-way ANOVA was run in Microsoft Excel on this dataset, followed by a Bonferroni corrected, post-hoc t-test between each group (see *Appendices*). This allowed us to model the average percentage of MRS types shared between males at five distinct distances.

2.3 Results

2.3.1 Tīeke at Shakespear

Tīeke from Tiritiri Matangi had spread throughout Shakespear but were primarily concentrated in Waterfall Gully and the north-eastern pocket of Shakespear, whereas Tāwharanui tīeke had predominately stayed in the eastern section of NZDF land (Figure

2.1). 19 tīeke from Tiritiri Matangi, four from Tāwharanui and 18 first-generation Shakespear tīeke were accurately identified by the end of the field season. Three pairs of tīeke were sighted on NZDF land, but their colour bands could not be ascertained and they could not be sound recorded due to restricted site access; their territories were located on active firing ranges that were in use by military during the entirety of the field season, making sighting and recording impossible. At least two tīeke have perished from the Tiritiri Matangi translocated population since the last census on March 2019 as they were originally located near the buffer zone of the park; an area with a heightened risk of depredation (Parker, 2018, 2019). They were also never seen throughout the field season, but their partners were seen with new partners and with dependent juveniles. Although tīeke are known to change partners post-translocation (Armstrong & Craig, 1995), once a mate has been chosen, they are extremely site and pair faithful and will normally only swap partners and territories if their original partner has died (Jenkins, 1977). Overall, 23 of the original 50 colour banded individuals (4/10 from Tāwharanui & 19/40 for Tiritiri Matangi) were accurately re-sighted, indicating a one-year post-translocation survivability of 46%, which is below the historical mean survivability (mean = 57.6%, range 41 - 81%, N = 10). This value is certainly an underestimate of survivability, as six banded individuals were known to exist (on the firing range) but could not be accurately identified. It is also possible that some first-generation unbanded individuals were unobserved in the park, however given the duration of the field season at Shakespear, the number of missed unbanded individuals is likely low.

2.3.2 Territories & Pairs

26 territories were mapped at Shakespear, though, three were excluded from subsequence analyses as the tīeke could not be accurately identified, and no recordings were conducted in those territories (Figure 2.1). Of the 23 individually identifiable territories, ten were settled

by males from Tiritiri Matangi, three were settled by males from Tāwharanui, and ten were settle by first-generation unbanded males (Figure 2.1). Both the male and their corresponding female partner were identified in ten of the 13 colour banded territories; there was one unpaired male on Territory 08, and two males (Territories 16 & 24) near the firing range whose partner could not be accurately identified (Figure 2.1). Of the ten pairs of tīeke, four were mixed; a male from Tiritiri Matangi was found with a female from Tāwharanui on one occasion (Territory 02), and every male from Tāwharanui was paired with a female from Tiritiri Matangi (Territories 18, 20 & 25)(Figure 2.1).

2.3.3 MRS Types

A total of 96 raw recordings were captured at Shakespear, yielding 359 tīeke vocalizations. Of these vocalizations, 294 tracks were identified to contain MRS, which resulted in a final total of 323 phrases (each representing an MRS) selected for further song analysis. These 323 phrases were categorised into 20 different MRS types, representing the total MRS repertoire of the population at Shakespear. Two tracks were later removed from the dataset as they were identified as extreme outliers (due to the poor quality of the recordings) during subsequent statistical analysis, resulting in a final working set of 321 phrases. The single experienced bird song researcher that was asked to replicate the same method of MRS type matching on Shakespear achieved an 89.5% agreement in MRS matching, grouping the subset of 200 MRSs into 22 MRS types.

An average of 2.2 MRS types per individual male was found at Shakespear (N = 23, range 1-4) (Figure 2.3). It should be noted that only one male has a repertoire size of four, and five males only sang one MRS type (Figure 2.4). There was no difference in the mean number of MRS types in an individual male's repertoire when comparing them by age (P = 0.934;

first-generation range 1-3, N = 10; greater than first-generation range 1-4, N = 13) or location (P = 0.971; Tiritiri Matangi range 1-4, N = 10; Tāwharanui range 2-3, N = 3; Shakespear-born range 1-3, N = 10) (Figure 2.3) (see *Appendices*). There were 13 different MRS types present in the group of first-generation males at Shakespear, whereas 15 different MRS types were found in the group of males older than one year (Figure 2.3). A total of five MRS types came from Tāwharanui, ten MRS types came from Tiritiri Matangi, and five MRS types were newly innovated by the unbanded first-generation males (Figure 2.3 & 2.4). However, two of the five innovated MRS types heard only had a single usable recording for each. They were still included in further analysis because they did not appear as outliers on the nMDS (Figure 2.6), and adherent or rare MRS types were notable in this case study (Figure 2.4). Proportionally, 40% of MRS types from Tāwharanui were sung by first-generation males (2/5 Tāwharanui MRS types, sung by 3/10 first-generation males) (Figure 2.3) and 60% of MRS types from Tiritiri Matangi were sung by first-generation males (6/10 Tiritiri Matangi MRS types, sung by 6/10 first-generation males) (Figure 2.3). Every first-generation male sang at least one Tāwharanui or Tiritiri Matangi MRS type, and every male tīeke shared at least one MRS type with at least two other male tīeke (Figure 2.4). Further, the maximum number of MRS types shared between any two males was two, however, no male tīeke sang both Tāwharanui and Tiritiri Matangi MRS at Shakespear (Figure 2.4). Finally, nine unique MRS types were found in the park that were not shared by any two birds; two were from Tiritiri Matangi, three were from Tāwharanui and four were from unbanded first-generation males (Figure 2.4).

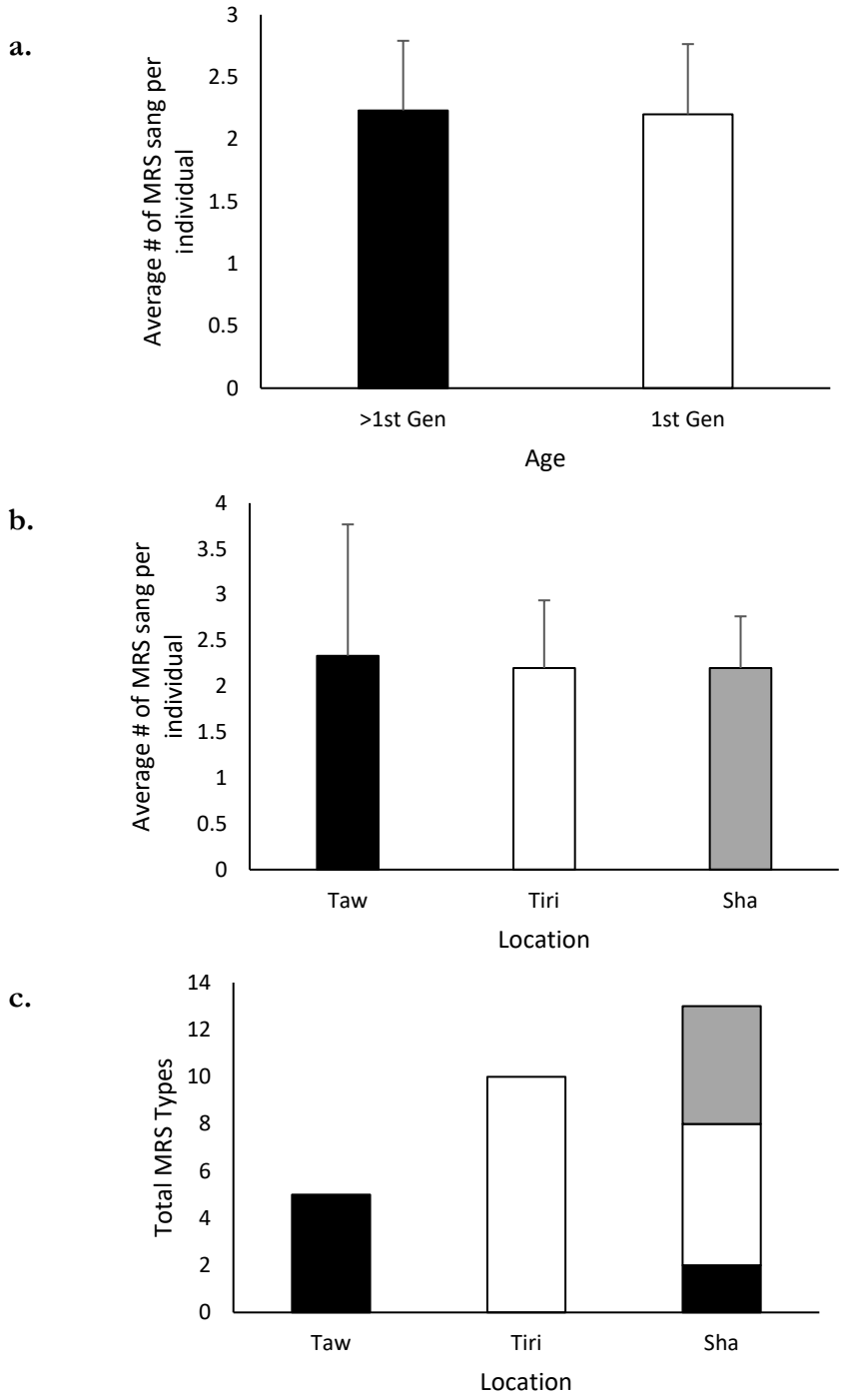


Figure 2.3: a) Average MRS repertoire size of first-generation males (1st Gen) and males that were older than one year (>1st Gen; males from Tiritiri Matangi and Tāwharanui combined) with 95% confidence intervals (see *Appendices*). **b)** Average MRS repertoire size comparing males from Tāwharanui (Taw), Tiritiri Matangi (Tiri) and Shakespear-born (Sha) males with 95% confidence intervals (see *Appendices*). **c)** A visual representation of the total number of MRS types in each group of males separated by location. First-generation bar shows the proportion of song types originating from Tāwharanui (black), Tiritiri Matangi (white), and unique to their generation (grey).

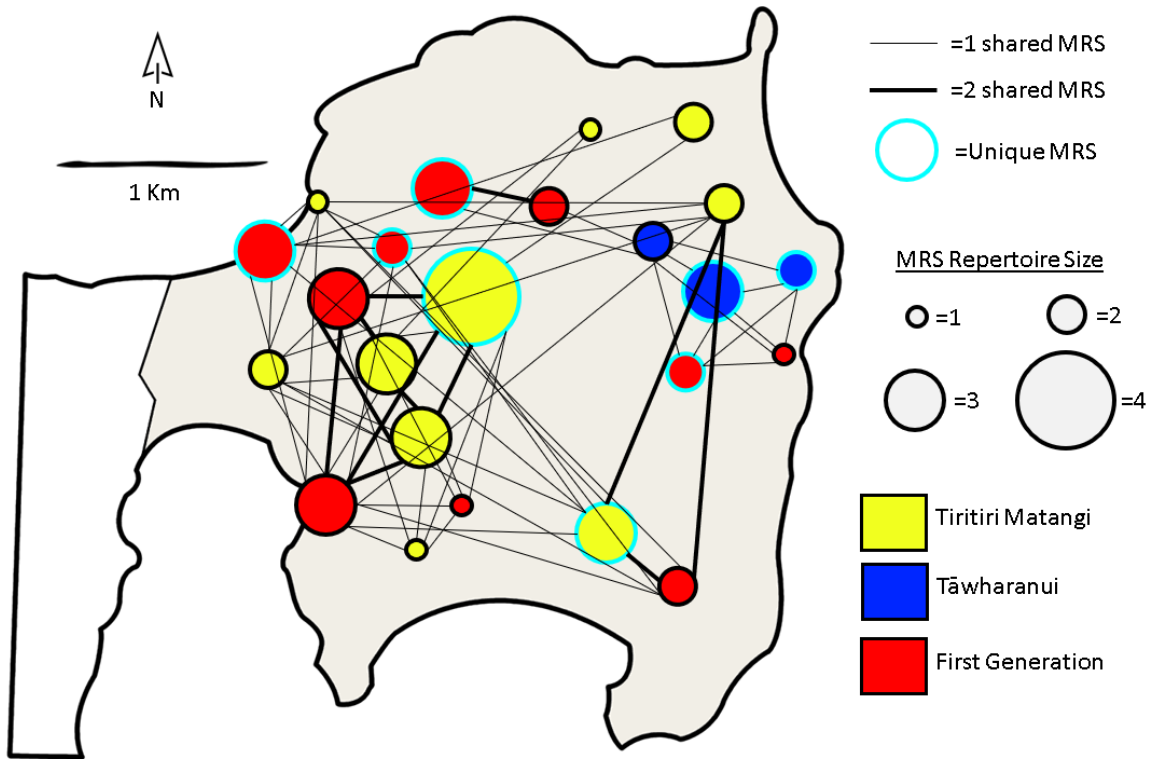


Figure 2.4: The degree of MRS type sharing between male tīeke at Shakespear. The location of each circle is relative to the location of the male's territory. The colour of each circle indicates the identity of the male of that territory. Circles outlined in blue indicate a unique MRS type that is not shared by any other bird. The size of the circle represents the individual's repertoire size. The thickness of the line connecting two circles represents the amount of MRS types shared between the two males. No male sings both Tāwharanui and Tiritiri Matangi MRS types.

2.3.4 Physical Distance & MRS Sharing

The ANOVA analysis indicated that there was a statistically significant difference between MRS types shared at different distances ($P < 0.001$). A Bonferroni corrected post- hoc t-test indicated that there was a statistically significant difference in the proportion of MRS types shared between males from 0-500m apart (N = 37) to song types shared between males from 501-1000m apart (N = 57, $P < 0.001$), 1001-1500m apart (N = 80, $P < 0.001$) and 1501-2000m apart (N = 68, $P < 0.001$) but not at distances greater than 2000m (N = 6, $P = 0.102$)

(Figure 2.5). There were no significant differences in MRS type sharing between any other two distances (Figure 2.5).

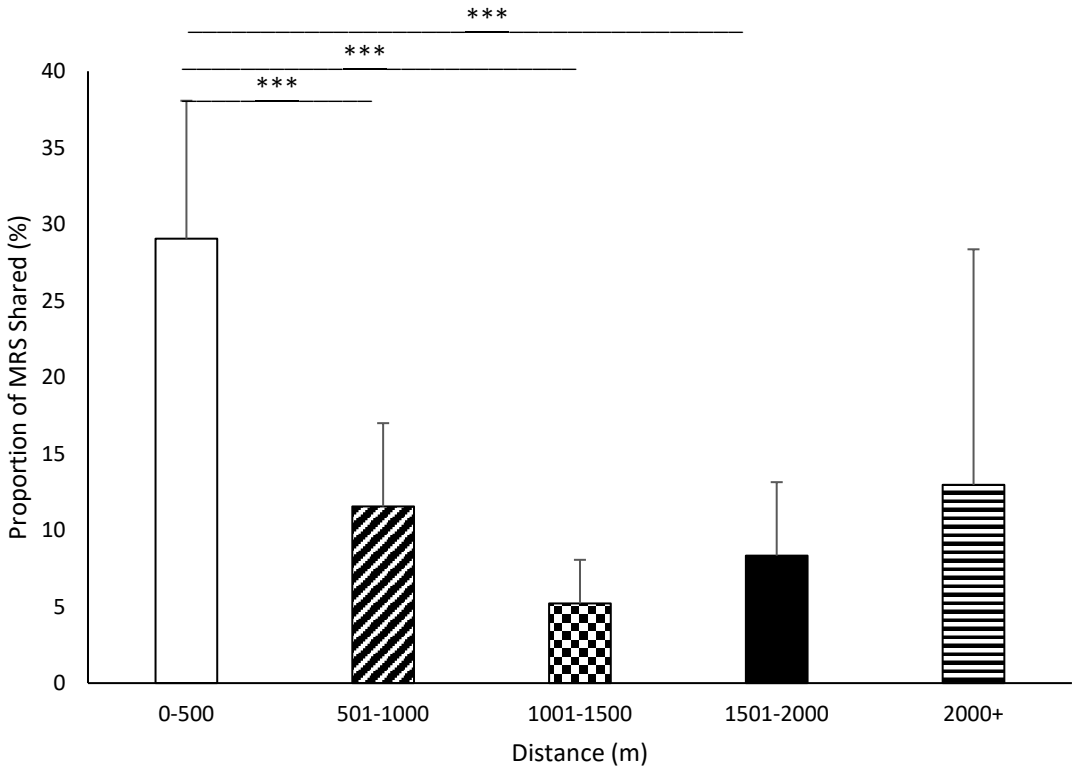


Figure 2.5: A bar chart visualisation of the proportion of MRS types shared at 5 different distances in Shakespear. A mean of 29.05% of MRS types were shared at distances between 0-500m, 11.55% at 501-1000m, 5.21% at 1001-1500m, 8.33% at 1501-2000m and 12.96% at distances greater than 2000m, all with 95% confidence intervals. Significant differences in song sharing were found only between 0-500m and the distances marked with an asterisk.

2.3.5 MRS Spectral Comparison

A spectral analysis of MRS types at Shakespear shows distinct clusters forming for each song type in the nMDS, all within similar non-dimensional acoustic space (Figure 2.6). Although 2D stress is high (2D stress = 0.18), it is within the acceptable limit and 3D stress was much lower (3D Stress = 0.09). Rare or potentially adherent MRS types (types 21, 27 & 35) were included in the nMDS as they did not alter or influence the relationships of other MRS types in non-metric space. There was an even distribution of first-generation male MRS

overlapping with both Tiritiri Matangi and Tāwharanui MRS types. There was no clear division between Tāwharanui and Tiritiri Matangi MRS types, though, there was notably very little overlap in non-metric acoustic space between adult male Tāwharanui and Tiritiri Matangi MRSs. For example, adult males that sung the most common Tāwharanui MRS types (2, 24 and 30) certainly occupied unique space in the nMDS.

2.3.6 MRS Type Sharing

Comparing shared MRS types shows two distinct clusters forming on the nMDS (stress = 0.01), indicating two distinct song neighbourhoods (Figure 2.7). This was formed using a dendrogram that gave similarity scores to each individual's song repertoire (see *Appendices*). First-generation males can be found in both song neighbourhoods, no adult males belong to a song neighbourhood different to their source population song neighbourhood (i.e. no Tāwharanui male falls within the Tiritiri Matangi song neighbourhood), and no first-generation bird belongs to both. These song neighbourhood boundaries were visualised on a map of Shakespear by dividing individuals based on which cluster in the nmMDS they belonged to (Figure 2.7).

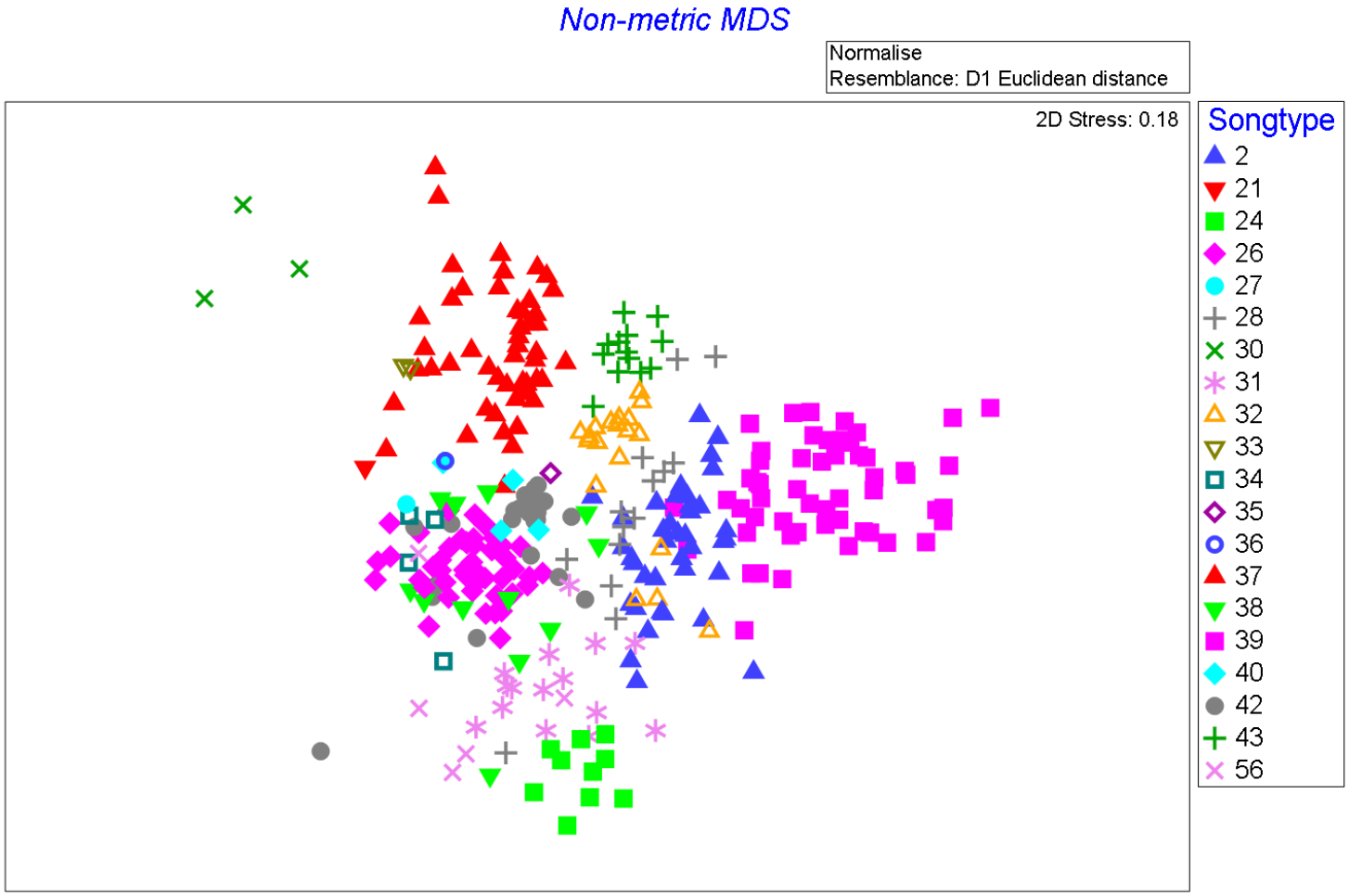


Figure 2.6: An nMDS of the MRS types at Shakespear. Each point represents a phrase and its 48 spectral features (see *Appendices*). Its proximity to another point represents the similarity of those 48 spectral features. The shape and colour of each point represents its MRS type classification (seen in legend). A total of 321 points exist and form 20 different MRS types. Normal distribution and clustering of MRS types indicates that song classification was accurate based on the spectral similarities of each phrase in relation to its MRS type.

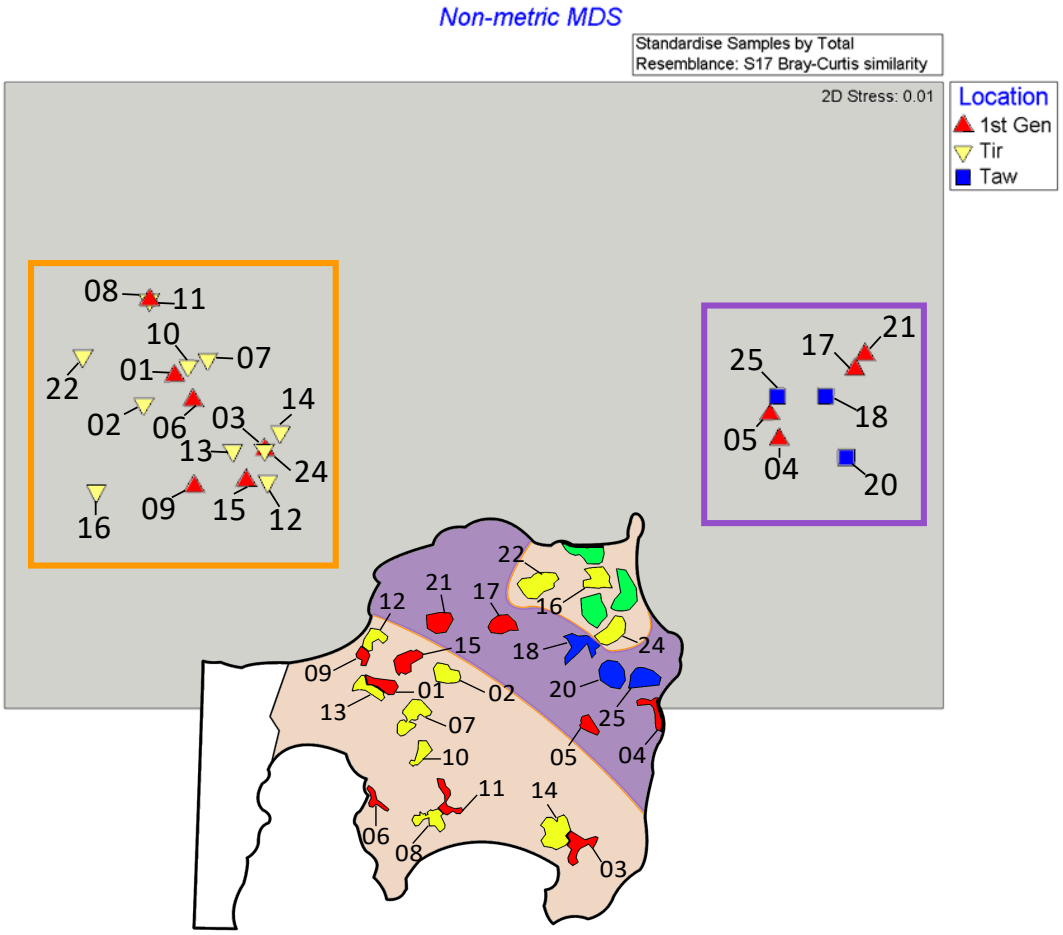


Figure 2.7: An nMDS showing the relationship between song repertoires of each individual male recorded at the park based on a Bray-Curtis similarity score (see *Appendices*). Each point represents an individual male's song repertoire, and its proximity to another point represents how similar the song repertoires of those males are. Points that are further apart have less MRS types in common. Colour and shape of each datapoint delineates the lineage of each male; Tāwharanui males in blue squares, Tiritiri Matangi males in upside-down yellow triangles and first-generation males in right-side-up red triangles. Numbers on the nMDS indicate the territory that the individual male belongs to and correlates with individual territory numbers above territory boundaries seen on the vectorised map of Shakespear. Two distinct clusters (enclosed in orange and purple) are present within the nMDS, representing two song neighbourhoods distinguished by the dialect sung. These neighbourhoods are visualised on the vectorised map of Shakespear; areas highlighted in orange represent Tiritiri Matangi song neighbourhoods and the area highlighted in purple represents the Tāwharanui song neighbourhood.

2.4 Discussion

2.4.1 Cultural Preservation

I found that the ancestral MRS types of two culturally distinct populations persist within Shakespear and were preserved by the next generation of male tīeke who learnt them. This hence *should* increase the cultural complexity at Shakespear as song culture from two distinct populations are now represented (see *Tāwharanui* chapter). Since unbanded juveniles could not be individually identified, and the origin of their paternity and natal territory was unknown, I was unable to confirm the identity of social song tutors (Jenkins, 1977). However, it should be noted that after one year, no first-generation tīeke sang both Tāwharanui and Tiritiri Matangi MRS types, despite many young males having contiguous neighbours from each ancestral population to learn from – counter to our prediction. This may be because juveniles that establish territories in culturally distinct song neighbourhoods learn MRS types of that song neighbourhood rather than their contiguous neighbour, or that not enough time had transpired to learn both Tāwharanui and Tiritiri Matangi MRS types. It is also possible that song learning bias based on individual male qualities may exist (Braaten & Reynolds, 1999; Laland, 2004; Rendell et al., 2011; Slabbekoorn & Smith, 2002); an aspect of social learning beyond the scope of this study. It is recommended that a future study should colour-band chicks in nests, track them to determine territory establishment post-fledging, and then monitor male song repertoire to test for song learning strategies and song tutor preferences. Doing so may further influence the criteria for founder population selection in males during conservation translocations. Males who are "good" tutors based on a criteria established from potential song learning bias exhibited by young males may make for better candidates to increase cultural complexity in newly established populations, and be advantageously selected for in future conservation translocations to compose the founder group.

2.4.2 Cultural Preferences

Despite the formation of culturally distinct song neighbourhoods, I found that females did not exclusively pair with males from the same ancestral population. Interestingly, every male from Tāwharanui paired with a female from Tiritiri Matangi. It is important to note that song is not the only factor for mate choice (Mays et al., 2008; Searcy, 1979; Slabbekoorn & Smith, 2002) and with limited mating options, simply mating with an individual from another culturally distinct population is preferential to not mating at all (Kaneshiro, 1987; Parker et al., 2012). Nonetheless, assortative pairing does appear to be happening, as many females did mate with males from the same source population. Although this matches our prediction, assortative pairing at Shakespear could have been influenced by the fact that birds from Tiritiri Matangi were released a few weeks prior to the Tāwharanui birds, consequently giving Tiritiri Matangi males first access to the best habitats for breeding territory establishment (Atkinson & Campbell, 1966), while also initially limiting the mate choices for Tiritiri Matangi females. Therefore, it is possible that simultaneous releases of birds may result in lower assortative pairing than what occurred at Shakespear, and that a greater amount of genetic mixing between culturally distinct populations would have occurred if introductions were to occur on the same day. Future research is required to confirm this prediction. Regardless, genetic mixing between two culturally distinct populations is occurring one-year post-translocation at Shakespear.

2.4.3 Cultural Neighbourhoods

The song sharing nMDS clearly shows two distinct clusters of MRS types, which is indicative of two culturally distinct song neighbourhoods forming one-year post translocation at Shakespear. Disconnected song neighbourhoods appear at Shakespear and is likely the result

of multiple founder males bringing the same common MRS types from their ancestral populations with them and establishing territories throughout Shakespear. Based on Jenkins' (1977) early work involving the formation of "song groups" in tīeke populations, I suggest that when tīeke from culturally distinct populations are released into the same area, they will create distinct song neighbourhoods that are representative of the dialect neighbourhoods of their ancestral population. However, it is possible that tīeke distribution at Shakespear could be driven by habitat quality through patterns of habitat selection, and the formation of culturally monogamous ancestral song neighbourhoods is a by-product of this (Armstrong et al., 2005; Johnson, 2005). Habitat is similar across the park, apart from the more mature and continuous forest in the NZDF land. Birds from Tiritiri Matangi were released a few weeks before birds from Tāwharanui, and therefore had the opportunity to establish their territories on the most suitable habitat in the park, which may have skewed the distribution of the tīeke at Shakespear (Johnson, 2005). Of course, this assumes that tīeke follow ideal distribution principles to habitat quality selection – a trait that was not tested for in my study. Therefore, a formal assessment of habitat quality and demographic variables in relation to tīeke dispersal could shed some light on other potential drivers for the song neighbourhood formation at Shakespear. Early research on tīeke culture demonstrated that tīeke song neighbourhoods persist both in space and time, where young birds will either replace old birds in a territory or establish a new territory in a song neighbourhood and learn the songs of the neighbourhood (Jenkins, 1977). More recent research has indicated that tīeke from different cultures do not respond as readily to one another (Parker et al., 2010). Consequently, these culturally distinct song neighbourhoods that have formed at Shakespear have the potential to inhibit genetic and cultural mixing within Shakespear if they remain intact and persist throughout subsequent generations, irrespective of how they were formed.

Geographic variation in song is well-studied and has been known to occur in several species of passerines (Catchpole & Slater, 2003; Edwards et al., 2005; Podos & Warren, 2007). For

example, Fernández Gómez et al. (2020) recently showed significant song variation in olive sparrows (*Arremonops rufivirgatus*) across two geographical levels (Fernández Gómez et al., 2020), and Bolus (2014) demonstrated that geographic variation in song is evident among common yellowthroat (*Geothlypis trichas*) populations across its North American range (Bolus, 2014). A caveat to many of these studies are that the variation in song detected takes place over extremely large geographical distances, whereas the population of tīeke at Shakespear is confined to an area of 507-ha. That being said, I found similar trends to song sharing within the population; there was an initial decrease in the level of song sharing between male tīeke with increasing physical distances between male tīeke, however, a slight increase was seen in song sharing between males at greater distances apart. So, although male tīeke who are closer together tend to share more MRS types, this relationship is not linear. Thus, this partly confirms my prediction that males that were more distant shared fewer MRS types. This nonlinear relationship is likely a result of males from Tiritiri Matangi sharing MRS types prior to being introduced to Shakespear and establishing territories on opposite ends of the park, coupled by the low sample size at that distance; there were only six males that had territories greater than 2000m apart from one another at Shakespear. These findings in song sharing with distance are consistent with the findings of distinct cultural song neighbourhoods at Shakespear.

I was unable to test if juveniles born from a culturally distinct song neighbourhood remained in their paternal song neighbourhood, or if they established a territory within a culturally distinct song neighbourhood different to their natal territory. This key element was beyond the scope of this project, though it has been shown that young tīeke males will establish territories far away from their social fathers and learn the local dialect of the area (Jenkins, 1977). However, Jenkins (1977) only tracked a small number of male progeny (N = 5), and young males dispersed a maximum distance of ~300m away from their social father. In the case of the population of Shakespear, if young males were to disperse a similar distance, they

would most likely remain within their paternal cultural neighbourhood and therefore inherit similar cultural dialects to their father (Jenkins, 1977; Parker et al., 2010).

Future research should be conducted to investigate whether male progeny remain within the culturally distinct, natal song neighbourhoods, and what MRS types they learn in relation to their social father, their contiguous neighbours, and the culturally distinct song neighbourhood. Research should also consider female song preferences reflected by their dispersal and choice in mate, and in relation to their natal song neighbourhood and social father's dialect. Dispersing males entering a vacant territory in a song neighbourhood will often adjust their MRS repertoire to match that of the neighbourhood, irrespective of their age – though older males are believed to learn new MRS slower than young males (Jenkins, 1977). However, no analytical data indicates the rate of repertoire change, whether it is influenced by density, and what the implications are for MRS sharing with distance or on the cultural integrity of song neighbourhoods. Quantifying these rates of change and exploring these questions could give an indication of how long these song neighbourhoods could persist and would provide insights into the rate of genetic and cultural mixing in new populations established with birds from different cultures.

2.4.4 Cultural Innovation

Innovative song makes up 25% of the total MRS types sung at Shakespear, indicating a rapid change in culture that is being driven by first-generation males innovating song. I discovered that five MRS types were innovated by four first-generation males, and counter to our prediction, these first-generation males appear to innovate song irrespective of their proximity to social tutors. Every first-generation male that innovated MRS also shared an MRS type with another male, indicating that they had social tutors to learn MRS types from,

but innovated regardless. This phenomena of tīeke failing to copy MRS types from a particular neighbour was first recognised by Jenkins (1977), and although the mechanism behind this feature in tīeke song learning could not be explained, it is the fundamental reason why tīeke song neighbourhoods proliferate in nature. It is possible that innovation may be an innate response of young males and could explain why such dramatic changes in tīeke culture are observed over short periods of time in many populations (see *Motuihe* chapter).

Innovation can occur in one of three ways; invention, improvisation and copy errors during learning (Hughes et al., 2002; Jenkins, 1977; Kroodsma et al., 1999; Marler & Peters, 1981; Slabbekoorn & Smith, 2002; Soha et al., 2016; Sonnenschein & Wickler, 1989; Tokarev & Tchernichovski, 2019). Invented song arises when elements of song are newly created. Passerines such as nightingales (*Luscinia megarhynchos*) and swamp sparrows (*Melospiza georgiana*) are known to create entirely new syllables and invent new song combinations from them (Hughes et al., 2002; Marler & Peters, 1981). It appears less likely that tīeke are spontaneously creating new song elements. The spectral features of the innovated phrases at Shakespear are within the range of the rest of the MRS phrases at Shakespear. Tīeke dialects were relatively homogenous as MRS types clustered nicely in an nMDS when comparing the spectral measurements of phrases for each MRS type. If these first-generation tīeke at Shakespear were randomly inventing new syllables, I would expect to see innovative MRS types show up as outliers in the nMDS since features like frequency, pitch and entropy are only limited by the physiologically restricted range of the bird (Gil & Gahr, 2002; Hall et al., 2013; Podos & Nowicki, 2004; Suthers & Zollinger, 2004). Though physiologically identical, populations of tīeke can be distinguished based on their spectral signatures, indicating that their innate spectral range can vary enough to differentiate populations from one another (Parker et al., 2012).

Innovation by poorly copied song occurs in many species of birds and is otherwise known as song learning errors (Baker & Cunningham 1985; Dawkins; 1976; Lynch, 1996). Poorly copied song can result in cultural mutations if the poorly copied song persists in a population (Baptista, 1992; Catchpole & Slater, 2003; Ellers & Slabbekoorn, 2003; Lynch, 1996; Slabbekoorn & Smith, 2002). This is known to occur in tīeke (Baker & Jenkins, 1987; Parker, 2011). Jenkins (1977) noted in his study-site at Cuvier that migratory males who filled vacant territories would sometimes incorrectly copy song types, which would result in a new song type forming if it was inherited by other contiguous neighbours. Parker (2011) demonstrated that song learning errors in tīeke are commonplace and are the hallmark indicator of the formation of divergent cultures. It is possible that the innovated MRS in first-generation males comes from song learning errors, and one may be tempted to speculate that the high rate of innovation seen at Shakespear is a reflection of the cultural mutation hypothesis, where the social transmission of MRS is subject to a higher rate of learning errors post-translocation (Jenkins 1977). However, it is relatively easy to audially identify the lineage of an incorrectly copied MRS, especially during the first year of song learning as demonstrated by Jenkins (1977). Although poorly copied MRSs may provide one explanation for high levels of innovation at Shakespear, poorly copied MRSs were easily distinguishable, and in the cases where a poorly copied MRS was recorded and identified, I selected for the most "correct" phrase within the MRS that best represented the MRS type the first-generation bird was trying to sing (see example in Figure 2.8).

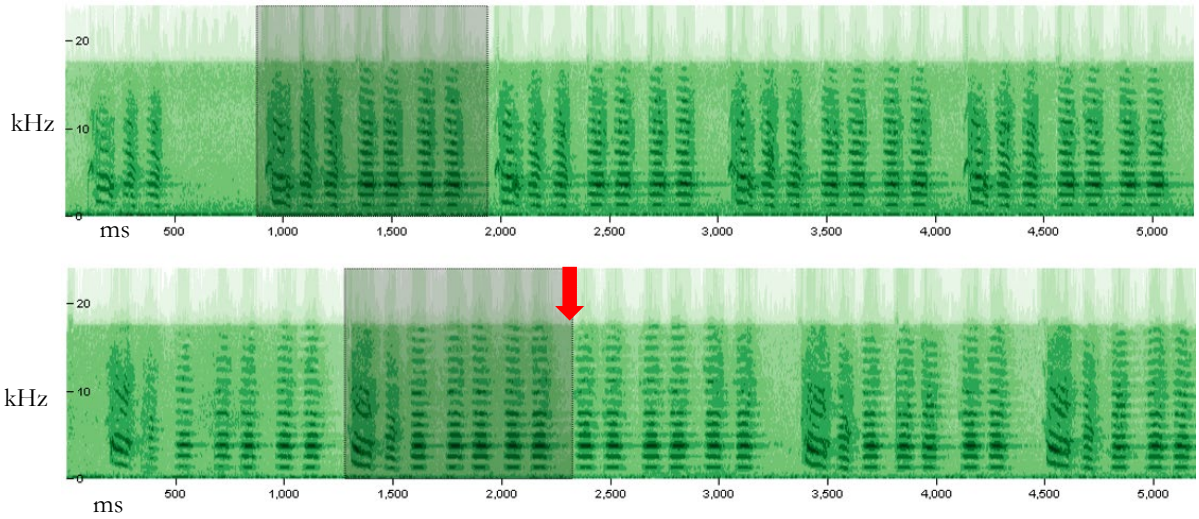


Figure 2.8: Phrases from a known MRS type (MRS type 2) sung by an adult male (above; Territory 20) and a first-generation male (below; Territory 05). Note that the "best" representative phrase of that first-generation male's MRS was selected for further analysis. The above spectrogram is the correctly sung version of the MRS type, and the below spectrogram is a poorly copied, yet-to-be-crystallised attempt at that MRS type. The red arrow indicates a forgotten syllable in a phrase, and the beginning and end of the MRS were sung incorrectly. These phrases were classified into the same MRS type as although the first-generation MRS was poorly sung by this male, the core of the song was easily distinguished both audially and visually, and usually the focal male would get one phrase within the MRS correct. Major differences primarily exist within the tempo that phrases or syllables were given, and consistency with which the first-generation male could hold a note.

Innovation via improvisation occurs when pre-existing syllables found in established song are rearranged to form new MRS types (Soha et al., 2016). This type of innovation can be seen in migratory passerines such as sedge wrens (*Cistothorus stellaris*), slate-coloured bulbuls (*Laniarius funebris*), grasshopper sparrows (*Ammodramus savannarum*) and swamp sparrows (*Melospiza georgiana*) (Kroodsma et al., 1999; Marler & Peters, 1981; Soha et al., 2009; Sonnenschein & Wickler, 1989). Evidence exists showing tīeke doing this at the phrase level, where pre-existing phrases belonging to different MRS types were combined, resulting in a new "hybrid" MRS type (Jenkins, 1977). The results I present here support innovation via improvisation for the new MRS types recorded at Shakespear. These first-generation males appear to be innovating MRS by learning syllables and/or phrases present in the population

and rearranging them, and their repetition within the MRS, to create their own distinct MRS; however, this has yet to be discretely tested.

It is possible that males from Tiritiri Matangi and Tāwharanui were also innovating song, but this was impossible to test. Historical recordings of male tīeke from Tiritiri Matangi were obtained (recorded in 2008), but given the rapid cultural changes found in tīeke, this comparison would be confounded (see *Motuihe* chapter). To elaborate, results from both Shakespear (25% innovation over one year) and Motuihe (74% innovation over 11 years) indicate that song culture (and thus MRS types) in male tīeke changes rapidly and therefore there would be little overlap between MRS types sung over a decade ago compared to those sung today from Tiritiri Matangi males. Further, a mass depredation of tīeke at Tāwharanui occurred between 2018-2019 diminishing the population from ~300 to ~65 individuals and likely resulted in a significant loss of MRS types (see *Tāwharanui* chapter). Future directions from this study could investigate the rate of change of known MRS types from the founder group of male tīeke post-translocation. Once the founder population has been identified, each male's repertoire should be recorded prior to release, and then re-recorded one-year post-release. This would give an indication of whether innovation may be an innate response of all male tīeke post-translocation.

Parker et al. (2012) speculated that first-generation male tīeke would innovate song if they did not have an adult social tutor to learn from. I therefore hypothesized that the low population-density settings following a translocation event could be the driver for song innovation in young males. However, it appears that young males innovate regardless of their proximity to adult social tutors, and that innovation may be an innate response of young males. Higher innovation predicted by low population-density situations like that of Shakespear may therefore be explained simply by young male survivability due to viable habitat availability rather than their proximity to social tutors. Low population-density and

high habitat availability in newly established populations leads to a higher survivability of young male tīeke (Armstrong et al., 2005). More young males can acquire a territory, and some of those males innovate (in Shakespear's case 40% of first-generation males) MRS either by using their innate chatter call as a template (Parker et al., 2012) or by rearranging culturally transmitted phrases and/or syllables available to them into new MRS types. The more young males that survive and establish territory, the more innovation that will be observed. In older, established populations, innovation appears rare, but it may not be because of the abundance of social tutors culturally transmitting MRS, but instead by juvenile survivability being highly sensitive to population density (Armstrong et al., 2005; Jenkins, 1977). Tīeke are territorial, long lived and a site faithful passerine who have low annual mortality rates in the absence of exotic predators (6.5% - 11%), and can retain the same territory for 20 years in the wild (Armstrong et al., 2005; Taylor et al., 2008). Although tīeke fecundity is heavily influenced by population density, it is conceivable that in most populations the rate of habitat becoming available for occupancy versus the rate of new males being born each year are not equal (Armstrong et al., 2005; Blackburn, 1966; Jenkins, 1977). Consequently, vacancies tend to be rare in relation to male recruitment, and new males have a difficult time establishing themselves in high-density populations. If new males cannot establish a viable territory, they either migrate off-island, out of sanctuary or are forced onto poor-quality habitat; either way their mortality rate is high. Thus, overall innovation in high-density populations is kept minimal, not because of the number of social tutors, but because of high mortality rates in young males who are unable to establish territories.

2.5 Conclusion

My prediction that males that were further apart from one another physically would share less MRS types with one another was found to be mostly true. Birds shared less MRS types with one another as distances increased, however the trend ceased at the greatest distances apart. This can be explained by limited space to move due to the size and shape of Shakespear, and founder males singing the same MRS types from the same source population prior to being translocated to Shakespear, and establishing territories on opposite ends of the park.

Assortative pairing did occur at Shakespear, but the degree of assortative pairing was likely an overestimate. Mate pairing within ancestral populations was not exclusive and therefore genetic mixing between two culturally distinct populations occurred rapidly after translocation. This finding suggests that previous concerns of birds from different cultures not mating with one another may be unwarranted and indicates that MRS is not solely sufficient enough to act as a pre-mating barrier between tīeke of different cultures.

First-generation males did inherit ancestral song, but not a single tīeke learned both source population dialects present at Shakespear, and were instead found within distinct cultural neighbourhoods that had formed one-year post-translocation. These cultural contact barriers at Shakespear may prolong or inhibit further genetic and cultural mixing if young males remain within their paternal neighbourhoods given the range of dispersal and the size of the current culturally distinct neighbourhoods. However, a caveat to this was the rapid innovation observed at Shakespear; young males innovating MRS may blur these neighbourhood boundaries and facilitate genetic mixing between neighbourhoods with each passing generation. Innovation by young males does not appear to be explained by first-generation male proximity to adult social tutors as predicted, and instead may be an innate

response of young males. The driver of innovation may still be explained by density, but in the context of habitat availability for density sensitive young males rather than the availability of social tutors.

To summarise, if the conservation translocation goal for Shakespear was to increase both cultural and genetic diversity, it was a hallmark of success. Genetic mixing occurred between the two populations, and their ancestral dialect was preserved, though, cultural evolution can already be detected.

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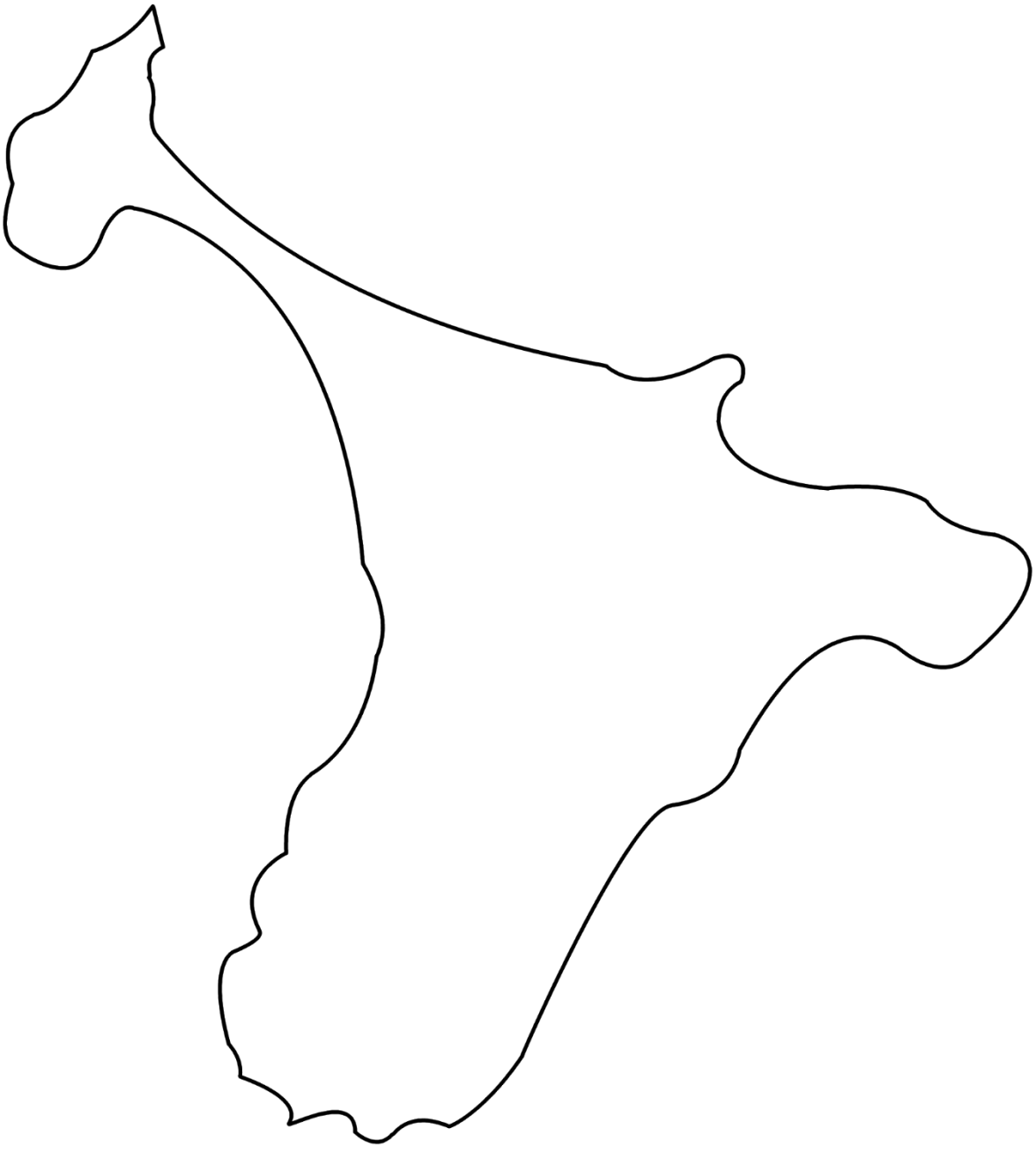
Chapter 3: Motuihe - rapid cultural evolution within a single-sourced population



3.1 Introduction

One of the most intriguing features of songbirds is their ability to form distinct, geographical song dialects – or "cultures" (Allen et al., 2013; Aplin et al., 2013, 2015; Catchpole & Slater, 2003). Cultures in oscine passerines emerge through the transmission of socially learned behaviours or skills being inherited between generations within a group or community over time (Aplin, 2019; Aplin et al., 2015; Laland & Janik, 2006). These socially transmitted traits can be anything from the emergence of new song types to the development of novel foraging techniques (Aplin, 2019; Aplin et al., 2015; Catchpole & Slater, 2003; Hunt & Gray, 2003; Logan et al., 2016; Slater, 2003). The formation of distinct song culture in oscines can develop through any combination of population structure, geographical variability, assortative mating and/or local conformity (Aplin, 2019). Over longer timescales, social learning could potentially also give rise to the natural development of new species through genetic evolution (Edwards et al., 2005; Lachlan & Servedio, 2004; Parker et al., 2010; Phillimore et al., 2006; Podos & Warren, 2007; Slabbekoorn & Smith, 2002). For example, Irwin (2000) demonstrated that the east and west forms of greenish warblers (*Phylloscopus trochiloides*) in Siberia do not interbreed with one another despite occupying the same habitat and having overlapping population ranges. He concluded that gradual interspecific structural changes to song through geographic variation eventually lead to a divergence of culture, which in turn caused a divergence into two subspecies (*P. t. viridanus* and *P. t. plumbeitarsus*) (Irwin, 2000).

In tīeke (North Island saddleback; *Philesturnus rufusater*), Male Rhythmical Songs (MRSs) are conspecific recognition signals (Jenkins, 1977) that are socially learnt and function to transmit information to members of the same species, and are known to change with geographical isolation over relatively short periods of time (< 50 years) (Parker et al., 2010, 2012). Parker et al. (2012) speculated that these changes were a result of cultural bottlenecks and cultural

mutations. Under the "cultural bottleneck hypothesis", the small founding population represents only a fraction of the total cultural diversity of the ancestral population, and as such newly established populations exhibit diminished song diversity (Baker & Jenkins, 1987; Hooson & Jamieson, 2003; Jenkins, 1977; Parker et al., 2012; Potvin & Clegg, 2015). Serial translocations heighten the effects of cultural bottlenecks and further diminish song culture in new populations (Figure 1.3) (Baker & Jenkins, 1987; Hooson & Jamieson, 2003; Parker et al., 2012). With the "cultural mutation hypothesis" (Dawkins, 1976; Jenkins, 1977; Lynch, 1996), socially transmitted songs such as MRS are subject to a high rate of learning error (Baptista, 1992; Catchpole & Slater, 2003; Ellers & Slabbekoorn, 2003; Lynch, 1996; Slabbekoorn & Smith, 2002). These errors can lead to changes in song diversity within and between populations (Jenkins, 1977; Parker et al., 2012). Over time, some of these cultural mutations accumulate and give rise to divergent song types (Ellers & Slabbekoorn, 2003; Irwin, 2000; Lynch, 1996; Tokarev & Tchernichovski, 2019).

Although the formation of animal cultures is a naturally occurring phenomenon in wild populations (Aplin, 2019; Galef, 1992; Heyes, 2012; Podos & Warren, 2007), conservation translocations conducted to lower the extinction risk of tīeke may have inadvertently accelerated this social process (Parker et al., 2010). Tīeke numbers had historically declined to approximately 500 birds that were restricted to a single, offshore island population by the late 1800s (Figure 1.2) (Atkinson & Campbell, 1966; Hooson & Jamieson, 2003; Lovegrove, 1996). Translocations were conducted to multiple islands and predator-controlled mainland sites over the last 100 years, and the species is now estimated at approximately 7000 birds (Parker, 2013) across 24 isolated populations (Figure 1.2 & 1.3). During this process of species recovery, distinct dialects have formed (Parker et al., 2012). If the formation of distinct song cultures in tīeke has been accelerated, it begs the question - notable to both conservation scientists and behavioural ecologists alike - of whether the processes of

population divergence and potential speciation have also been accelerated (Lachlan & Servedio, 2004; Lambert et al., 2005; Parker et al., 2010, 2012).

To address this question, a series of playback experiments were conducted on a population of tīeke on Motuihe Island to quantify whether the process of change in MRS between populations had any functional significance as a communication signal for individual tīeke populations (Parker et al., 2010). Fundamentally, Parker et al. (2010) investigated early signs of population divergence by testing whether the tīeke from Motuihe responded differently to conspecific signals from increasingly culturally distant populations via serial translocations (Figure 1.3). Tīeke were tested with playbacks of familiar MRS of the island and unfamiliar MRS from Hen and Cuvier islands and their responses were quantified. The study concluded that the delayed response seen when tīeke heard MRS from Hen and Cuvier indicated that discriminatory behaviours to unfamiliar song developed rapidly (<25 years) (Parker et al., 2010). The ability to discriminate between song types and respond differently is important for mate preferences, juvenile dispersal, and spatial patterns of settlement (Catchpole & Slater, 2003; Jenkins, 1977; Lynch, 1996; Podos & Warren, 2007; Slater, 2003). Furthermore, song is known to facilitate gene flow through sexual selection (Catchpole & Slater, 2003; Lambert et al., 2005; Phillimore et al., 2006; Slabbekoorn & Smith, 2002; Slater, 2003), hence could be a precursor for human induced allopatric speciation (Parker et al., 2010). With the long-term goal of eventually reintroducing the isolated populations of tīeke back to their native home-range, these findings are relevant to conservation biologists who aim to secure the future of New Zealand's endemic species (Armstrong & Davidson, 2006). Therefore, quantifying the natural process of MRS change *within* an isolated population's song repertoire is an integral component to fundamentally understanding whether tīeke born from separate, culturally distinct populations will eventually recognize, and ultimately mate with one another when introduced into the same area. Three years post-translocation, the entire Motuihe population's song repertoire was recorded which, when used as a baseline measurement for

tīeke culture at Motuihe, provided a unique opportunity to study how a completely isolated population's song culture can change with time. I revisited the island 11 years later in 2019 and collected audio recordings of male tīeke MRS. This allowed me to specifically investigate the rate of change in and/or increase to MRS types on the island. Tīeke on Motuihe were analysed at two discrete time periods (2008 and 2019), and as such will be considered as two separate populations and referred to by the year that they were recorded for the duration of this case study.

In this chapter I quantify the natural process of MRS change *within* an isolated population on Motuihe Island (Figure 1.7). This is an integral component to fundamentally understanding the rates of change of tīeke song dialects within the context of a single-source translocation to locations in the process of habitat restoration. I also compare the MRS types of the population at the time of translocation with the now well-established tīeke population 11 years later (i.e. 2008 vs 2019). Specifically, I compare population-level MRS diversity, assess the changes to population-level MRS repertoire and identify any changes to MRS variability in an 11-year time span. Together with the other chapters of my thesis, this study improves our current understanding of song culture evolution in relation to conservation.

For this study I predicted that:

1. The population song repertoire has changed over a timescale of 11 years – there will be new MRS types present in the 2019 population in addition to the loss of founding MRS types.

2. Song diversity has increased as the population has grown – there will be more MRS types present and move individuals in the 2019 population compared to the 2008 population.
3. Variability in song structure has increased (measured by the physical acoustic characteristics) within the 2019 population as a result of population size and population establishment.

3.2 Methods

3.2.1 Study-site & Population

Motuihe Island is a 179-ha recreation reserve located 19km east of Auckland City in the Hauraki Gulf (Figure 1. & 1.3). It is jointly managed and controlled by the Department of Conservation (DOC) and the Motuihe Trust (Motuihe Trust, 2019). The island has served many purposes - from a quarantine station during the smallpox pandemic to a prisoner of war camp during World War I – and as such, its lands have been heavily modified (Motuihe Trust, 2019). However, when DOC acquired the land in 1987, ecological restoration of Motuihe followed soon thereafter (Motuihe Trust, 2019). In 1993 and 1995, poison drops were administered to eradicate Norway rats (*Rattus norvegicus*) and mice (*Mus musculus*) from the island (Parker & Laurence, 2008). Restoration of Motuihe was further intensified with the establishment of the community led Motuihe Island Restoration Trust in 2000 (Motuihe Trust, 2019; Parker & Laurence, 2008; Parker, 2011). A subsequent eradication operation involving poison drops, poisoned bait, traps, and specialist hunters and dogs (*Canis familiaris*) was conducted to eliminate all rabbits (*Oryctolagus cuniculus*) and cats (*Felis catus*) on the island (Motuihe Trust, 2019; Parker & Laurence, 2008). The operation was a success and Motuihe was declared pest-free in 2004 (Motuihe Trust, 2019; Parker & Laurence, 2008). Shortly

thereafter, tīeke were the first native passerines reintroduced onto the island (Parker & Laurence, 2008). Incursions of rats have been known to occur at Motuihe Island as a result of the frequent island visits by boaters. As such, extensive poisoned bait stations, camera traps and trap lines are maintained by DOC and the Trust to rapidly eliminate any intruding pests. Many of the island's forests are a result of intensive replanting efforts made by conservation volunteers and make for suitable tīeke habitat once properly established. Intensive replanting of native vegetation across the island began in 2003, and therefore only 18-ha of forested land (aptly named the Tīeke Trail) located on the south-western coast of the island is old growth. The majority of the tīeke population can be found in this area, but tīeke have spread across the entire island, occupying habitat as it becomes viable.

The group composition of tīeke selected to be reintroduced to Motuihe was composed of birds from a single island (Parker & Laurence, 2008). An even sex ratio of 20 colour banded birds were sourced from Tiritiri Matangi – an offshore island population established in 1984 by 24 tīeke from Cuvier (Figure 1.3) (Hooson & Jamieson, 2003; Lovegrove, 1996; Parker & Laurence, 2008). The birds were released onto Motuihe Island on February 26th, 2004, thus making Motuihe a third-level translocated population as the population of tīeke used to establish Motuihe had gone through three serial bottleneck events (Parker & Laurence, 2008). At the time, single-sourced, serial translocations were quite common (Hooson & Jamieson, 2003; Lambert et al., 2005) as emphasis was put more on the survivability of the translocated individuals rather than the conservation of the song dialects (Lovegrove, 1996; Taylor et al., 2005). In this respect Motuihe was a breakthrough translocation, having a 70% survivability one year post-translocation; the second highest survival rate ever recorded at the time for tīeke and well above average (mean = 56%, range 41-79%, N = 5) (Parker & Laurence, 2008).

3.2.2 Field Methods

Access to Motuihe Island was limited by the unexpected closure of public access to the wharf after a storm in September 2019, hence start and end dates were based on the DOC supply boat schedule to access the island. As such, audio-recording took place during a fieldtrip from December 1st to the 8th, 2019. I collected the audio-recordings using a Marantz PMD661MKII Handheld Solid-State Recorders, Sennheiser MKE 600 Shotgun microphone and a Rycote Softy wind guard mounted on a Rycote pistol grip. Raw recordings were in .WAV format with a sample rate of 48-kHz, and 24-bit sampling precision. The raw files were given a unique file name which included the name of the recorder, date of recording, and area of recording for future use. Recordings of tīeke did not occur on days with rain or high wind. Due to access constraints and a previous underestimation of the number of tīeke on the island, I focused on recording vocalisations rather than plotting territories. Therefore, the island was arbitrarily divided into north, east, south, and west sections. Each section of the island was sampled a minimum of three times, on different days, alternating between morning (sunrise to 1130) and evening (1500 to sunset) recordings. For example, the east section of the island would be sampled in the morning, west in the evening, then west in the morning, east in the evening of the following day. This ensured even sampling durations throughout the park to capture as many MRS types as possible. Emphasis was put on trying to capture the entire population-level MRS repertoire rather than the repertoires of individual males. I primarily followed permanent tracks to first detect males (visually or aurally), and only went off-track if necessary to record focal tīeke after finding singing males. Tīeke vocalise frequently and loudly and can be heard from distances of over 100m away (Jenkins, 1977; Parker, 2011). When I found a male tīeke singing an MRS, I would follow it for up to 30 minutes while audio-recording its song and making general remarks about the focal bird's behaviour, then continue down the trail. I also made a general statement of the area and

location for each recording by use of the Google Earth (Google LLC, 2020) app on an iPhone 6s (Apple Inc, 2020).

3.2.3 Song Processing

Tīeke MRS are easy to distinguish from one another both visually (from digitally rendered spectrograms) and aurally (Figure 3.1) and as such this remains the most widely accepted method of categorising bird song type (Parker, 2011). I did all the song analysis and segmentation to standardise selection criteria across all populations and remove any differences due to the observer. The Motuihe raw recordings of tīeke from 2019 were first inspected in Raven 1.6 (Cornell Lab of Ornithology, Ithaca, NY, USA). High quality tīeke vocalisations were then cut out of the raw recording and new .WAV files (sample size = 24 bits, pad size = 1.1 seconds) were created for each track. Each track was given a unique, annotated filename which included the type of vocalisations (chatter, MRS, or quiet call), recordist, date, and location of the recording. Tracks which included MRS were subsequently uploaded to KOE (Fukuzawa et al., 2020; Webb, 2020) (FFT = 512, overlap = 50%) and the single most repeated phrase within the MRS was manually segmented to be analysed as a representative of the entire MRS following the method outlined by Parker et al. (2012) (Figure 3.1). These segmented MRSs were sorted by duration and compared using KOE's features "Unit table" and "Exemplars". These tools allow researchers to bulk label, and visually and aurally inspect and compare all spectrograms and song type classifications in an automatically generated reference page based on specific selections. Song types were then assigned to each MRS based on audio and visual similarities (matching). MRS matchings were generally conservative, but allowances were made for individual variation present between birds within Motuihe i.e. small variations in tempo, pitch, or the number of repeated syllables within a phrase (Figure 3.1). A class of 57 undergraduate students with no prior

experience with birdsong or audio programs were asked to replicate phrase type matching on a subset of Motuihe song (containing 191 MRSs and 20 different MRS types) following the same method of classification using the same KOE program. MRS types were compared between each student and my originally categorised phrases to check for agreement.

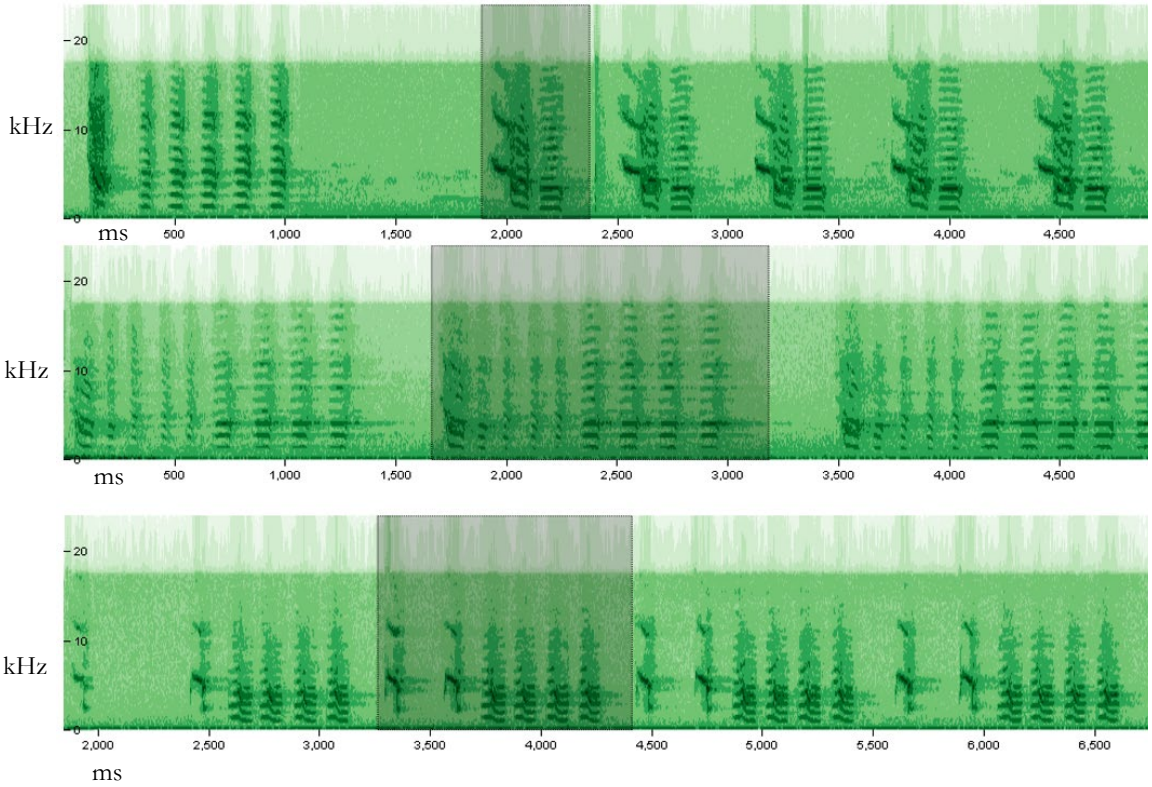


Figure 3.1: Spectrograms showing three different MRS types sung by male tīeke at Motuihe. The grey rectangle indicates the single phrase selected to represent the song type and to be measured for spectral analysis.

3.2.4 Collection & Song Processing of Historic Recordings

I obtained the historic recordings from Parker et al. (2012), which were collected from December 2004 to November 2008 from the following island populations: Hen, Cuvier, Red Mercury, Whatupuke, Stanley, Tiritiri Matangi, Little Barrier, Moutohora, Lady Alice, Coppermine, Kapiti, Mokoia and Motuihe (Figure 1.2). These historic recordings were used

along modern recordings to determine what spectral features best distinguish tīeke song culture between populations. Each of the 13 established populations were visited for 5-15 days, by 1-4 researchers, on 1-4 occasions (Parker et al., 2012). Recordings were taken with Sony Hi MD MZ-NH700 mini disc recorders, Sennheiser K6 recording modules and M66 shotgun microphones fitted with Rycote Softy wind guards and mounted on Rycote pistol grips (Parker, 2011). Raw recordings were inspected (FFT = 256, Hann window, 5.8ms, 50% overlap) using Raven 1.2.1 (Cornell Lab of Ornithology, Ithaca, NY, USA) (Parker, 2011). High quality tīeke vocalisations were then cut out of the raw recording and new .WAV files were created for each track containing MRS using Sony SonicStage (Sony Corporation 2001 - 2007) software with 16-bit sampling precision and a 44 kHz sampling rate (Parker et al., 2012). I uploaded the historic island recordings to KOE (FFT = 512, overlap = 50%) in 2019 and manually segmented them following the same procedural method of selection as previously stated (see *Song Processing* section), though only the phrases from Motuihe in 2008 were classified into MRS types.

MRS types existing in the population of tīeke at Motuihe in 2019 and 2008 were then compared, and any type that was audially and visually similar between the two populations were labelled with the same MRS type classification name. This gave me an indication of the level of change in song diversity between the two time frames, as well as insight on how the song repertoire of the population had changed in the last 11 years.

Historic recordings of Little Barrier Island were considered as two separate populations (LBI C & LBI W) as the northeast and southeast quarters of this large island (2817-ha) were established from different translocation events (Figure 1.3) (Parker et al., 2012). For analysis, Motuihe recordings were separated into two groups based on the time period sampled (2008 vs 2019). Therefore, although 15 of the 24 populations were analysed (Figure 1.2 & 1.3), 17 datapoints are represented.

3.2.5 Spectral & Statistical Analyses

A spectral analysis was conducted in KOE on each phrase selected for all modern and historic populations (see *Tāwharanui* chapter). The spectral features were exported to Microsoft Excel (Microsoft Corporation, 2002) and the mean, median, standard error and standard deviation were then calculated for each feature of each phrase. These measurements represent multiple physical acoustic measures of each recording and were analysed using a range of multivariate techniques. All multivariate analyses were run using the PRIMER v7.0.17 computer program (Quest Research Limited, 2015) with the PERMANOVA+ add-on package (Anderson et al., 2008). A Linear Discriminant Analysis (LDA) was run using every population to determine which features best explained the relationships between populations. Populations were averaged and translocation levels (Ancestral, First, Second, Third, or Mixed) (Figure 1.3) for each recorded population and were used to provide the replicates for the LDA, which highlighted the physical acoustic features that best explain the relationships between the populations (see *Appendices*). These "between-population" features were checked for normal distribution by running a draftman plot for each feature for each population (see *Appendices*) (Anderson et al., 2008). It was determined that none of the between-population features needed to be transformed prior to further analysis. Each population was individually scrutinized for extreme outliers, resulting in nine songs being removed from the dataset.

To directly compare song variability between the 2008 and 2019 populations at Motuihe in non-dimensional acoustic space, a non-metric multi-dimensional scaling (nMDS) ordination plot was run containing only the between-population physical acoustic features of each manually segmented and measured phrase, from both populations. The acoustic features were first standardised, then a Euclidean Distance Matrix was calculated, and finally the relationship among the two populations were visualised using an nMDS. The features were

not averaged at the population level, so each MRS as a function of its spectral features existed as a single point in the nMDS. The proximity between points represented how similar one MRS was from another – points on the nMDS that were closer together shared more spectral similarities.

Two more nMDSs were run in the same fashion as previously mentioned but using the "within-population" discriminatory acoustic features that best delineate song types as determined by an LDA using only known song types within a population and averaging at the song type level to provide the replicates for the LDA (see *Shakespear* chapter). The first nMDS contained only the overlapping song types of the two populations to see if there were notable acoustic differences and was colourised in two separate ways: at the song type level and at the population level (Figure 3.5a). The second contained all song types of both populations and was colourised at the population level (Figure 3.5b). To determine the drivers for the acoustic differences seen between all songs of 2008 and 2019, the within-population discriminatory features were overlaid as vectors onto the nMDS where the length and direction of a vector represented the strength and direction of influence of a particular feature (Figure 3.6) (Anderson et al., 2008).

Biologically relevant acoustic measurements (as defined by Parker et al. (2012)) from Motuihe songs of 2008 and 2019 were collated into a separate spreadsheet. These relevant features that are commonly used in the analysis on tīeke song were: duration, mean amplitude modulation, and both the mean and variance of pitch, entropy, frequency modulation, goodness of pitch and frequency (Parker et al., 2012). These 10 spectral features were averaged at the population level (i.e. Motuihe in 2008 vs Motuihe in 2019) resulting in a single value for each feature (Table 3.1). Descriptive statistics were calculated for the averages of each feature for Motuihe song in 2008 and 2019. A one-way ANOVA was run between the overlapping MRS types of 2008 and 2019 Motuihe to test for any significant changes to their

physical acoustic characteristics (Figure 3.7). Another one-way ANOVA was run using the same 10 features but this time containing every song of Motuihe in 2008 and 2019 (Figure 3.8).

3.3 Results

3.3.1 Tīeke at Motuihe

In 2008 it was conservatively estimated that Motuihe could support up to ~80 individuals as long as the island remained pest-free (Parker & Laurence, 2008). This estimate was based on available habitat suitable for tīeke at the time of translocation (18-ha). Work effort for the 2019 season was based from this estimation, however, by the end of the 2019 field season the population was estimated at three times the predicted amount (N ≈ 240). This was likely due to habitat becoming rapidly available post-revegetation (Figure 3.3). With replanting initiatives expanding viable habitat from 18-ha in 2004, to presently ~165-ha (Figure 3.3), tīeke were found spread relatively uniformly throughout the entire island in the 2019 season, though more densely packed territories tended to be in mature coastal forested areas (Atkinson & Campbell, 1966). No tīeke were seen with colour bands, which indicates that none of the original founder population of tīeke are still alive at Motuihe – it is possible they were missed as tīeke can live up to 20 years in the wild (Taylor et al., 2008) with quite low annual mortality rates (6.5 - 11%) (Armstrong et al., 2005). However, 75% of the founder population was comprised of adult birds older than a year (Parker, 2011), so if they were alive, it would have been very close to the end of their known maximum lifespan. Since tīeke could not be individually identified, and there was not enough time to quantify and confirm each territory on the island, it is possible that singing males were missed in the 2019 season,

and that the same individual was recorded multiple times, especially if they were a prolific singer.

3.3.2 Sampling Effort

Recording effort was proportionate for the 2008 and 2019 field seasons; the date of recording, duration spent on the island, start and end times of recording, and the number of researchers in the 2008 and 2019 seasons were comparable. Work effort, however, was disproportionate; there were many more male tīeke spread across a much wider area of land during the 2019 season. The field season in 2008 was confined to 18-ha of habitat containing roughly 23 singing males (Parker & Laurence, 2008). The 2019 field season encompassed nearly the entire island (179-ha) with approximately 120 males singing. Due to the larger distance and more tīeke present, proportionately less time was spent per individual bird in 2019 but resulted in 177 more MRSs being recorded when compared to 2008. As males could not be individually identified, and little time was spent identifying territory boundaries of each male recorded, I am unsure if the entire population's repertoire was captured. Therefore, the results that I present here are conservative and may underestimate larger, underlying differences.

3.3.3 Quantitative Song Types

A total of 73 raw recordings were captured at Motuihe in 2019, yielding 280 tīeke vocalisations. Of these vocalisations, 221 tracks were identified to contain MRS, which resulted in a final total of 235 phrases (each representing an MRS) manually selected for further analysis. These 235 phrases were categorised into 27 different phrase types (each

representing an MRS type), which composed the total MRS repertoire of the 2019 Motuihe population. The song sorting technique was validated by 57 independent undergraduate students who had no prior experience with bird song analysis or sound analysis programs. An average song matching score of 69.3% (range = 34.5% - 90.1%) was achieved. It should be noted that this practical was conducted virtually during the Covid-19 lockdown period and may have affected the clarity of instructions and motivation of many students.

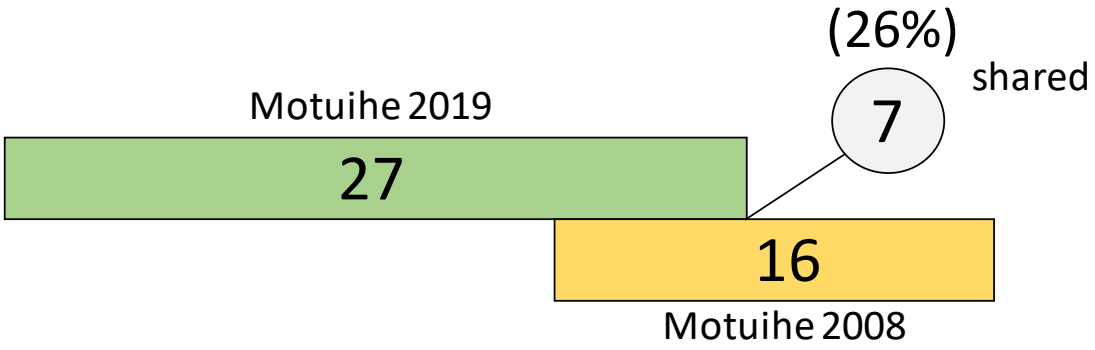


Figure 3.2: A visualisation of the quantity of MRS types present in 2008 and 2019, and how many overlap between the two distinct times.

A total of 141 raw recordings were captured at Motuihe in 2008, yielding 137 tīeke vocalisations. Of these vocalisations, 36 tracks were identified to contain MRS, which resulted in a final total of 58 phrases (each representing an MRS) manually selected for further analysis. These 58 phrases were categorized into 16 different phrase types (each representing an MRS type), representing the total MRS repertoire of the 2008 Motuihe population. This change in the total amount of song types between 2008 and 2019 indicates that there has been a 59% increase (N = 11) in the amount of song types present on the island since 2008 (Figure 3.2). The 16 MRS identified for the 2008 population were compared to the 27 types identified for the 2019 population. It was found that 26% (N = 7) of song types were present in both 2008 and 2019, whereas 74% (N = 20) of the songs were only found present in the 2019 population (Figure 3.2). Of the seven song types that

were shared by both time periods, four were the most prolific MRS in both populations. Interestingly, one rare type from 2008 (N = 1) was recorded in 2019 on a number of occasions (N = 11) and another rare MRS type heard within the 2008 population (N = 1) was also found in the 2019 population, and was still one of the rarest in the population (N = 1) (see *Appendices*).

3.3.4 Comparative Spectral Song Characteristics

A grand total of 4,426 MRSs were manually segmented from 17 populations (mean = 295, range = 45 - 628). The spectral analysis conducted in KOE resulted in 233 measured and potentially useable features per phrase (each representing an MRS) for every population (see *Tāwharanui* chapter). The LDA determined that seven out of the 223 measured spectral features best discriminated song between populations (see *Tāwharanui* chapter) and 48 out of the 233 best discriminated between MRS types within populations (see *Shakespear* chapter). At the population level, I found that the nMDS for 2008 and 2019 highlighted that the spectral variables of Motuihe in 2019 occupied a broader range of acoustic space than the 2008 population (Figure 3.4). Although stress was high in the 2D nMDS (stress = 0.18), it remained within acceptable levels and the 3D nMDS was much lower (stress = 0.11), indicating that this was a reliable representation of the physical acoustic nature of both populations in non-dimensional space.

An nMDS was run using the 48 discriminatory features that best reflected the relationship between MRSs within a population (see *Appendices*). It contained only the MRS types shared between the 2008 and 2019 populations. A weak clustering of MRS types was observed from the resulting nMDS (Figure 3.5a). However, when overlapping MRS types were identified based on the year, a clear division and shift of acoustic space between songs from 2008 and

songs from 2019 is observable (Figure 3.5b). The same trend can be seen when all MRS types are compared in a similar fashion (Figure 3.6). Vectorised overlays of the 48 discriminant features indicates that most of the changes in song position between the two populations in the nMDS were a result of changes in Mel Frequency Cepstral (MFC)-derived features and coefficients (Figure 3.6).

MRS types found in both 2008 and 2019 showed no statistically significant changes to any biologically relevant physical acoustic measurements (Figure 3.7). However, when the biologically relevant features of every song type for 2008 and 2019 were compared, there were statistically significant changes to the duration, variation in entropy and mean goodness of pitch (Figure 3.8). The 2019 samples had increased in both song duration (P = 0.029, mean = 955ms, range 284 - 1887, N = 235) and variance in entropy (P = 0.016, mean = 1.506-dB, range 0.276 - 4.05, N = 235), and a decrease in mean goodness of pitch (P = 0.0001, mean = 0.223-Hz, range 0.11 - 0.434, N = 235) (Figure 3.8 & Table 3.1).

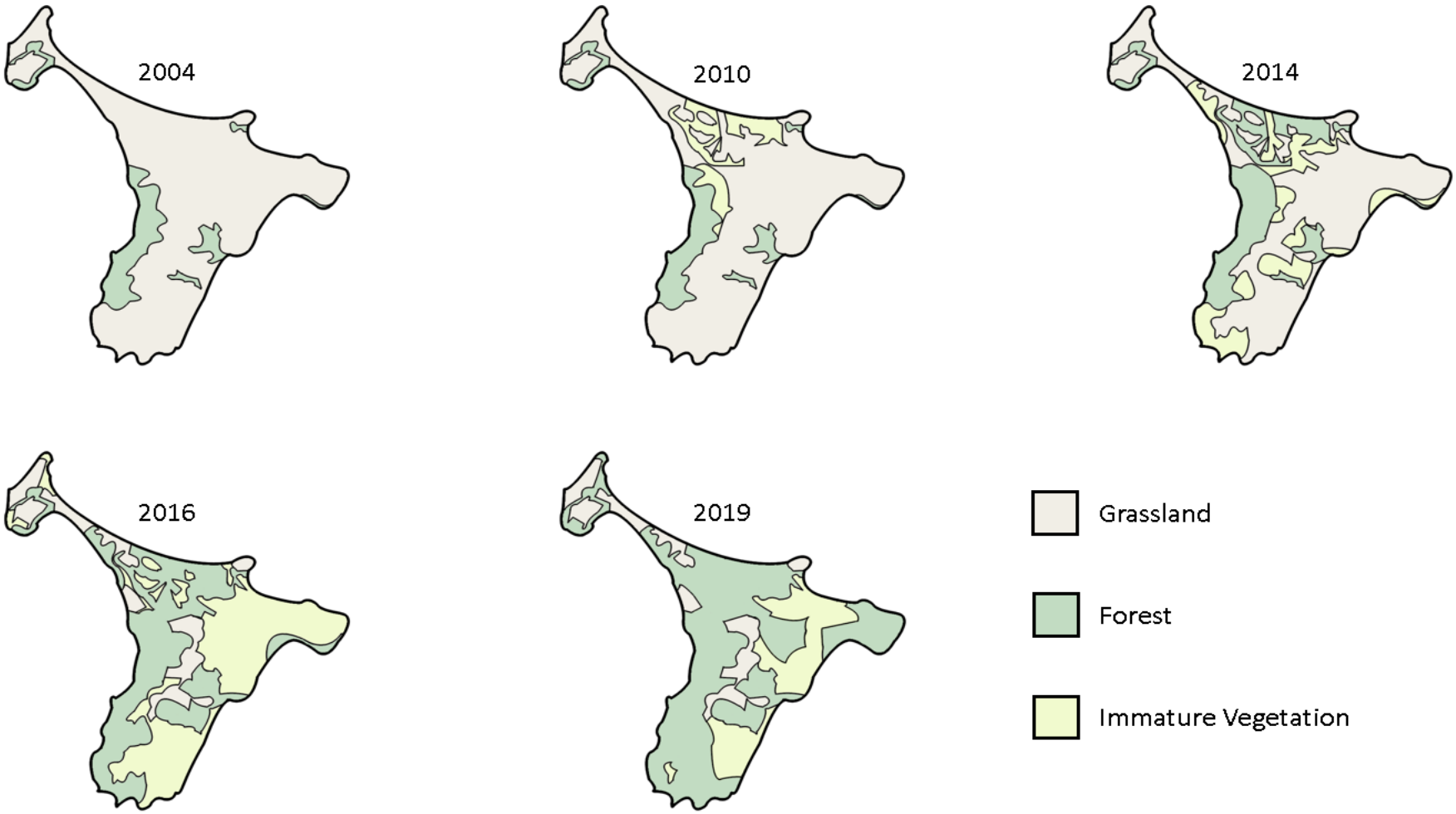


Figure 3.3: Vectorized image of vegetation cover on Motuihe, referenced from satellite imagery (see *Appendices*). Grey areas are uninhabitable areas in the park, often composed of remnant paddocks, roadways, or infrastructure. Areas highlighted in green are forested areas that are suitable habitat for tīeke. The quality of the habitat could not be assessed via satellite imagery. Areas highlighted in yellow are recently revegetated sections of the park and contain immature vegetation most likely not suitable for tīeke to establish territories on.

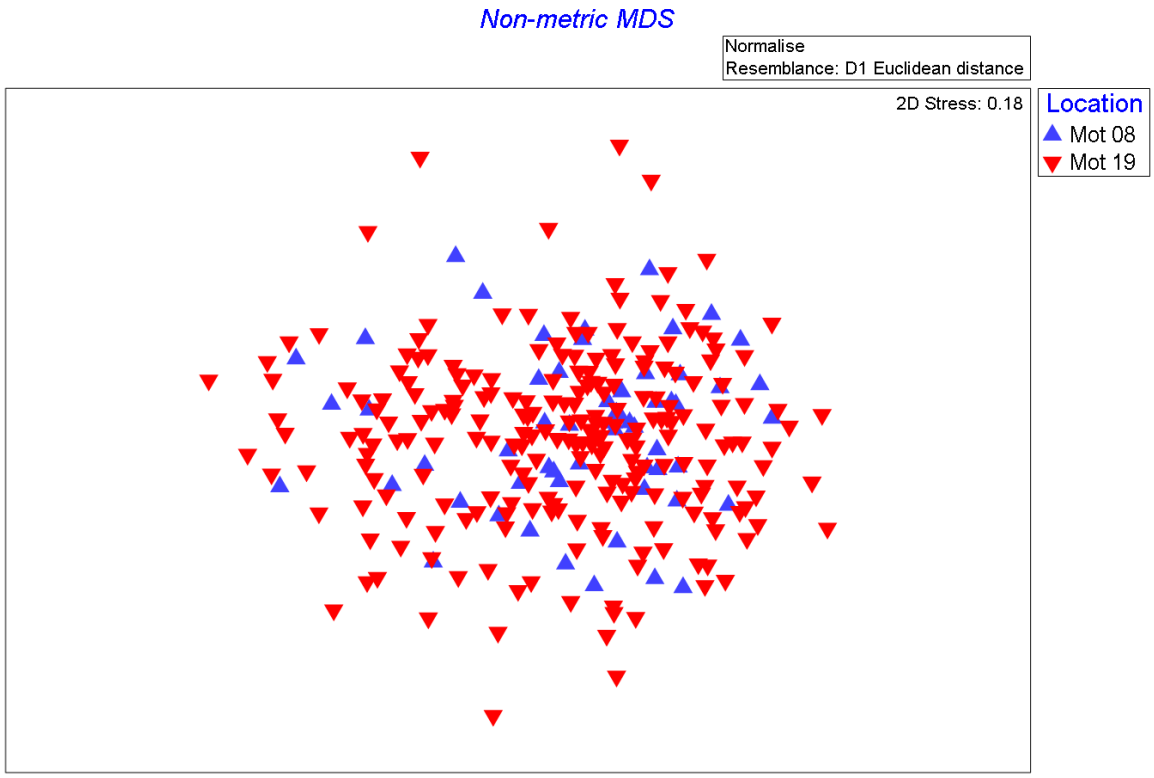


Figure 3.4: An nMDS of MRS based on Euclidean distances of the normalised physical acoustic variables for individual male tīeke in at Motuihe in 2008 and 2019. Each point represents a phrase and its seven spectral features that best discriminate between populations based on an LDA. Each points proximity to another point represents the similarity of those seven spectral features. "Mot 08" in upright blue triangles represents the singing population of males in 2008 and "Mot 19" in red inverted triangles represents the 2019 population of singing males. There is greater variation in the physical acoustic variables for songs recorded in 2019 to that observed in 2008 as "Mot 19" occupies a larger swath of non-metric acoustic space.

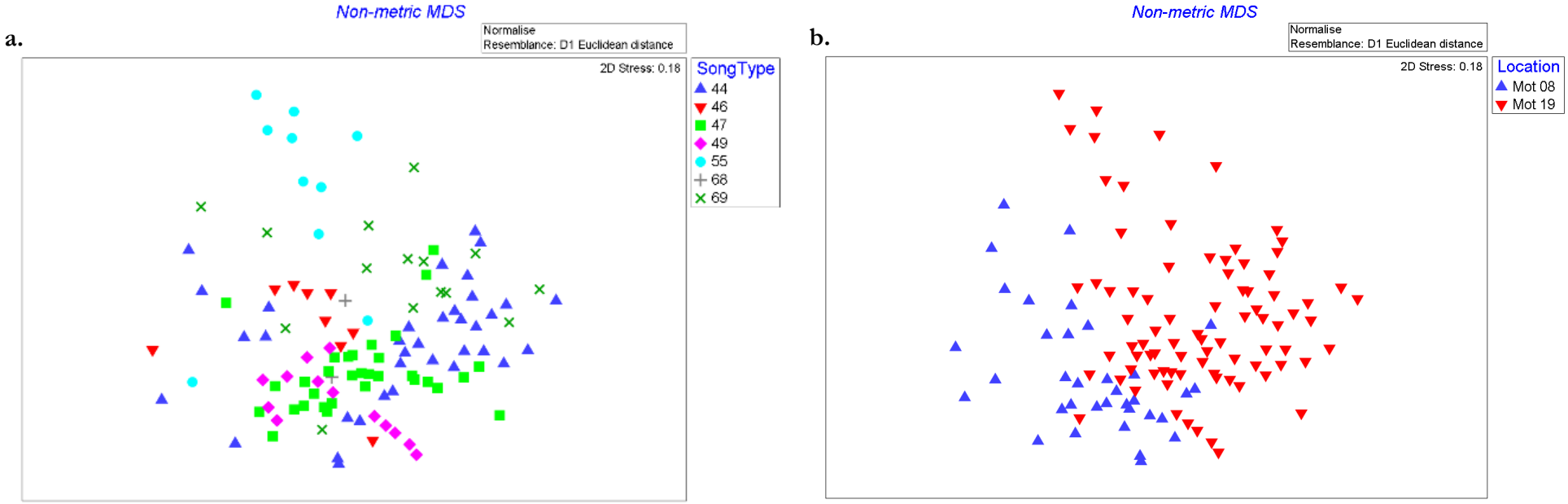


Figure 3.5: a) An nMDS containing the shared song types between the 2008 and 2019 population. Each point represents the 48 spectral features of a phrase representing an MRS. The 48 features were chosen based on an LDA, and best discriminate differences in song within a population. A point's proximity to another point represents their spectral similarities. Points closer together have more similar spectral qualities. Points in different shapes and colours indicate different MRS types (seven MRS types in total). **b)** The same nMDS in a) but points are coloured to indicate what year (2008 vs 2019) each MRS came from. Right-side-up blue triangles are MRS from 2008 (Mot 08) and inverted red triangles are MRS from 2019 (Mot 19).

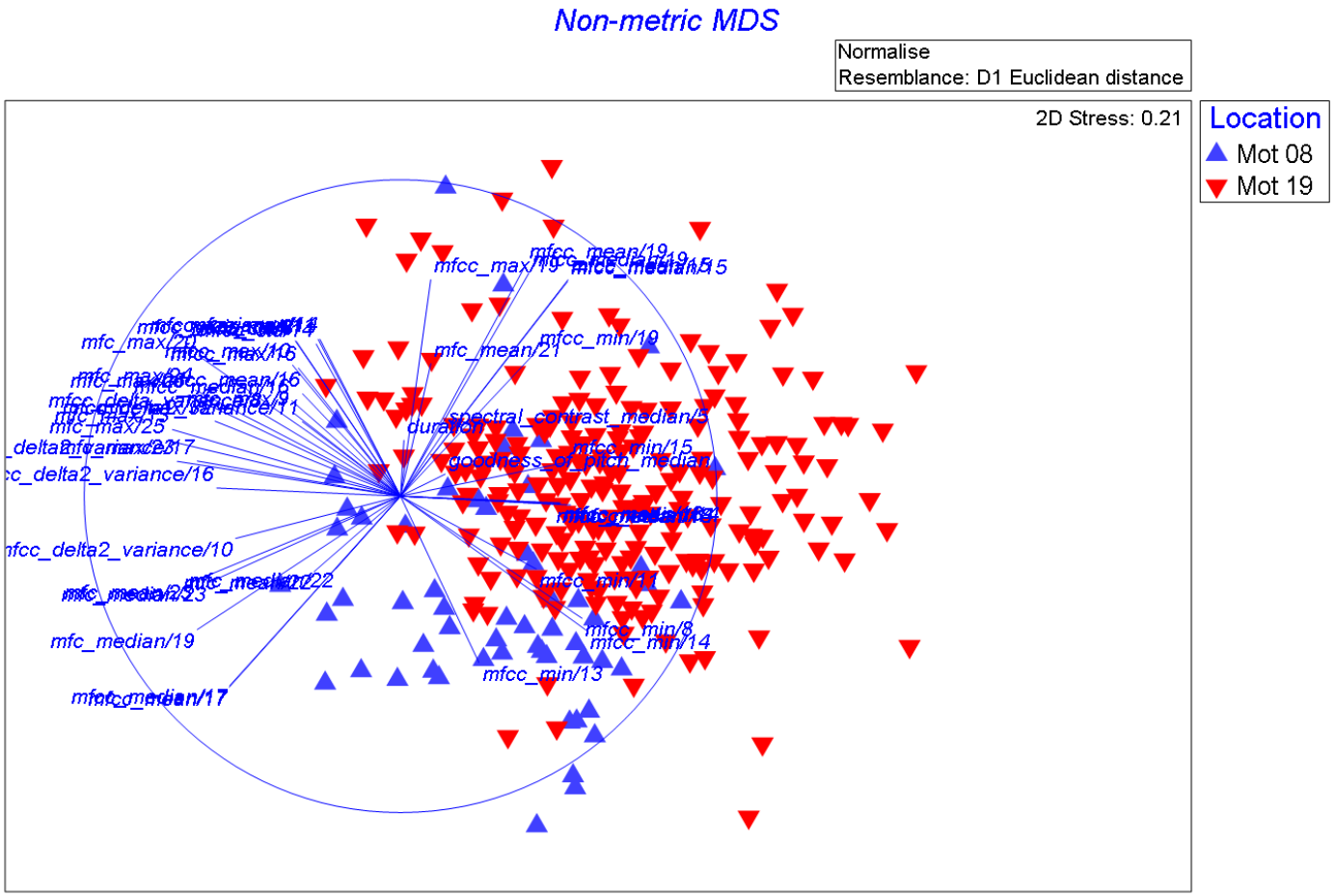


Figure 3.6: An nMDS containing every MRS from 2008 and 2019 indicating the same general shift at the population level. The 48 spectral features responsible for the position of each nMDS are overlaid onto the model. Their direction and size of each vector indicates the strength and direction of influence on the placement of each MRS.

Table 3.1: Descriptive statistics for biologically relevant spectral variables measured from overlapping MRS and total MRS from Motuihe tīeke populations in 2008 and 2019. Yellow highlighted boxes denote means which differ significantly from one another using a single factor ANOVA comparison.

Overlapping MRS Type Comparison	**2008**		**2019**		P-value
	Mean	S.E.	Mean	S.E.	
Duration (ms)	830.978	62.353	809.195	40.809	0.771
Mean Frequency Modulation (Hz)	0.256	0.02	0.22	0.012	0.136
Mean Amplitude Modulation(dB)	-0.0005	0.0003	0.002	0.002	0.622
Mean Entropy (dB)	-4.859	0.118	-4.702	0.068	0.228
Mean Goodness of Pitch (Hz)	0.267	0.012	0.246	0.006	0.104
Mean Fundamental Frequency (Hz)	498.272	48.97	418.68	26.906	0.129
Variance in Frequency Modulation (Hz)	0.09	0.013	0.085	0.008	0.75
Variance in Entropy (dB)	1.191	0.105	1.449	0.078	0.064
Variance in Goodness of Pitch (Hz)	0.022	0.002	0.024	0.002	0.54
Variance in Fundamental Frequency (Hz)	778000.673	78135.053	743306.998	49197.456	0.704

All MRS Type Comparison	2008		2019		P-value
	Mean	S.E.	Mean	S.E.	
Duration (ms)	829.829	40.995	955.664	26.648	0.029
Mean Frequency Modulation (Hz)	0.255	0.017	0.227	0.007	0.107
Mean Amplitude Modulation(dB)	-0.0005	0.0004	0.0003	0.001	0.735
Mean Entropy (dB)	-4.882	0.088	-4.725	0.0385	0.078
Mean Goodness of Pitch (Hz)	0.26	0.01	0.222919	0.004076	0.000101
Mean Fundamental Frequency (Hz)	495.045	40.136	435.045	15.834	0.111
Variance in Frequency Modulation (Hz)	0.091278	0.010347	0.087	0.005	0.69
Variance in Entropy (dB)	1.26	0.083	1.506	0.046	0.016
Variance in Goodness of Pitch (Hz)	0.022	0.002	0.021	0.0009	0.65
Variance in Fundamental Frequency (Hz)	789989.9	60347.28	864691	36473.15	0.347

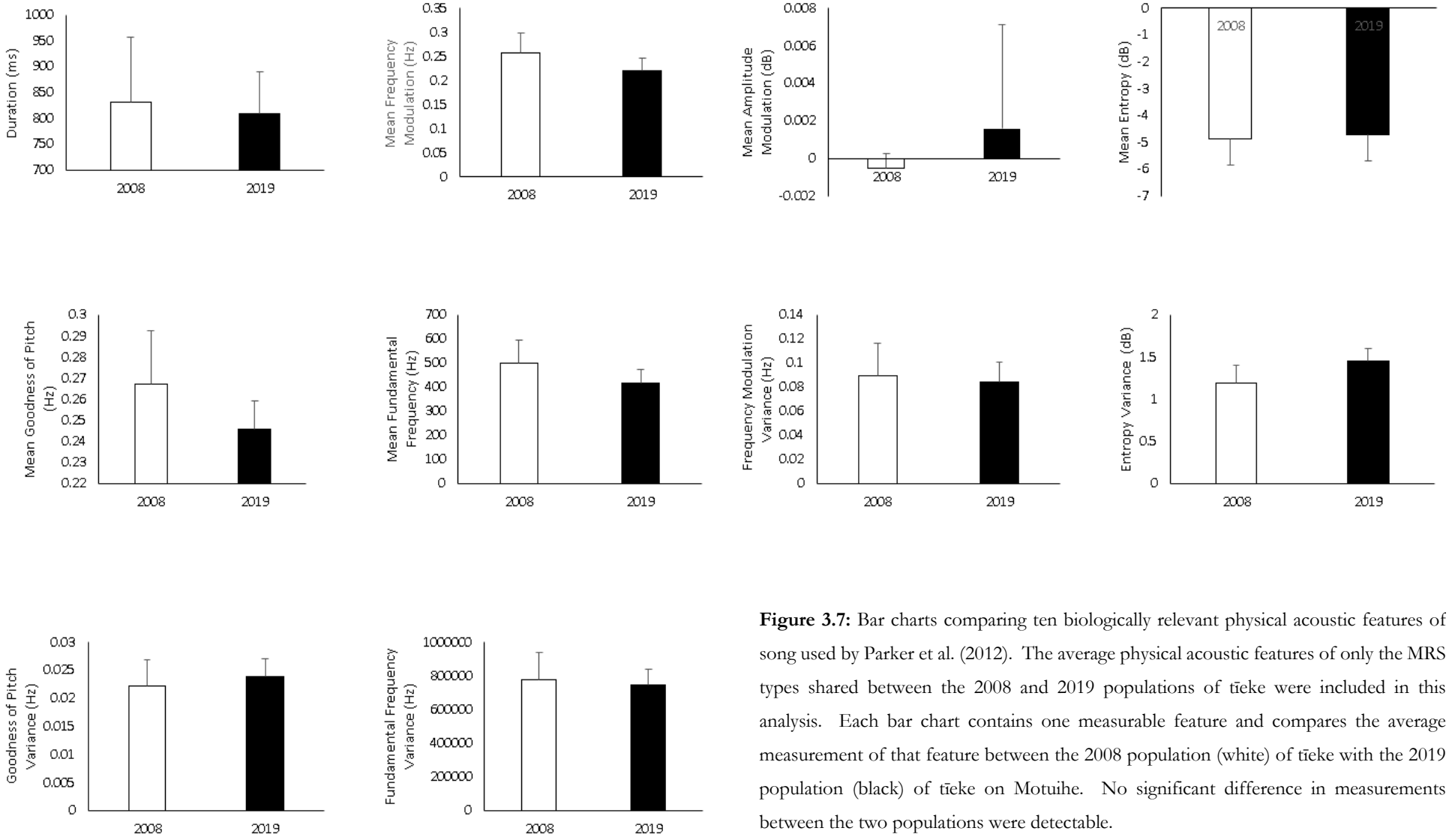


Figure 3.7: Bar charts comparing ten biologically relevant physical acoustic features of song used by Parker et al. (2012). The average physical acoustic features of only the MRS types shared between the 2008 and 2019 populations of tīeke were included in this analysis. Each bar chart contains one measurable feature and compares the average measurement of that feature between the 2008 population (white) of tīeke with the 2019 population (black) of tīeke on Motuihe. No significant difference in measurements between the two populations were detectable.

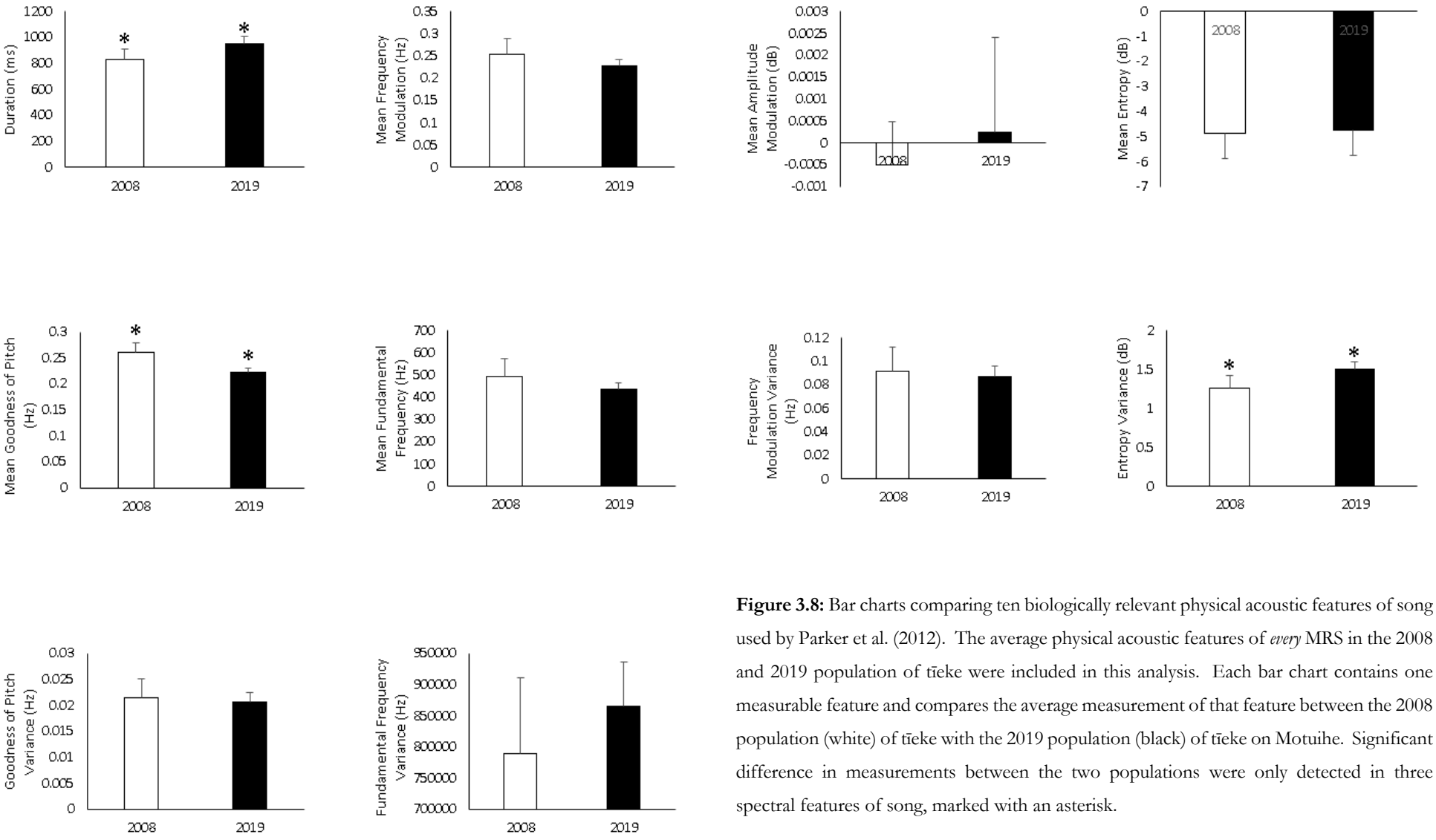


Figure 3.8: Bar charts comparing ten biologically relevant physical acoustic features of song used by Parker et al. (2012). The average physical acoustic features of *every* MRS in the 2008 and 2019 population of tīeke were included in this analysis. Each bar chart contains one measurable feature and compares the average measurement of that feature between the 2008 population (white) of tīeke with the 2019 population (black) of tīeke on Motuihe. Significant difference in measurements between the two populations were only detected in three spectral features of song, marked with an asterisk.

3.4 Discussion

3.4.1 Song Diversity

The increase in cultural complexity observed in 2019 is consistent with predictions of the cultural mutation hypothesis (Dawkins, 1976; Jenkins, 1977; Lynch, 1996). In newly formed (founder) populations, this process has not had the time to develop new song types, however cumulative learning errors persisting in older populations have the potential to increase song diversity (Lynch, 1996). The lower song diversity seen in 2008 can be explained by the cultural bottleneck hypothesis (Jenkins, 1977; Parker et al., 2012). Parker et al. (2012) highlighted these drivers when addressing changes in song diversity between island populations, and although the basic principles seem to apply well to explain differences in song diversity within a population, we intend to explore some site-specific features that may have contributed to the high rates of changes in song diversity at Motuihe. A driver for the exceptionally high rate of song learning errors (and substantial rise in song diversity) seen at Motuihe is the increase in suitable habitats due to replanting efforts influencing the distribution of young males (Figure 3.9).

In small geographic scales (such that of Motuihe island), animal dispersal can occur randomly, uniformly or via a clumped distribution (Molles & Manuel, 2008). Random distribution is the least common form of dispersal in nature and largely occurs when placement of an individual is determined by uncontrollable factors (i.e. wind or currents), or where strong social interactions are not found within a species (Molles & Manuel, 2008). It is unlikely that young males on Motuihe followed this form of distribution, as tīeke are a highly social passerine (Parker, 2011). Uniform distribution occurs in populations where areas between individuals are maximised usually through social interactions (i.e. territories) or for resource competition (Molles & Manuel, 2008). Uniform distribution is known to

occur in high-density, territorial, well established populations (Molles & Manuel, 2008), but Motuihe is a relatively young population (15 years), and there is still ample habitat yet to be settled on, so uniform distribution is unlikely. Clumped distribution is the most common type of distribution found in nature and predominantly occurs in environments where resources are patchy or scarce (Molles & Manuel, 2008) and best explains the current environmental conditions at Motuihe Island (Atkinson & Campbell, 1966; Motuihe Trust 2019). Therefore, it is likely that tīeke fit a clumped distribution at Motuihe, though this was not discretely tested for.

Following the cultural mutation hypothesis, an accumulation of song learning errors persisting in a growing population and being inherited by other males will likely give rise to an increase of song types (Lynch, 1996). This effect is increased by the expansion of the population due to improvements in suitable habitat, such as the yearly replanting of native vegetation on former grasslands on Motuihe (Atkinson & Campbell, 1966; Brunton & Stamp, 2007; Motuihe Trust 2019). Although Motuihe Island is relatively small (179-ha), the distribution of tīeke across the island likely trailed the remediation of grasslands to forested land on the island (Figure 3.9) (Atkinson & Campbell, 1966; Brunton & Stamp, 2007). Tīeke are extremely site faithful and once they acquire a territory they remain on that territory for the remainder of their lives (Armstrong et al., 2005; Jenkins, 1977; Parker, 2011; Parker et al., 2012; Thorne, 2007), meaning that older males who settled on the best available habitat at the time will not relocate to another habitat once it becomes available. Hence, new habitat would likely be occupied by dispersing juveniles. This settlement behaviour resulted in the clustering of older males (who act as social tutors for younger males) to the only location on Motuihe with mature forest at the time of translocation (an 18-ha patch of forest) (Atkinson & Campbell, 1966; Brunton & Stamp, 2007). A similar division of tīeke age with relation to habitat occupancy has been observed previously in a tīeke population on Tiritiri Matangi (Brunton & Stamp, 2007). When sampling for seasonal and habitat-related changes in tīeke

densities, Brunton & Stamp (2007) observed significantly more juveniles inhabiting replanted forest patches than mature adults, and less juveniles in remnant mature forests. In 2008 when the entire Motuihe population was recorded, the population was small (N ≈ 23) and contained to this one area (Parker & Laurence, 2008). Song diversity would have already been diminished as the founding population was subjected to a cultural bottleneck and represented a subset of MRS types from their source population (Baker & Jenkins, 1987; Parker et al., 2010, 2012). Song diversity would have continued to remain low until revegetated habitat became mature enough to support dispersing juveniles (Atkinson & Campbell, 1966). As such, dispersal across the island would not have been random or uniform, and young males would have likely all dispersed into the new suitable unoccupied habitat at the time - void of older males who could act as social tutors for the neighbourhood (Figure 3.9). This trickling effect of new habitat for tīeke would have caused a patchy distribution of social tutors and naive young males, and potentially influenced the rate of errors in song learning. The generalisability of this finding needs to be confirmed by examining the rate of change of MRS types in other, similar tīeke populations. Future studies that involve recording the repertoires of multiple populations during two finite periods of time would allow us to understand the rates of cultural change and cultural diversity within a population, and the role of habitat and dispersal patterns as drivers of change.

3.4.2 Song Variability

I found more variability within the 2019 songs than the songs sampled in 2008 i.e. the 2019 population occupied a larger proportion of non-metric acoustic space in the nMDS. Weak clustering observed within the same MRS type also indicates greater variation within discrete MRS types in 2019. Although some of the MRS types persisted, overall the repertoire had substantially changed during the 11-year period. This shift in acoustic space can largely be

attributed to changes in MFC-derived features and coefficients. MFC features and coefficients are commonly used in human speech recognition (Webb, 2020), however, it is currently unclear what their significance is from a biological perspective for songbirds. MFC is a non-linear spectrum of sound that represents distinct units of sound (Xu et al., 2004); essentially many spectral qualities are stripped away so that only the pure shape of the sound is observed (Ganchev et al., 2005). It is beyond the scope of this study to explore whether changes in MFC and coefficients has any functional significance to the communication signalling of oscines, and it is recommended that further research be conducted on MFC features and coefficients and their function as drivers for changes in birdsong.

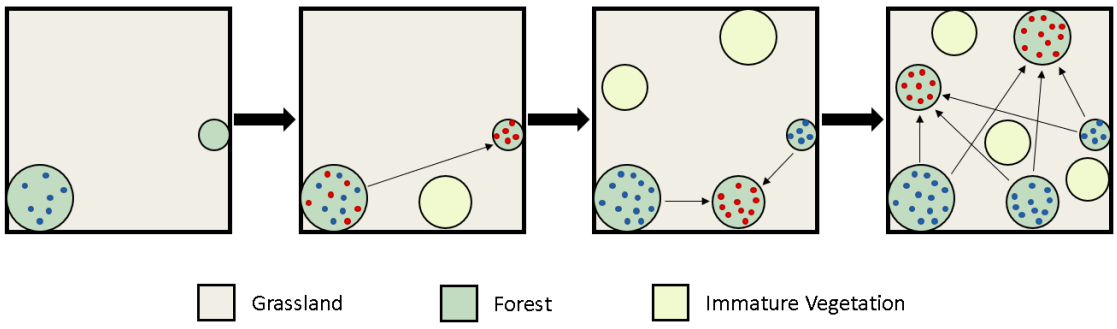


Figure 3.9: A visual repetitive model of the basic distribution principle likely occurring on Motuihe. Blue dots represent older mature males, and red dot represent the dispersing younger male tīeke. Moving from left to right demonstrates the changes to vegetative cover at Motuihe, and the subsequent dispersal pattern of young males following these changes.

Variability in song within a species has been attributed to morphological changes (predominantly to body size and beak size/shape) (Derryberry et al., 2018; Gil & Gahr, 2002; Podos & Nowicki, 2004), though it is unlikely that this would be a driver for the variability witnessed on Motuihe given the time frame (11 years). Greater variation within the older, 2019 population is consistent with Parker et al.'s (2012) findings that population age plays a significant role in the pattern of song variability, where island populations that have been established for a longer period of time exhibit greater variation in song characteristics. This

study compared song variation between island populations, not within, and Parker et al. (2012) speculated that less variation in newer populations could be a result of younger birds singing innovative, spectrally consistent MRSs based from their innate chatter call, due to the lack of social tutors in low-density populations. Similarly, I demonstrated that young tīeke will innovate irrespective of a social tutor in low-density populations (see *Shakespear* chapter). Regardless, in low-density populations, young males will innovate MRS, with the method of innovation being reflected in the spectral qualities of their song; MRS based from a chatter call would be more stereotypic and acoustically structured, with low variability (Jenkins, 1977; Parker et al., 2012).

In situations where there are multiple social tutors to learn from (similar to that of the male tīeke), young male zebra finches increase variation in their song by copying song elements from more than one song type (Williams, 1990) – something that tīeke are known to do as well when creating "hybrid" MRS types (Jenkins, 1977). In fact, individual song variation has been documented in a number of species where multiple social tutors provide source material for a young males' song, and even young birds being tutored from the same individual will show striking differences in their song structure (Catchpole & Slater, 2003; Feuth et al., 2000; Williams, 1990). In such cases, individual variation plays a vital role in the total cultural variability seen within a population; the larger and denser the population, the more chances there are to copy song from multiple tutors and increase variation in song. Though this may explain the variation seen in the larger 2019 population, the seemingly linear relationship does not hold true in some island populations of tīeke. Many newer populations of tīeke have large populations but exhibit less variation in their song than in older, well-established populations (Parker et al., 2012). This, in part, can be explained by founder effects and the cultural bottleneck hypothesis - many of these older, well-established populations only underwent a single translocation, whereas many newer populations were subjected to multiple serial bottlenecks (Hooson & Jamieson, 2003; Lambert et al., 2005;

Lovegrove, 1996; Parker et al., 2010, 2012) – and by the accumulation of song learning errors over time in older populations under the cultural mutation hypothesis (Jenkins, 1977; Lynch, 1996; Parker et al., 2012). As such, new populations *should* see an increase in song variability if they are established with many individuals, sourced from multiple populations each with their own unique translocation history and culture (see *Tāwharanui* chapter).

3.4.3 Song Innovation

Interestingly, the overlap of shared MRS over time is similar to the amount of shared MRS between isolated island populations. Of the MRS types recorded and identified by Parker et al. (2012) spanning across 14 populations, 25% (N = 50) were shared across more than one island (shared MRS types were recorded on 2.94 ± 0.21 islands), whereas 75% (N = 150) of MRS types were only recorded on a single island. On Motuihe, 26% (N = 7) of songs were shared between 2008 and 2019 and 74% (N = 20) were unique to 2019. This potentially indicates that changes to song culture within a population occurs at a similar rate to cultural changes between populations. Most notably, there may be specific MRS types that are inherently more persistent within the species both in time and in space. Within Motuihe, there did not seem to be an obvious trend for a specific MRS type persisting in the population; both common and uncommon MRSs of the 2008 population were found in the 2019 population and were equally common or uncommon (see *Appendices*) (Boyd & Richardson, 1985; Laland, 2004). Social learning strategies were not tested for in this thesis and present an avenue for future studies. Future research could explore the MRS types shared across populations and within populations to try and highlight why they may persist, and possibly identify any forms of song learning bias or spectral qualities of these particularly robust MRS types that lends to their cultural endurance (Laland, 2004; Slater, 1989; Wheelwright et al., 2008).

Much like the increase to song diversity on Motuihe, and in innovation seen across populations in Parker et al.'s (2012) study, the increased innovation seen at Motuihe is likely explained by the cultural mutation hypothesis (Dawkins, 1976; Jenkins, 1977; Lynch, 1996). Essentially, individual male tīeke on Motuihe make copying mistakes when trying to learn existing MRS types, and some of these mistakes gave rise to the formation of new MRS types, thus increasing the total number of MRS types present in the population. Other studies have shown that selective pressures for certain song features could give rise to new song types that are better optimized for the transmission of information from signaller to receiver (Endler, 1993; Irwin, 2000; Morton, 1975; Slabbekoorn et al., 2002, 2007). Testing for selective pressures on song features of the tīeke was beyond the scope of this project. It is therefore recommended that future studies investigate any potential selective pressures for tīeke song features, and whether potential pressures could influence fundamental changes to tīeke song. This may help explain the statistically different changes to duration, entropy variance and mean goodness of pitch observed, and the division between the 2008 and 2019 song culture in non-metric acoustic space.

Entropy is a measure of spectral width and uniformity, and the variance of this measure has been used as an indicator for song acoustic diversity (Alward et al., 2013, 2016, 2017; Derégnaucourt et al., 2005; Tchernichovski et al., 2001). Variability in entropy in a bird's song is indicative of less song structure; the greater the entropy variance, the more acoustic diversity (or less acoustic stereotypy) within the population (Alward et al., 2017). The greater variance in entropy exhibited by the 2019 population indicates more acoustic diversity than in the 2008 population. Testosterone is a known hormone that influences the rate of stereotypy in songbirds (Arnold, 1975; Bottjer & Hewer, 1992; Heid et al., 2010; Whaling et al., 1998). For example, decreases in the variance of entropy was shown in castrated male canaries (*Serinus canaria*) artificially injected with testosterone (Alward et al., 2017), and high variability in song was detected well into adulthood in castrated male song sparrows

(*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*) (Marler et al., 1988). Older male passerines have notably more testosterone than younger male birds and sing more stereotyped song (Bottjer & Johnson, 1997). An increase in entropy variance seen in the 2019 population may indicate proportionally more young birds within the population, since older male passerines have notable more testosterone and sing more stereotyped song (Bottjer & Johnson, 1997). This complements my other findings which suggests a proportionately younger population in 2019, though, since hormonal assays were not conducted, I was unable to determine the age demographic of the population. As such future studies could compare individual *within*-population age with population acoustic features.

Goodness of pitch is a biologically relevant feature of birdsong that detects harmonic structure and is an estimate of harmonic pitch periodicity (Lipkind & Tchernichovski, 2011; Tchernichovski, 2012; Webb, 2020). Lower values observed in 2019 indicates more pure tones and may represent diminished physical acoustic structure, poorer quality songs or simply just a louder acoustic background (Tchernichovski, 2012). To start, it is unlikely that the acoustic background of Motuihe Island has changed between 2008 and 2019, as for this to be the case one would expect to see a statically significant increase in entropy values, which were not observed (Tchernichovski, 2012). These findings could, however, corroborate with Parker et al.'s (2012) speculation that young male tīeke innovate MRS using their chatter call; a call that has a consistent physical acoustic structure and thus inherently greater in goodness of pitch. It would suggest that there are proportionately fewer males innovating MRS by use of their chatter call template in 2019, and follows the trend observed in Parker et al.'s (2012) between-population study showing older populations increasing in song variability and in goodness of pitch values.

Song duration can carry information about male quality, current condition or motivation (Gil & Gahr, 2002) and like most features of song, may be important for social interactions such

as mate choice and territory defence (Catchpole & Slater, 2003). Changes in duration can be elongated or shortened to convey information by one of two methods; either by changing their singing effort by producing more or less phrases per bout, or by lengthening/shortening the phrases within the song bout (Cuthill & Macdonald, 1990; Nelson & Poesel, 2011). Since phrases were discretely measured for their acoustic features and used as a representative of the tīeke's MRS, any detectable changes to duration would be solely reflective of changes in phrase length, not the duration of a song bout. In many species of songbirds, song duration has been shown to indicate aggressive motivation (Nelson & Poesel, 2011; Slabbekoorn et al., 2002). For example, male ortolan buntings (*Emberiza hortulana*) (a small Eurasian passerine with a small repertoire size similar to that of the tīeke), respond more strongly to elongated song during playback experiments, indicating that longer songs are perceived as a higher threat value in territorial songbirds (Osiejuk & Jakubowska, 2017). This response to song duration has been observed in many passerines, and most notably the opposite pattern of stronger responses to shorter songs has not been detected (Nelson & Poesel, 2012). Thus, it is evident that song duration can be used as a response to potential rivals in acoustic territorial defence. With the population in 2019 being notably bigger, an increase in individuals creates more territorial conflicts in an acoustically saturated environment. This in turn could have increased the duration of male tīeke MRS, though this study can only show increases to phrase length. Therefore, further research could be conducted through playback experiments, where the duration of an MRS is kept the same, but the duration of phrases within the MRS are changed, and observations are made on the response rates of a focal tīeke. Doing so could elucidate the increases to phrase duration observed in 2019.

Finally, acoustic signals are also known to be affected by, and adapted for the physical properties of the habitat – this is known as the "acoustic adaptation hypothesis" (Catchpole & Slater, 2003; Endler, 1992; Forrest, 1994; Irwin, 2000; Morton, 1975). Birdsong in forested land is prone to scattering by vegetation, and as such have acoustically adapted to be lower

in frequency, longer in duration, and with more pure tones (Derryberry et al., 2018; Irwin, 2000; Kirschel et al., 2009; Morton, 1975; Slabbekoorn et al., 2002; Wiley, 1991), whereas bird song in open areas such as grasslands can be affected by wind and as such have acoustically adapted to cope with these environmental conditions (Blumstein & Turner, 2005; Richards & Wiley, 1980; Wiley & Richards, 1978). An example of this can be seen within populations of dark-eyed juncos (*Junco hyemalis*) in California, where significantly higher minimum frequencies of song, and generally shorter songs were found in urban populations (Slabbekoorn et al., 2007). Though the changes in habitat were more subtle at Motuihe, its vegetative cover certainly has matured since the reintroduction of tīeke to the island (Figure 5). Future research could investigate the impacts of forest density and habitat variables with their potential influences on the acoustic signalling of tīeke (Irwin, 2000). Doing so may illuminate potential drivers for cultural change in populations.

3.5 Conclusion

In this chapter I have identified a rapid increase in song innovation (74% of MRS types are new), a rapid increase in song diversity (20 more MRS types) and a rapid increase in song variability (MRS types of 2019 population occupied more acoustic space) in an isolated, single-sourced, serially translocated population of tīeke. These findings demonstrate that the cultural evolution of wild tīeke populations can occur in less than 11 years. The immense changes to Motuihe's song culture can be explained by the cultural bottleneck and cultural mutation hypotheses (Dawkins, 1976; Jenkins, 1977; Lynch, 1996), where the rate of cultural mutation was amplified, potentially due to the steady improvements in suitable habitat causing an expansion of the population and a patchy distribution of social tutors and naive young males across the island.

Specifically, phrases are longer, less consistent and have less structure in 2019 MRS compared to 2008 MRS. Though changes to these features of song are likely multifaceted, inconsistencies and less structure exhibited in phrases are at least partially due to imperfections in song learning made by young males. Keeping in mind that 75% of the founder population were adults, and all progeny were confined to 18-ha of usable territory until at least 2008, the proportional decrease in consistency and structure detected in 2019 is indicative of a proportionately younger population in 2019 – though this remains speculative as no empirical tests on population age were conducted. Further, song features are known to change with changes to forest density and may also partially explain changes to song features, though habitat variables and their impact to song were not inspected in this thesis.

Overall, my key findings indicate that future conservation translocations may not need to apply as much emphasis on conserving culture from a founder population selection perspective; I have shown that in one of the youngest, most serially translocated populations, song culture changes rapidly. Instead, if conservation translocations aim to conserve ancient dialects, consideration must be made on the future restoration initiatives of potential locations. I believe that the population at Motuihe demonstrates that an uneven distribution of social tutors to young males caused by remediating habitat post-translocation exacerbates song learning errors in populations. If one wants to preserve tīeke culture, one must mitigate the effects of cultural mutation. This chapter elucidates that one method may be to ensure an even distribution of adult social tutors across the landscape of a newly formed population.

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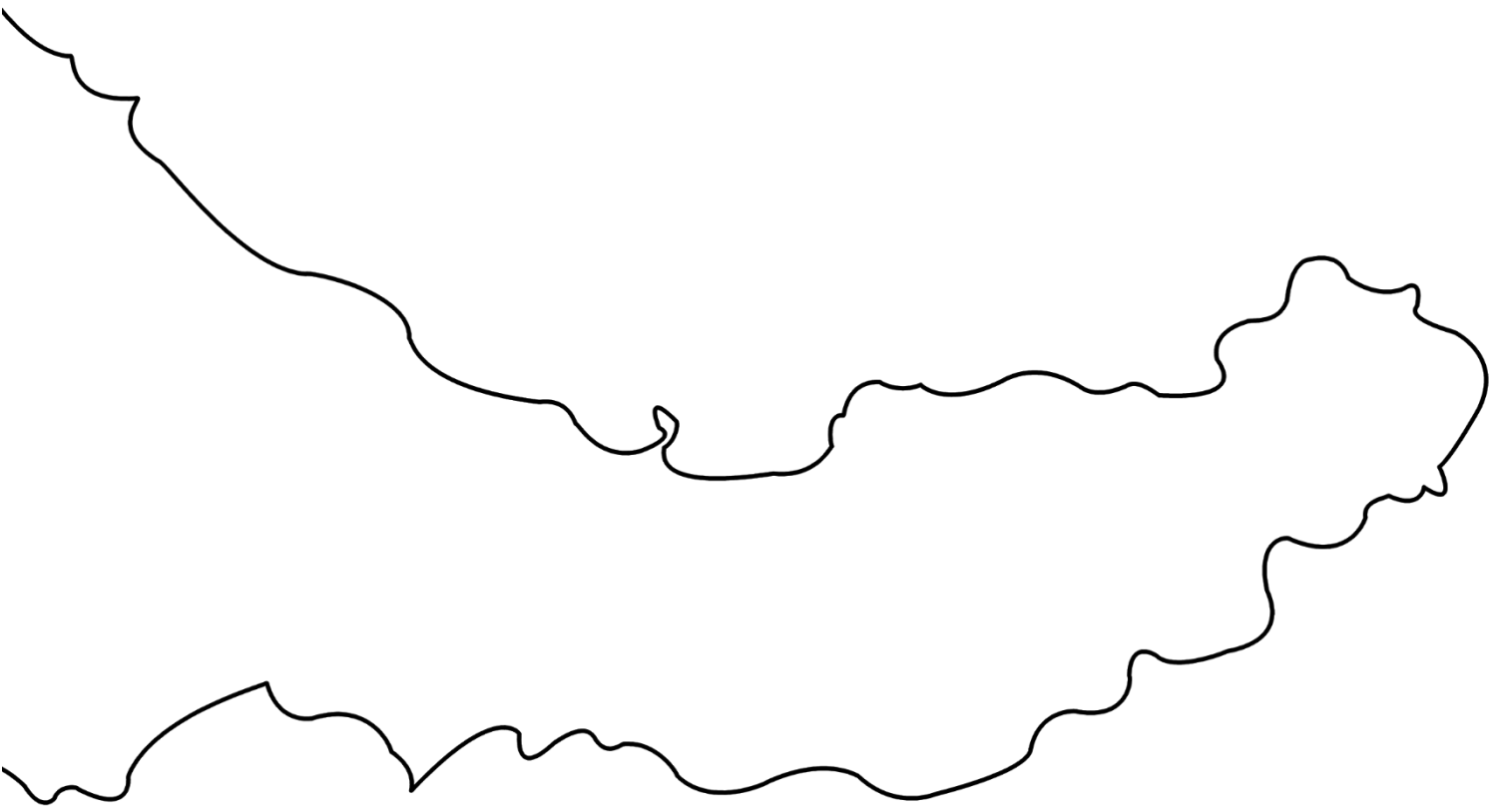
Chapter 4: Tāwharanui - the effects of varied conservation translocations and cultural bottlenecks on cultural diversity



4.1 Introduction

As the human population continues to grow and expand across the planet, habitats suitable for wildlife continue to be degraded, and the rate of species extinction increases (Saunders & Norton, 2001; Tennyson & Martinson, 2006; Thorn, 2007). Species extinction rates in New Zealand are further exacerbated by characteristics of its distinctive yet fragile ecosystems; ecosystems that have evolved in isolation since the departure of New Zealand's foundational landmass from Gondwanaland roughly 80 million years ago (Tennyson & Martinson, 2006; Wilson 2004). The relatively recent human arrival to New Zealand and the subsequent degradation of habitat and hunting of wildlife lead to a rapid and massive loss of species diversity (Holdaway et al., 2001). Hence, conservation scientists in New Zealand have developed a variety of pioneering species recovery programmes to conserve its unique biota (Salmon, 2013). The use and success of offshore islands as sanctuaries for species recovery acts as a foundation for the development of New Zealand's conservation strategies (Atkinson, 1990; Saunders & Norton, 2001). The method of intentionally releasing indigenous species into either new locations or locations where the species had been extirpated - a technique known as a 'translocation'- was first initiated in New Zealand by Sir Richard Henry in the 1890s (Armstrong & McLean, 1995; Miskelly & Powlesland, 2013). This approach, when implemented on offshore islands in conjunction with effective predator control techniques, remains highly successful and facilitated rapid and effective conservation strategies for species recovery throughout New Zealand (Griffith et. al., 1989; Wilson, 2004).

The endemic, forest-dwelling birds of New Zealand were hit particularly hard by invasive mammalian predators, given that many species have developed poor flight abilities and conspicuous, inquisitive behaviours in the absence of many traditional ground predators (Lovegrove, 1992; Saunders & Norton, 2001; Wilson, 2004). However, since the early 1900s, the pioneering translocation approaches of conservation management have played an integral

role in the recovery and preservation of some of New Zealand's most threatened bird species (Saunders & Norton, 2001). One such species is the tīeke (North Island saddleback; *Philesturnus rufusater*); a once endangered species of forest passerines who had been completely eradicated from mainland New Zealand by the 1900s and confined to a single remnant population of roughly 500 individuals on Hen island (Hooson & Jamieson, 2003; Jenkins, 1977; Lovegrove, 1996; Merton, 1965). Early translocations of the species were ultimately met with failure, and the first successfully translocated population wasn't realised until 1964 when a small population of tīeke persisted on Whatupuke Island (Figure 1.2 & 1.3) (Lovegrove, 1996). The early failures and subsequent success of the mid-1900s resulted in a key breakthrough in the form of the identification of the tīeke's inability to coexist with specific invasive predators (Hooson & Jamieson, 2003; Lovegrove, 1996; Merton, 1965). After the success of 1964, 25 more translocations of tīeke were conducted over 33 years, resulting in 15 new island populations being established via translocation (Figure 1.2 & 1.3) (Hooson & Jamieson, 2003; Lovegrove, 1996). Though offshore translocations were largely successful, it was apparent that any attempts at establishing a mainland population in the absence of effective predator control would be met with failure. If tīeke were to be translocated to their historic mainland ranges, then species such as cats (*Felis catus*) rats (*Rattus rattus* & *R. norvegicus*) and stoats (*Mustela erminea*) must be eliminated (Lovegrove, 1992). As such, the historic return of tīeke to the mainland was not realised until the advent of mainland "sanctuaries" – carefully selected areas of land on the mainland where predator-proof fencing can be erected to keep predators out, and the restoration and rehabilitation of native biota is conducted by various trusts, government organizations and private enterprises (Hooson & Jamieson, 2003; Innes et al., 2012; Maitland, 2011; Saunders & Norton, 2001). The culminative efforts of 100 years of conservation management came to fruition in 2002, when the first population of tīeke were translocated to establish a population at a mainland sanctuary called Zealandia – the first mainland population in nearly 150 years (Figure 1.2 &

1.3) (Campbell-Hunt, 2002; Hooson & Jamieson, 2003). The development of mainland sanctuaries in conjunction with the success of offshore translocations has allowed the species to grow over 53 years from a single, remnant population of 500 individuals, to currently 24 populations with estimates of 7000 individuals (Figure 1.2 & 1.3) (Hooson & Jamieson, 2003; Lovegrove, 1996; Parker, 2013). In 2012, another ambitious mainland translocation took place; tīeke from three different source populations were released together to establish a single *mixed* population at Tāwharanui (Figure 1.2 & 1.7). Here, the aim was to preserve genetic *and* cultural diversity of the species (K. Parker pers. comm., 2019). It was also paramount to avoid serial bottlenecks, as Parker et al. (2012) speculated that this phenomenon was a key component for song divergence within the species.

Cultural bottlenecks arise from the fragmentation of a population, where small founder populations cannot contain all the cultural diversity present within the source population (Hooson & Jamieson, 2003). Cultural bottlenecks are known to follow events such as translocations (Hooson & Jamieson, 2003; Parker, 2008; Parker et al., 2012), habitat degradation (Harbison et al., 1999) or drastic declines in population numbers from mass population mortality (O'Loghlen et al., 2013). Cultural bottleneck events do not only occur in social passerines, and do not only affect song culture. For example, the demographic history of ancestral populations of killer whales (*Orcinus orca*) suggests that populations experienced cultural bottlenecks, which gave way to small isolated populations forming unique hunting behaviours to eat specific prey (Foote et al., 2016; Whitehead, 2020). Although these populations are no longer isolated from one another, these culturally distinct populations of killer whales continue to occupy novel hunting niches that are preserved through social learning (Foote et al., 2016), and now seem responsible for restricted geneflow between populations (Whitehead, 2020). With respect to song dialects in oscine passerines, cultural bottlenecks have played a similar role in the divergence of song in island populations of silvereye (*Zosterops lateralis*) across Australasia where shared syllables between populations

decreased with increasing serial founder events (Potvin & Clegg, 2015). A similar result can be seen within chaffinches (*Fringilla coelebs*) populations on the sequentially colonised Atlantic Islands, where, relative to the mainland European population, there has been a progressive reduction in syntactical structure with each serially established population (Lachlan et al., 2013). Further, a single cultural bottleneck was likely the cause for the divergence of culture in the small population of Eurasian tree sparrows introduced to North America form Germany in 1870 (Lang & Barlow, 1997). In many cases, these divergences in song types are at least partly responsible for speciation (Irwin, 2000; Lachlan & Servedio, 2004; Slabbekoorn & Smith, 2002; Slater, 1989). Thus, when establishing the tīeke population at Tāwharanui, it was critical that a large founder group be used, composed of birds from culturally distinct populations and varying translocation histories. This unique translocation and resulting population, in conjunction with historic recordings provided by Parker et al. (2012) of 14 populations, allowed me to investigate the impacts of mixing populations from a cultural perspective.

At the inception of this research project, the aim was to focus on the tīeke population at Tāwharanui to quantify the cultural evolution of tīeke song culture over an eight-year period when birds are sourced from multiple, culturally distinct populations. *Do individuals from source populations form distinct neighbourhoods? Does the resulting mixed population have greater cultural diversity, and does it develop faster than in single-sourced populations? Do some song types persist from ancestral populations?* Unfortunately, initial exploratory work followed by consultation from various stakeholders at Tāwharanui indicated that the tīeke population was in steep decline following multiple predator incursions into the park and an inability to bring these predators under control (K. Parker & M. Puckett pers. comm., 2019). Therefore, the aims and questions were modified to explore other aspects of cultural evolution of tīeke song, and the populations at Shakespear and Motuihe were included into the overall project. Shakespear (a newly translocated mixed population) allowed me to compare how song types change one-

year post-translocation, while Motuihe allowed me to investigate how song types change during a discrete timeframe. The rapid reduction in population size and other negative impacts of invasive predators on the Tāwharanui population from 2018 onwards has meant that the population underwent two successive bottlenecks within a relatively short period of time. Hence, the scope of this study shifted to focus on better understanding the impacts of introduced predators on the song culture of the Tāwharanui population, and address questions about the impact of population bottlenecks on song culture. As such, I recorded socially transmitted conspecific recognition signals, known as Male Rhythmical Song (MRS), of male tīeke at Tāwharanui that are primarily used for mate attraction and territorial defence (Jenkins, 1977). Variants of the MRS play a significant role in the cultural evolution of the species, and different tīeke populations have distinct MRS types (Parker et al., 2012).

In this chapter I summarise my findings on the cultural complexity of tīeke in relation to different conservation management strategies. Doing so allows for a critical evaluation of the translocation history of the species with respect to changes in population-level MRS features. Here I provide an empirical comparison of tīeke culture between 17 isolated populations using historic and recent audio recordings of tīeke MRS. With these recordings, I identified the cultural complexities of 17 culturally distinct populations in relation to the ancestral spectral signature of Hen Island. I also highlight the impacts that recent bottlenecks have had on the MRS diversity within Tāwharanui. Lastly, I investigated whether mixing culturally distinct populations had any effects on maximising cultural diversity within mixed-sourced populations.

For this study I predicted that:

1. Due to the recent successive bottleneck events at Tāwharanui, it will be the least culturally complex population of the 17 analysed when population-level spectral signatures are compared to that of the ancestral Hen Island's spectral signature.
2. Given that Shakespear had only recently been established by a small founder group (thus also recently underwent a cultural bottleneck event), it will have similar levels of cultural complexity as Tāwharanui when its spectral signature is compared to the other 16 tīeke populations.
3. Since age plays a significant role in the complexity of tīeke song culture, Motuihe's cultural complexity in 2019 will change from its original complexity in 2008, and its spectral signature in 2019 will be more similar to populations of the same age.

4.2 Methods

4.2.1 Study-site & Population

Tāwharanui Regional Park is a 558-ha mainland, open wildlife sanctuary located 75km northeast of Auckland City, at the eastern tip of the Tokatū Peninsula (Auckland Regional Council, 2010) (Figure 1.2 & 1.7). It is composed of approximately 254-ha of native, mixed growth forests and wetlands, 50-ha of beach and 254-ha of active grazing paddocks dispersed throughout the park for sheep (*Ovis aries*) and cattle (*Bos taurus*). In 2004, a 2.7km coast to coast pest-proof fence was completed, turning Tāwharanui into a 'mainland island', though the fence is open at its coastal ends during low tide (Auckland Regional Council, 2010; Day & MacGibbon, 2007). A multi-species mammalian pest eradication followed soon thereafter and was largely successful, though mice (*Mus musculus*) and rabbits (*Oryctolagus cuniculus*)

persisted within the park and incursions of cats, rats (*R. rattus* & *R. norvegicus*), stoats and common brushtail possums (*Trichosurus vulpecula*) are known to occur (Maitland, 2011). A monthly culling of rabbits is carried out to keep population densities as low as possible (M. Maitland & M. Puckett pers. comm., 2019), and mice remain in high densities at the park (Goldwater et al., 2012). Poisoned bait stations and extensive trap lines are maintained by the park's rangers in the event that an incursion does occur (Maitland, 2011), and occasionally specialist hunters and dogs (*Canis familiaris)* are brought in to exterminate some larger, evasive mammals (M. Puckett pers. comm., 2019).

Multiple species translocations (birds and reptiles), and extensive replanting occurred following the installation of the predator proof fence in 2004 (Murdoch, 2008). Many of the forest patches in the park are a result of intensive replanting efforts by the local community group (known as the 'Tāwharanui Open Sanctuary Society' – TOSSI) and make for suitable habitat for tīeke once established (Atkinson & Campbell, 1966). The only old growth forest in the park (known as the Ecology Bush) is located at the park's centre (Murdoch, 2008). The majority of the tīeke population can be found in this forest, though they have dispersed to various other forest patches throughout the sanctuary (Figure 4.1).

Following new approaches to conservation translocations to maximise song diversity (Angeloni et al., 2008; Anthony & Blumstein, 2000; Parker & Laurence, 2008), the group composition of tīeke selected to be reintroduced into Tāwharanui was composed of birds from three culturally distinct island populations. 90 tīeke were selected from populations differing in translocation lineage, translocation level and population age; 30 tīeke came from Lady Alice Island, 30 from Mokoia Island and 30 Red Mercury Island (Maitland, 2012). These birds were successfully translocated and consecutively released into Tāwharanui on March 10th, 20th and 26th respectively in 2012 (K. Parker pers. comm., 2019). Although the re-establishment of the population was successful from a conventional conservation

standpoint (Armstrong & Davidson, 2006; Taylor et al., 2005), little is known about the population's cultural complexity.

Tīeke are poor flyers and roost in cavities year-round, making them highly susceptible to predation by introduced mammalian predators (Lovegrove, 1992). 2019 was a particularly bad year for incursions at the park and may have resulted from the exceptionally large masting event that New Zealand experienced in the summer of 2018-2019 (Department of Conservation, 2019). Park rangers and I reported multiple sightings of cats, rats (*R. rattus* & *R. norvegicus*), stoats and common brushtail possums during data collection at Tāwharanui in 2019. In December 2017, the population of tīeke at Tāwharanui was approximately 300 individuals (K. Parker pers. comm. 2019). This reduced to approximately 65 individuals (K. Sutherland pers. obs., 2019), mostly consolidated to the inner Ecology Bush by September 2019 – less than the original number of 90 individuals used to establish the population in 2012 (Maitland, 2012). Virtually all tīeke were locally eradicated from the north eastern tip of the park (known as Tokatū Point); the original release point for the founding population and the only area where banded individuals were spotted earlier in 2019 before the field season commenced (Figure 4.1).

New predator trapping methods have been implemented in the park using a combination of hay, eggs, cages and serval (*Leptailurus serval*) urine supplied to the park by Auckland Zoo. This new technique has seen great success in capturing cats in the park, catching six individuals in the first month of use in August 2020 (M. Puckett pers. comm., 2020). It also appears that the tīeke population decline has levelled off as of March 2020 and is expected to make a full recovery provided Tāwharanui continues to eradicate feral cats and prevents any more invasive predators from entering its grounds (K. Parker pers. comm., 2020). Since tīeke could not be individually identified, it is possible that singing males were missed in the 2019 season, though, enough time (roughly 30 days) was spent in the field to confidently

identify each territory in the park, which should have mitigated over or under sampling individuals.

4.2.1 Field Methods

I first visited Tāwharanui on April 2nd -18th and May 1st-10th 2019 with 1-2 field technicians and a Garmin GPS (Garmin Ltd, 1996-2020). These initial trips allowed me to become familiar with the park, tīeke territories, and with the recording equipment. Intensive audio recordings of tīeke took place between September 16th, 2019 to October 24th, 2019. Recordings of MRS were taken by 1-4 trained field technicians all using Marantz PMD661MKII Handheld Solid-State Recorders, Sennheiser MKE 600 Shotgun microphones and Rycote Softy wind guards mounted on Rycote pistol grips. Raw recordings were in .WAV format with a sample rate of 48 kHz and 24-bit sampling precision. The raw files were backed up on external hard drives and Massey University cloud drives and given a unique file name which included the name of the recorder, date of recording, and area of recording for future use. Recordings of tīeke did not occur on days with rain or high wind.

The entire park was divided between researchers and evenly sampled irrespective of how many tīeke were in the area. Later in the season, the greatest effort was put into the forested areas least effected by the recent incursions of exotic predators (namely the Ecology Bush and Possum Gully). Effort was made to ensure as many individual song repertoires as possible were captured. Researchers spent several days in their designated section of the park, spanning from shortly after sunrise till 1130 and/or 1400 till shortly before sunset. Hiking trails and predator trap lines were used to navigate through the native bush in search of tīeke, though, following birds for recording also involved considerable off-trail searching to get to areas where tīeke had been seen or heard. When a tīeke was located, researchers

followed the singing individual for 10 – 60 minutes depending on how frequently the focal male was singing, and on how often that area (and thus likely the male) had been sampled previously.

While following an individual male, researchers would take GPS coordinates to be later used in Google Earth (Google LLC, 2020) to determine territory boundaries (Figure 4.1). The territories could be visualized while in the field on an iPhone 6s (Apple Inc, 2020) and the Google Earth (Google LLC, 2020) app to give a general idea of where each male could be found, and which birds have or have not been sampled. It should be noted that as the males in the park were not colour banded, they could not be individually identified with full certainty. However, as tīeke are site faithful (Jenkins, 1977; Parker et al., 2010), territory boundaries and a population estimation could be determined based on the number of birds present in different areas (Figure 4.1). Playback was not used in the park to capture recordings, however near the end of the season, playback was used on one day (October 22nd) at the north-eastern-most tip of the park (known as Tokatū Point) to confirm that no tīeke were in the area. The absence of tīeke in this area was again confirmed during a brief tīeke banding session in early 2020, headed by park rangers and a private conservation organization where playback was extensively used to lure tīeke into mist nets (K. Parker & B. Harrison pers. comm., 2020).

4.2.3 Territory Mapping

Each territory was plotted on Google Earth (Google LLC, 2020) by transcribing GPS points taken in-field into .KML polygon shapes (Figure 4.1). Since males could not be individually identified, these territory boundaries were primarily used as a rough guide for field technicians looking for birds and helped to mitigate over or under sampling individuals.

Figure 4.1: Estimated territory boundaries outlined in red for territorial male tīeke at Tāwharanui. Yellow circles indicate colloquially named areas within the park.

4.2.4 Song Analysis

Different variants of tīeke MRS are easy to distinguish from one another both visually (from digitally rendered spectrograms) and aurally (Figure 4.2) and as such this remains the most widely accepted method of categorising bird song type (Parker, 2011). I did all the song analyses and segmentation so as to standardise selection criteria across all recent and historic recordings, and to remove any differences due to the observer. Raw recordings of birds at Tāwharanui were first inspected in Raven 1.6 (Cornell Lab of Ornithology, USA). High quality tīeke vocalisations were then cut out of the raw recording and new .WAV files (sample size=24 bits, pad size=1.1 seconds) were created for each track. Each track was given a unique, annotated filename which included the type of vocalisations (chatter, MRS or quiet call), recordist, date, and location of the recording. Tracks which included MRS were subsequently uploaded to KOE (Massey University SNCS, New Zealand) (Fukuzawa et al., 2020; Webb, 2020) (FFT=512, overlap=50%) and the single most repeated phrase within

the MRS was manually segmented to be analysed as a representative of the entire song following the method outlined by Parker et al. (2012) (Figure 4.2). These segmented MRSs were sorted by duration and compared using KOE and the features "Unit table" and "Exemplars". These tools allow researchers to bulk label, and visually and aurally inspect and compare all spectrograms and MRS type classifications in an automatically generated reference page based on specific selections (Fukuzawa et al., 2020; Webb, 2020). Song types were then assigned to each MRS based on audio and visual similarities (matching). MRS matchings were generally conservative, but allowances were made for individual variation present between birds within Tāwharanui i.e. small variations in tempo, pitch, or the number of repeated syllables within an MRS.

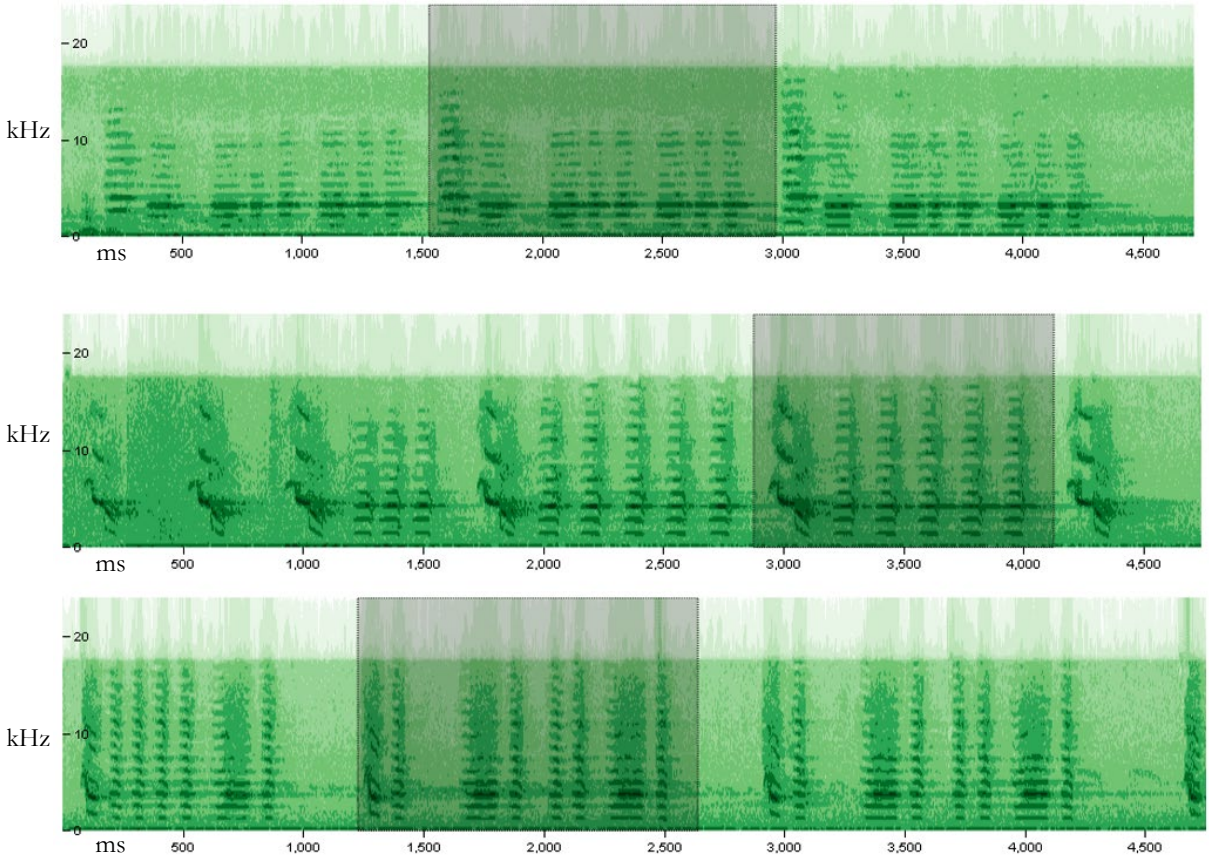


Figure 4.2: Spectrograms showing MRS of three different MRS types sung by male tīeke at Tāwharanui. The grey rectangle indicates the single phrase selected to represent the song type and to be measured for spectral analysis.

4.2.5 Historic Recordings

The historical recordings I used for comparisons were collected from December 2004 to November 2008 from the following island populations: Hen, Cuvier, Red Mercury, Whatupuke, Stanley, Tiritiri Matangi, Little Barrier, Moutohora, Lady Alice, Coppermine, Kapiti, Mokoia and Motuihe (Figure 1.2) (Parker et al., 2012). Each of the 13 established populations were visited for 5-15 days, by 1-4 researchers, on 1-4 occasions (Parker et al., 2012). Recordings were taken with Sony Hi MD MZ-NH700 mini disc recorders, Sennheiser K6 recording modules and M66 shotgun microphones fitted with Rycote Softy wind guards and mounted on Rycote pistol grips (Parker, 2011). Raw recordings were inspected (FFT = 256, Hann window, 5.8ms, 50% overlap) using Raven 1.2.1 (Cornell Lab of Ornithology, Ithaca, NY, USA) (Parker, 2011). High quality tīeke vocalisations were then cut out of the raw recording and new .WAV files were created for each track containing MRS using Sony SonicStage (Sony Corporation 2001-2007) software with 16-bit sampling precision and a 44 kHz sampling rate (Parker et al., 2012). Historic island recordings were uploaded to KOE (FFT = 512, overlap = 50%) in 2019 and manually segmented following in the same procedural method of selection as previously stated (see *Song Analysis* section).

Historic recordings of Little Barrier Island were considered as two separate populations (LBI C & LBI W) as the northeast and southeast quarters of this large island (2817-ha) were established from different translocation events (Figure 1.3) (Parker et al., 2012). For analysis, Motuihe recordings were separated into two groups based on the time period sampled (2008 vs 2019). Therefore, although 15 of the 24 populations were analysed, 17 datapoints are represented (Figure 1.3 & 4.3).

4.2.6 Spectral Analysis

Spectral analyses were conducted in KOE where 223 bioacoustics measurements were taken from a single phrase (Figure 4.2) within each MRS for all populations. The spectral features were exported into an .XLSX file in Microsoft Excel (Microsoft Corporation, 2002) and the mean, median, standard error and standard deviation were then calculated for each feature for each phrase. All multivariate analyses were run using the PRIMER v7.0.17 computer program (Quest Research Limited, 2015) with the PERMANOVA+ add-on package (Anderson et al., 2008). A Linear Discriminant Analysis (LDA) was run using every population to determine which features best explained the relationships between populations. Populations were averaged and translocation levels (Ancestral, First, Second, Third, or Mixed) (Figure 1.3) for each recorded population and were used to provide the replicates for the LDA, which highlighted the physical acoustic features that best explained the relationships between the populations (see *Appendices*). These "between-population" features were checked for normal distribution by running a draftman plot for each feature of each population (see *Appendices*) (Anderson et al., 2008). It was determined that none of the between-population features needed to be transformed prior to further analysis.

Each population was then separately analysed and checked for extreme outliers using the discriminatory features determined by the LDA. This was done by first normalising the "between-population" features for each population; a Euclidian-Distance resemblance matrix was then formed for each separate population and was used to run a non-metric multi-dimensional scaling (nMDS) ordination plot to check for normal clustering within each population. This resulted in nine tracks being removed from the dataset chiefly due to their quality.

The between-population spectral features for each population were then collated into a master spreadsheet and averaged at the population level to give a single value for each

discriminant feature for each population (i.e. the LDA determined that 7/223 spectral features best discriminated between populations, each population would therefore have seven measurements when all recordings for each population were averaged at the population level). The data was examined for approximate normality and it was determined that no features needed to be transformed prior to further analysis. The features were then standardised, and a Euclidean distance matrix was calculated. The relationships between populations were then visualised using an nMDS (Figure 4.3a), where each point represents the populations song repertoire, and its proximity to another point represents how similar each population's acoustic features were.

To determine a general relation of source population MRS dialects persisting within Tāwharanui, the between-population acoustic features were used again to compare spectral similarities of Tāwharanui song to Lady Alice, Red Mercury, Mokoia and Hen islands in non-metric acoustic space. (Figure 4.3b). This was done following the same procedure as the all-population nMDS method, but only contained acoustic features from Hen, Lady Alice, Red Mercury and Tāwharanui.

4.3 Results

4.3.1 Quantitative Song Types

A large database of modern and historic audio recordings of tīeke from 17 study-sites (N = 4,127) was assembled. MRS for all locations were identified and segmented manually (mean = 243, range = 36 - 602) from audio recordings. Audio recordings varied in duration and quantity of MRS, with some recordings being a few seconds long containing only one MRS, and other recordings being hours long containing multiple MRSs. The resulting

segmentations yielded a total of 4,426 manually segmented MRSs (mean = 295, range = 45 - 628). The segmentation process took me approximately 160 hours to complete using KOE, and the categorical sorting of MRS from Motuihe and Shakespear took me approximately 160 hours, also using KOE (Fukuzawa et al., 2020). The spectral analysis conducted in KOE resulted in 233 measured and potentially useable features per phrase (each representing an MRS) for every population. The LDA determined that 7 out of the 223 measured spectral features best discriminated song between populations (see *Appendices*). They were the mean and median of spectral contrast, minimum spectral bandwidth, and Mel Frequency Cepstral (MFC)-derived features and coefficients.

4.3.2 Historical Analysis

Parker et al. (2012) originally analysed the historical recordings of 14 study-sites from a song sharing perspective. He classified >3,500 recordings into 2513 MRS types (Parker et al., 2012). These MRS types were then compared across study-sites to look for degrees of song sharing in population-level repertoires (Parker et al., 2012). Parker et al.'s (2012) resulting analysis showed a decreased level of song sharing between islands with increasing levels of translocation from the ancestral population.

4.3.3. All-Population nMDS

The all-population nMDS (Figure 4.3a) demonstrates a general trend of populations being further away from the ancestral population of Hen Island with each serial translocation event. Populations that were established from a direct translocation from Hen Island have more similar spectral acoustic features to that of the ancestral Hen Island than do secondary,

tertiary, and mixed translocated populations. There is also some indication that less cultural complexity exists within younger populations (Figure 1.3 & 4.3a). Interestingly, it appears that mixed populations did not see a large increase in cultural complexity based on my analysis where Hen Island represents the most culturally complex population. The all-population nMDS (Figure 4.3a) resulted in a stress factor of 0.08 which is well within the acceptable levels and indicates that the nMDS is an accurate representation of bio-acoustic similarities at the population level in non-metric acoustic space.

Tāwharanui is the farthest away from Hen Island, indicating that it is the least spectrally similar to Hen Island and thus the least culturally diverse of the 17 study-sites included in my analysis (Figure 4.3a). Shakespear is the newest population in the nMDS plot (Figure 4.3a) and is similar to Tāwharanui in its distance from Hen Island, so is therefore similar in cultural complexity and spectral similarity. Motuihe shows a clear placement change between the 2008 and 2019 recorded population (Figure 4.3a), indicating that there have been fundamental changes to the measurable spectral acoustic features of the population within 11 years. The population recorded in 2019 is most spectrally similar to the Mokoia population – a population that was 16 years old when recorded (Figure 4.3a). Interestingly, the 2019 recorded population of males on Motuihe are quite close to Hen Island's (Figure 4.3a), exhibiting a similar spectral complexity and cultural diversity as first order translocated populations.

4.3.4 Tāwharanui nMDS

The nMDS ran specifically for Tāwharanui's translocation history (Figure 4.3b) shows that Tāwharanui is the most distant population from Hen Island, and the relative location of this subset of populations in the nMDS are comparable to their location in the all-population

nMDS. That is, their distance from Hen Island is a reflection of their translocation level; Red Mercury, (a direct descendant of Hen) is closest to Hen, followed by Lady Alice (a second-level translocated population) followed by Mokoia (a third-level translocated population). Out of the three founder populations, Tāwharanui is most similar to Mokoia in non-metric acoustic space, and equally dissimilar to Lady Alice and Red Mercury (Figure 4.3b). Stress was non-existent in this nMDS, indicating an accurately depicted relationship between the populations.

Figure 4.3: a) An nMDS based on Euclidean distances of the averaged, normalized physical acoustic variables for individual male tīeke from 17 different study-sites. The populations studied are: Hen (Hen), Whatupuke (Wha), Red Mercury (Red), Cuvier (Cuv), Little Barrier (LBI W & LBI C), Tiritiri Matangi (Tir), Moutuhora (Mou), Lady Alice (Lad), Coppermine (Cop), Stanley (Sta), Motuihe (Mot 08 & Mot 19), Kapiti (Kap), Mokoia (Mok), Tāwharanui (Taw) and Shakespear (Sha). Each point represents an individual population and is composed of the seven measured acoustic features of phrases sang by males belonging to that population. Populations that are closer together on the ordination have greater similarity in spectral features than those further apart. Hen Island (in green) is comprised from ancestral dialect and as such is considered the most culturally complex. Populations farther away from Hen Island are therefore considered less culturally complex. Similarities among populations are evident and exist between populations sharing common translocation history (delineated by colour and shape). 2D stress is 0.08 and well within the accepted levels, indicating a reliable representation of the data. **b)** An nMDS run specifically for Tāwharanui's translocation history. It contains the ancestral Hen Island, and Tāwharanui's three founder populations: Red Mercury (Red), Lady Alice (Lad) and Mokoia (Mok). 2D stress is non-existent indicating an accurate representation of the relationship between these populations in non-metric acoustic space.

4.4 Discussion

4.4.1 Measurable Bio-acoustic Drivers of Change

My findings indicate that rapid cultural evolution is taking place based on the differences in the physical acoustic properties of the tīeke populations analysed. This further validates Parker et al.'s (2012) findings, which he based on song sharing across populations. This rate of cultural evolution is uncommon in free-living, social learning species as many species exhibit strong selective forces for population-level song stability (Harbison et al., 1999; Nelson et al., 2004; Paxton et al., 2019; Wright et al., 2008). Killer whales (*Orcinus orca*) for example, live in stable groups with group-specific vocal repertoires made up of highly stereotyped, structurally stable whistles (Riesch et al., 2006; Strager, 1995; Yurk et al., 2002). Specifically, the whistles of resident killer whales of British Columbia showed essentially no structural changes and have been completely stable over at least 13 years, with zero overlap with any other culturally distinct groups (Riesch et al., 2006). In songbirds, avifauna such as the Galápagos medium ground finch (*Geospiza fortis*) are hallmarks of consistency with respect to their song characteristics. The acoustic structure of a population of Galápagos medium ground finch was compared using song recordings from 1961 and 1999 (Goodale & Podos, 2010). The results showed highly conserved song structure occupying remarkably consistent acoustic space over 40 years (Goodale & Podos, 2010). Many free-living species that do exhibit cultural evolution do so at a slow pace. The song of Kent Island savannah sparrows (*Passerculus sandwichensis*) exhibited substantive cultural evolution over a 30-year period where three out of the four elements of their song analysed showed spectral changes (Williams et al., 2013). Further, as mentioned earlier, Lang & Barlow (1997) demonstrated that the North American population of Eurasian tree sparrows (*Passer montanus*) exhibited a considerable divergence of culture with respect to their ancestral German population, but this was over a 115-year time frame. Similar to my predictions, it was thought that cultural bottlenecks,

founder effects and cultural mutations were largely the reason for the divergence in song (Lang & Barlow, 1997). It is therefore apparent that very few field-based studies have been able to show such rapid cultural evolution of song like that of the tīeke populations.

Indeed, it is apparent that changes to song cultural may be accelerated in small, declining or patchy populations (Lynch, 1996). In tīeke, Parker et al. (2010) empirically demonstrated that cultural evolution was occurring in < 25 years in isolated populations, but my findings would suggest that it is more rapid (< 11 years), and the process of cultural evolution can be detected from the first year of translocation through young males innovating song (see *Shakespear* & *Motuihe* chapters). The fundamental differences to the measurable spectral acoustic features of MRS song between the study-sites analysed is best explained by changes to spectral contrast, minimum spectral bandwidth, and MFC-derived features and coefficients.

Spectral bandwidth is defined as the magnitude-weighted average of the differences between the spectral components and the spectral centroid (Fukuzawa et al., 2020). In the context of birdsong, bandwidth plays a role in signal transmission, and studies have shown that spectral bandwidth is known to change in passerines through acoustic adaptations (Phillips et al., 2020). Phillips et al. (2020) demonstrated that white-crowned sparrows (*Zonotrichia leucophrys*) develop narrow bandwidths in response to living in urban environments. The habitats of tīeke across all populations are all similar, so it is unlikely that acoustic adaptation explains changes seen to spectral bandwidth across populations. A more reasonable explanation could be that a subset of founders represented a subset of the acoustic space of their source population (due to chance) (Baker & Jenkins, 1987; Baker et al., 2006; Parker et al., 2010, 2012) and therefore the new population was predisposed to singing MRS with a particular bandwidth.

Spectral contrast is defined as the level of differences between peaks and valleys in a spectrum (Yang et al., 2003). It is a result of power regulation along the frequency axis, and is closely related to harmonicity (So et al., 2020). In the context of birdsong, spectral contrast is a ubiquitous feature in vocalisations used by birds to perceive and distinguish auditory communication from other sounds in the environment, and respond with a behavioural cue (So et al., 2020). So et al. (2020) demonstrate that spectral contrast is a behaviourally relevant feature of song by studying neurological pathways in zebra finches (*Taeniopygia guttata*). This further emphasises that isolated populations of tīeke are culturally distinct, given that differences in spectral contrast indicate fundamental differences to what tīeke will respond to in MRS. This was demonstrated by Parker et al.'s (2010) playback experiments of tīeke on Motuihe Island, where tīeke from Motuihe were less responsive to MRS from other populations (see *Motuihe* chapter).

MFC is a non-linear spectrum of a spectrum that represents distinct units of sound (Xu et al., 2004); essentially many spectral qualities are stripped away so that only the pure shape of the sound is observed (Ganchev et al., 2005). No empirical studies have been conducted to test if changing MFC-derived feature and coefficients elicits a behavioural response in songbirds, or their functional significance for communication signalling. I therefore recommend that further research be conducted on MFC features and coefficients and their function as drivers for changes in birdsong.

4.4.2 All Populations

This was a completely new analysis using Parker's (2011) data in a newer, more comprehensive sound analysis program, KOE (Fukuzawa et al., 2020), with the addition of modern recordings of three populations. Although Parker et al.'s (2012) original analysis was

primarily comparing MRS type sharing between populations, the trend observed in his 2012 study is comparable to the trends seen in my analysis when comparing physical acoustic spectral measurements. To elaborate, by comparing the quantity of MRS types shared between populations, Parker et al. (2012) empirically demonstrated that culturally distinct tīeke populations form due to rapid changes in their culture, and that song sharing decreased with each serial translocation. He speculated that founder effects, bottleneck effects and cultural mutations may drive this phenomenon (Parker et al., 2010, 2012). In the nMDS that I developed containing 17 study-sites, the positioning of each population empirically demonstrates that acoustic characteristics of male tīeke song also vary between populations and correlate with the translocation history of each population. Populations that have undergone more serial translocations have lower song diversity indicated by their distance from the ancestral dialect signature of Hen Island. My findings also show that population age plays a key role in the complexity of male song culture; lower song diversity is found in younger populations. These findings corroborate the research by Parker et al. (2012), and I speculate that the "cultural bottleneck hypothesis" and young male song innovation drive this observed phenomenon (Parker et al., 2010, 2012). With the cultural bottleneck hypothesis, a gradual decrease in song sharing results from the inability of small founder populations to represent the entire repertoire of their ancestral island, thus cultural complexity erodes with each step in serial translocation (Jenkins, 1977; Parker et al., 2012).

Further, in low density populations such as those of newly translocated populations, the survivability and recruitment of young male tīeke onto territories is amplified (Armstrong et al., 2005). Parker et al. (2012) speculated that in these low-density scenarios, where contiguous adult song tutors are absent, young males tend to innovate MRS based on the tīeke generic "chatter" call template (Jenkins, 1977; Parker et al., 2012). This call has acoustic properties that are simple and innate, and hence reduce the diversity of songs within newer populations (Parker et al., 2012). My findings from Shakespear (see *Shakespear* chapter) seem

to further complement this speculation. In Shakespear (a recently translocated, low-density population established in 2018), I found that 25% of the MRS types present in the population were innovated MRS types coming from young, first-generation males.

One observation of the structure within the nMDS is that the newly recorded populations appear to occupy similar acoustic space, and the historic populations all tend to occupy a different region of acoustic space. In an attempt to standardise MRS selection, I segmented all phrases, from every population, using the same standardised selection criteria (see *Methods* section) for this thesis, rather than using the historically segmented phrases selected by Parker (2011). Since recording equipment was different, and historic MRSs were initially converted in a different method with different computer software to the 2019 recordings, it is possible that some acoustic features were affected, and this may have influenced the nMDS. This could be explored further but is beyond the scope of this study given the technological advancements seen in the last decade with respect to recording equipment and bio-acoustic user software. I believe that the observed differences in occupied space between the recordings of 2019 and the recordings of 2004-2008 is best explained by cultural drift (Lynch, 1996; Mundinger, 1980; Parker, 2011; Slabbekoorn & Smith, 2002) within the species and further exemplifies fundamental changes to tīeke song with time.

Similar to genetic drift, cultural drift is defined as neutral changes over time in cultural traits in isolated subpopulations (Aplin, 2019). In the context of passerines, it is a random progression of changes to song repertoires over time (Baker & Jenkins, 1987; Parker et al., 2012; Potvin & Clegg, 2015). They may occur directly (i.e. via acoustic adaptations to the environment, where better transmitting vocalisations are favoured) (Cardoso & Atwell, 2011; Derryberry, 2009) or indirectly (i.e. via morphological changes to bill shape or size causing alterations in vocalisations) (Podos, 2001; Potvin, 2013). Cultural drift can affect multiple taxa of social learning species, including birds (Bartlett & Slater, 1999), bats (Boughman,

1998) and cetaceans (Deecke et al., 2000; Sayigh et al., 1995). Cultural drift in oscines has been shown to have more pronounced effects on smaller, or generationally fragmented populations (Baker & Jenkins, 1987; Cardoso & Atwell, 2011; Lynch, 1996; Mundinger, 1980; Parker et al., 2012; Paxton et al., 2019; Potvin & Clegg, 2015; Slabbekoorn & Smith, 2002; Tietze, 2018). An example of cultural drift in a free-living population of passerines can be found within the convergent acoustic characteristics of three species of Hawaiian honeycreeper (*Carduelinae*), whose declining population's convergent song features may be explained by cultural drift over 40 years (Paxton et al., 2019). Further, cultural drift emanating from a bottleneck event has caused a divergence of song culture across free-living populations of silvereye (*Zosterops lateralis*) throughout Australasia (Potvin & Clegg, 2015). The results of Potvin & Clegg (2007) suggest that cultural drift influences syllable repertoires in newly colonised populations. Cultural drift is known to expedite divergence in culture in the naturally small and isolated populations of tīeke (Jenkins, 1977; Parker et al., 2012), and likely plays a role in the division between the historically recorded and recently recorded populations.

Interestingly, it would appear as though tīeke populations that were established from several donor populations at the onset of their formation may not have maximised the cultural diversity of the founding population. No obvious increase to cultural complexity was observed in the all-population nMDS (Figure 4.3a) for the mixed populations, Shakespear and Tāwharanui. Though, I am aware that limitations exist using Tāwharanui as a model population since the population has been declining, and that there may be a delayed response to increasing cultural diversity when creating a new population with a mixed founder group (see *Shakespear & Tawharanui* chapters). From a genetic management perspective, the simultaneous release of multiple, isolated populations into the same area likely promoted heterozygosity and helped to maintain evolutionary potential (although this was beyond the scope of this study to test) at Shakespear and Tāwharanui (Jamieson & Lacy, 2012; Keller et

al., 2012; Lambert et al., 2005). However, from cultural management perspective, the translocation strategy employed at Shakespear and Tāwharanui appeared to have little if any effect on increasing the new population's cultural diversity. Given this, and that Motuihe – a single-sourced, third-level translocated population – had a rapid increase to its cultural diversity over a relatively short period of time (11 years), this may indicate that the careful selection of culturally diverse source populations, and avoidance of serial translocations is not necessary to maximise or increase cultural diversity in new populations. Further recommendations were made to sustain culture in new populations by using larger numbers of founding birds (Parker, 2011; Parker et al., 2012), however, my nMDS does not indicate that the populations established from small number of founders suffered any more of a loss to cultural complexity than those established from large founder groups.

Further, since population age plays an integral role in the song complexity of tīeke populations (Parker et al., 2012), one would predict the youngest population (in this case Shakespear) in the nMDS to be the farthest away from Hen Island. Given its translocation initiative, Shakespear *should* have had a boost to its initial cultural complexity that belies its age since males from two culturally distinct populations were present and singing at Shakespear. However, that does not appear to be the case; populations such as 2008's Motuihe - a population that was only 3 years old at the time of recording - are closer (and therefore more culturally complex) to Hen Island than Shakespear. This is despite the 2008 Motuihe population being only two years older than Shakespear, and established from a single-source, third-level translocation event. This may signify that population age is the key driver in relation to the maintenance of cultural complexity, though, further research is needed to test this idea. I recommend that populations such as Shakespear be monitored and re-recorded on a semi-annual basis, and compared to single-sourced, serially translocated populations over a similar period to better understand the interplay between cultural complexity, translocation history and population age.

4.4.3 Shakespear

The Shakespear tīeke population was established using a similar approach to Tāwharanui; mixed sourced founder populations were used to maximise genetic and cultural diversity (K. Parker pers. comm., 2019). The two source populations used to establish Shakespear were Tāwharanui and Tiritiri Matangi (Figure 1.3) (K. Parker pers. comm., 2019), but the proportion of each resulted in a soundscape at Shakespear biased towards Tiritiri Matangi, with 50% of MRS types coming from Tiritiri Matangi males and only 25% from Tāwharanui (see *Shakespear* chapter). It was therefore surprising that the song characteristics sampled showed a greater similarity to Tāwharanui than Tiritiri Matangi. However, this could be a methodological issue as the statistical comparison undertaken used data from the Tiritiri Matangi dialects recorded in 2008. As with all the tīeke populations, song variants continue to evolve, and although the samples used were representative of the MRS types sung 11 years ago, they may not reflect MRS types at the time of the Shakespear translocation. Insights on rates of change can be drawn from my findings on the Motuihe population, where upwards of 70% of MRS types were newly innovated during an 11-year period (see *Motuihe* chapter). Supporting this idea is the similarity of the Tāwharanui dialects to Shakespear samples. I used recordings from Tāwharanui collected in 2019, only one year after Tāwharanui males were introduced to Shakespear, hence these represent "real-time" dialects of both populations compared to old dialects for Tiritiri Matangi. Given how rapidly MRS types change, and the age discrepancies for the dialect data used to compose points for Tiritiri Matangi, Tāwharanui and Shakespear in non-metric acoustic space, Shakespear's position is likely misrepresented on the nMDS. This issue illustrates the complexity of designing and planning long-term experiments in the field with wild populations. Future research should aim to update all dialects of tīeke populations within a small timeframe of a few years to give the best, real-time representation of the acoustic relationships between these populations.

The dataset collected for the population at Shakespear provides an excellent foundation for further research questions. For example, it is possible to track juvenile male dispersal by colour banding juveniles in nest and tracking their movement. With this, and the known territories mapped of 2019, and individual song repertoires known for each bird from the 2019 season, one could look at potential song learning bias in young males at Shakespear (Braaten & Reynolds, 1999; Laland, 2004; Rendell et al., 2011; Slabbekoorn & Smith, 2002). MRS types of the population could also be re-recorded annually to track rates of changes in song diversity, complexity and innovation. This could help to corroborate my findings of the rates of change to song culture observed in the Motuihe population and shed light on the relationships between population age, translocation history and cultural complexity.

4.4.3 Motuihe

The tīeke population on Motuihe appears to have gone through rapid cultural evolution during the decade and a half following the translocation. The Motuihe population is spectrally similar to Mokoia, and has a similar cultural trajectory based on the age and translocation history of the two populations (Figure 1.3). Motuihe and Mokoia both belong to the same lineage, came from the same source population, and are both third-level translocated populations. At the time of Parker et al.'s (2012) sampling, the tīeke population had been on Mokoia for 16 years. At the time I sampled tīeke on Motuihe, the population was 15 years old. This supports the idea that cultural mutation rates (and potentially cultural complexity) are likely to be similar between the two populations and can be seen in Motuihe's shift in acoustic space in the nMDS.

The increase in song cultural complexity in Motuihe over an 11-year period has been dramatic. This increase in complexity has meant that the population is more similar to Hen

Island in terms of song diversity now than it was at the time of translocation. This expansion of song variants can be explained by the "cultural mutation hypothesis" (Dawkins, 1976; Jenkins, 1977; Lynch, 1996), where socially transmitted song like MRS is subject to a high rate of learning error (Baptista, 1992; Catchpole & Slater, 2003; Ellers & Slabbekoorn, 2003; Lynch, 1996; Slabbekoorn & Smith, 2002), which leads to an increased rate of cultural mutation and rapid changes in song diversity within and between populations (Dawkins, 1976; Jenkins, 1977; Lynch, 1996; Parker et al. 2012). There are many forms of cultural mutation – from the modification of existing cultural traits, to the creation of new cultural traits all together – and song learning errors are known to occur in many social learning oscine species (Ellers & Slabbekoorn, 2003; Irwin, 2000; Lynch, 1996; Tokarev & Tchernichovski, 2019). For example, Cardoso & Atwell (2011) analysed long-ranged songs of two dark-eyed junco (*Junco hyemails*) populations in California – one urban population, and one mountain population. Both populations have distinctive measurable differences in the spectral features of their song, and thus distinctive song cultures (Slabbekoorn et al., 2007). Results concluded that 56% of the magnitude of population divergence between these two populations (in relation to their song culture) could be explained by modifications of existing song types through cultural mutations (Cardoso & Atwell, 2011). An accumulation of these learning errors persisting in older populations like 2019 Motuihe may have the potential to increase song diversity (Lynch, 1996; Paxton et al., 2019). It is important to make the distinction that male MRS types at Motuihe weren't just forgotten and subsequently replaced by more complex MRS, but that MRS types actually increased over the years, with many (43%) of the original MRS types of 2008 still persisting within the population (see *Motuihe* chapter). Although there are other populations with a similar age as Motuihe in the nMDS, we speculate that Motuihe may have had an exceptionally high rate of song learning errors as a result of the replanting efforts influencing the distribution of young males on the island (Parker et al., 2012).

4.4.5 Tāwharanui

Initially I predicted that I would see a higher degree of cultural diversity at Tāwharanui in relation to its population age given its unique translocation history – I suspected that song types from Mokoia, Lady Alice and Red Mercury would persist within the park and thus increase the population-level song diversity. Hence, I expected that although Tāwharanui was a relatively "new" population (< 8 years old), its position in non-metric acoustic space would belie its age; Tāwharanui would appear closer to much older, culturally complex tīeke populations. However, the recent population decline exemplified by my inability to relocate banded individuals during the field season (particularly at Tokatū point) has likely altered both the genetic and cultural landscape.

As a result, Tāwharanui is now one of the least culturally complex population I analysed. Tāwharanui has undergone two rapid serial bottleneck events and its song culture has been greatly diminished. The large decrease in population numbers due to invasive predators likely disrupted the social system of the tīeke at Tāwharanui and could have had detrimental effects on the means by which male tīeke learn song (Jenkins, 1977; Parker et al., 2012). Normally, tīeke are long lived passerine and annual mortality rates are low (< 12%) (Armstrong et al., 2005; Armstrong & Davidson, 2006; Taylor et al., 2008), therefore territorial vacancies are normally quite rare (Jenkins, 1977), and in established populations, this creates ample social tutors for new males to learn song from (Jenkins, 1977). Contrasting this, in situations such as mass predation and extreme population decline, population density decreases and territorial space is abundant - mimicking a newly translocated population. As such, young males may lack adult social tutors, or, may have lost their contiguous adult tutor before fully learning an MRS type. I speculate that this potential withdrawal from the learning process may also explain the low levels of cultural complexity exhibited in the population (Parker, 2012; Price 2008).

When comparing Tāwharanui's spectral signature to its founder populations, my results show that, post-population decline, Tāwharanui is the closest in cultural complexity to Mokoia, a similarly aged population. The results of Tāwharanui's lack of cultural complexity undercuts the efforts of conservation scientists' carefully planned conservation translocation strategy and possibly downplays the importance of mixed founder populations that was suggested by Parker et al. (2012) to maximise cultural diversity. Once the biological consequences of conservation management to the behavioural evolution of the tīeke were identified, future recommendations were made to maximised both genetic and cultural diversity in newly established populations (Parker et al., 2010, 2012). Parker et al (2010) emphasised that populations should be founded by multiple doner populations at the onset of establishment. By using the completely known translocation history of the species, conservation scientists could advantageously select for doner populations to assemble a culturally rich founder population by avoiding serial translocations (Parker, 2008). Research conducted on other socially learning species has indicated that social learning is likely a key element in the successful establishment of a reintroduced population (Brown & Laland, 2001; Tear et al., 1997; Whitehead, 2010). For example, research on fish indicates the efficacy of social learning to improve translocation success (Brown & Laland, 2001). The survivability of hatchery-raised fish reintroduced to the wild may be improved by manipulating social learning in captivity (Brown & Laland, 2001), and predator avoidance was improved through social learning in Saimaa Arctic char (*Salvelinus alpinus*) (Vilhunen et al., 2005). These studies were primarily focused on animal cultural from a behavioural communication perspective, not a vocal communication perspective, but it still may highlight potential avenues for future translocation strategies. Future studies could potentially investigate aviary-reared tīeke subjected to MRS recordings from Hen Island as a potential strategy for preserving ancient cultural dialects. If indeed these hatchery-raised tīeke can learn MRS from historic playback, they could be incorporated into a founder group to be translocated to a mainland or offshore

sanctuary. Further, research has also indicated that it is crucially important that founder groups form a cohesive population (Ryan, 2006). Although concerns about diminished functional population size arose as a result of MRSs potential to act as a cultural contact barrier, my research on Shakespear indicates that, despite there being culturally distinct founder groups, the population is unified after one-year post-translocation. Indeed, it is apparent that animal culture plays a vital role in the evolutionary pathway of a species, and although conservation scientists aim to preserve this, it is apparent that in New Zealand the conservation trajectory of the species can be drastically influenced by but a few invasive mammals. If invasive species cannot be properly controlled, the best intended conservation strategies for many of New Zealand's species quickly becomes unhinged.

Since the arrival of early human settlers, over 40% of New Zealand land birds are now extinct (Clout, 1997). Although the decline in New Zealand's avifauna is likely multifaceted, introduced species currently disproportionately threaten over 50% of threatened New Zealand bird species (Collar et al., 1994; Dowding & Murphy, 2001). The early arrival of humans, Pacific rats (kiore; *Rattus exulans*) and dogs alone were responsible for the extinction of at least 32 species of birds over 1000 years (Gill & Martinson, 1991). Other mammalian predators introduced in the last 200 years have had the greatest impact on New Zealand avifauna, causing a further nine extinctions over a short period of time (Gill & Martinson, 1991). With that said, conservation efforts have reversed the decline in many New Zealand species through mammalian predator removal and habitat restoration (Burns et al., 2012; Dowding & Murphy, 2001; Innes et al., 2012; Moorhouse et al., 2003; Robertson et al., 2012; Salmon, 2013; Saunders & Norton, 2001; Towns et al., 2001). An example of the impacts of controlling exotic mammalian predators can be found in predator controlled and uncontrolled breeding sites of the kaka (*Nestor meridionalis*), a threatened, endemic New Zealand parrot (Moorhouse et al., 2003). At sites were invasive mammals like stoats and common brushtail possums were controlled, the nesting success of the kaka was significantly

higher (> 80%) than in unmanaged sites (< 38%) (Moorhouse et al., 2003). Further, predation of adult females was also significantly less (5%) in predator-controlled sites than in uncontrolled sites (65%) (Moorhouse et al., 2003). Building on this, most of New Zealand's native terrestrial reptile fauna are considered needing urgent conservation action, with the most apparent problem being predation by introduced mammals (Towns et al., 2001). Predation by invasive mammals initially caused severe extinctions and range declines in New Zealand reptiles, but through reactive and carefully planned conservation strategies, reptiles are now seeing a resurgence in numbers (Towns et al., 2001). Many reptile recovery programs involve targeted predator control and innovative conservation approaches similar to that taken to restore and protect New Zealand's avifauna (Towns et al., 2001).

Innovative species recovery programs involving translocations, predator control and erections of predator-proof fencing have indeed shown promising results for ecosystem restoration and fauna conservation (Burns et al., 2012; Innes et al., 2012; Parker, 2008; Smuts-Kennedy & Parker, 2013). Though many of these conservation strategies have rehabilitated endangered species of passerines (Butler & Merton, 1992; Hooson & Jamieson, 2003; Merton 1975; Miskelly & Powlesland, 2013), Tāwharanui exemplifies the impacts that mammalian predators have on native species, and how they can alter the direction of species recovery programs. Therefore, future conservation campaigns should strongly evaluate the potential of mammalian invasions to endemic sanctuaries (be it on the mainland or offshore) and continue to develop robust contingency plans to manage incursion events as quickly and effectively as possible. The decline of the tīeke population and the undoing of the carefully planned conservation efforts around the establishment of the population at Tāwharanui should serve as an example for future conservation efforts. As our knowledge of a species increases, and as conservation technologies improve and develop, the more effective our conservation management strategies can become.

4.5 Conclusion

My findings with the modern and the historically recorded populations indicate that the interplay between cultural drift, cultural mutations, founder effects and cultural bottlenecks have caused distinct, spectrally measurable differences to the song culture of each population (Baker & Jenkins, 1987; Hooson & Jamieson, 2003; Jenkins, 1977; Lynch, 1996; Mundinger, 1980; Parker, 2011; Parker et al., 2010, 2012; Slabbekoorn & Smith, 2002). Importantly, my findings highlight the simplicity of Tāwharanui's song culture in relation to the ancestral Hen Island dialect despite it having a complex translocation procedure involving a historically large founder group composed of three culturally distinct populations (K. Parker & D. Brunton pers. comm., 2019). Tāwharanui *should* have been more culturally diverse given this translocation initiative (K. Parker & D. Brunton pers. comm., 2019), but during the field season the population had declined to fewer birds than were released during the original translocation. This emphasises the impacts that invasive mammals can have on the conservation direction of a species.

Specifically, despite the Tāwharanui finding going against the predicted outcome of the translocation strategy implemented at Tāwharanui, it still confirms our predictions that since Tāwharanui had gone through two rapid, successive bottlenecks events, its song culture would be greatly diminished. Most notably, Tāwharanui's population-level acoustic signature is most similar to Shakespear's. Counter to our prediction, Shakespear is much closer to Tāwharanui in non-metric acoustic space than Tiritiri Matangi (Figure 4.3a). This indicates that Shakespear shares more similar spectral features with Tāwharanui than Tiritiri Matangi despite 50% of the MRS types at Shakespear coming from Tiritiri Matangi male tīeke. The 2019 tīeke dialect on Motuihe is most similar to Mokoia (a population which was 16 years old when recorded) in terms of their spectral signatures. This supports our prediction that Motuihe would be most spectrally similar to a population of a similar age. The 2019

population has shifted much closer to the spectral signature of Hen Island, indicating an increase to the complexity of its population-level song repertoire (Figure 4.3a).

In summary, the events at Tāwharanui show the vulnerability of many New Zealand species, as the population declined to fewer birds than were released during the original translocation and as such it had come close to extirpation. The cause was incursions into the park by cats, rats (*R. rattus* & *R. norvegicus*), common brushtail possums and stoats, and was only halted by the hard, ingenious work of park rangers and pest control crews. This tumultuous event further exemplifies the importance of predator control and the tīeke's inability to coexist with such exotic predatory species (Lovegrove, 1992). It is a direct reflection of what must have happened across the mainland upon the early introduction of these invasive species during the European colonization of the country. On a personal note, it was a stark experience to walk into a familiar forest and hear unaccustomed quietness. This was only further exacerbated by the realisation that this focal population – originally the primary study-site for my research– was likely experiencing a massive decline in numbers. If this study has shed light on anything, it was that the primary emphasis of conservation science in New Zealand needs to be directed at predator control to preserve its uniquely fragile biota. Although genetic diversity is obviously paramount for the maintenance of healthy species, and conservation input by genetic management should continue to be given to maintain species evolutionary potential (Keller et al., 2012; Lambert et al., 2005), other studies indicate that tīeke are not genetically complex and there are no obvious fitness or fecundity defects from inbreeding depression (Jamieson et al., 2009; Lambert et al., 2005; Taylor et al., 2005, 2008). My findings indicate that from a cultural perspective, reduced cultural complexity does not affect the breeding choices of tīeke, and that cultural complexity seems to increase given time. The operative word being *time*, which is the reason why the maximization of both genetic and behavioural diversity of *any* tīeke population moving forward is fundamentally underpinned by the removal of exotic mammalian predators.

4.6 References

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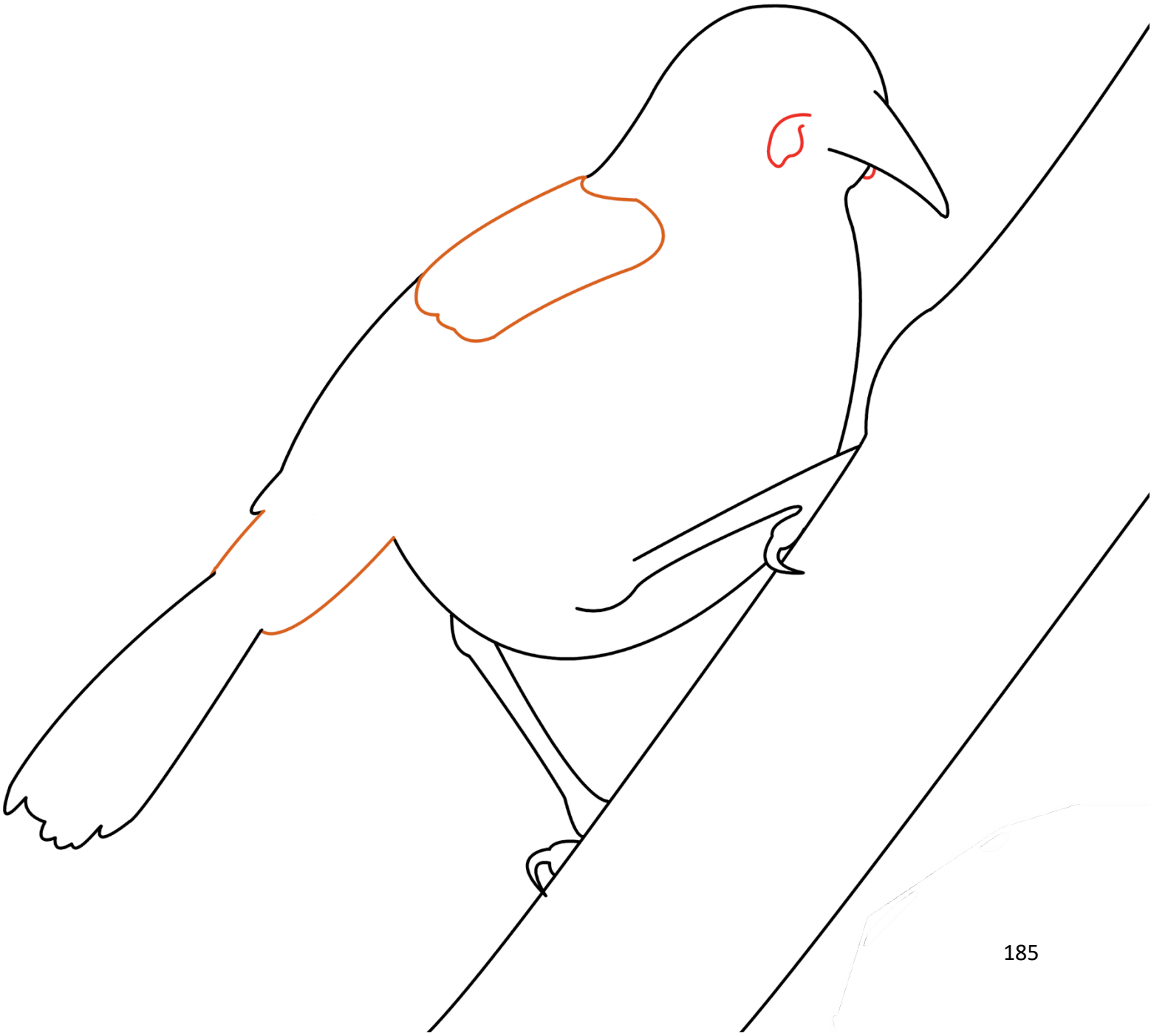
Chapter 5: Conclusions



The restoration of tīeke (North Island saddleback; *Philesturnus rufusater*)is one of New Zealand's greatest conservation success stories. The conservation efforts of the last 100 years have essentially given the tīeke a second chance in New Zealand and has seen the population grow from one remnant offshore site, to a total of 24 mainland and offshore sites across the North Island (Hooson & Jamieson, 2003b; Lovegrove, 1992). Although tīeke numbers have increased 14-fold since 1910 (Merton, 1965; Parker, 2013), their sensitivity to invasive mammalian predators warrants continuous hard work by conservationists to ensure locations with tīeke remain free from mammalian predators and these populations are secured. Indeed, though conservation recovery programmes have largely been efficacious, potentially irreversible damage has been done to the species from a genetic, and potentially cultural perspective. Early studies have demonstrated that the tīeke have low genetic diversity (Jamieson et al., 2009; Lambert et al., 2005; Taylor et al., 2005, 2008), so conservation translocations have been conducted with this in mind in an attempt to maximise genetic diversity at each site, but it was only until relatively recently that concerns about tīeke culture arose (Parker et al., 2010, 2012).

The thought behind conserving tīeke culture stems from a playback experiment conducted by Parker et al. (2010) on Motuihe Island. Tīeke were tested with playbacks of familiar conspecific recognition signals (known as Male Rhythmical Songs; MRSs) of the island and unfamiliar conspecific recognition signals from Hen and Cuvier islands and their responses were quantified (Parker et al., 2010). Results indicated that tīeke responded significantly faster to the familiar playback of Motuihe MRS than to playback of MRS from other populations. Parker et al. (2010) speculated that these results indicated that tīeke fit within the early stages of acoustic divergence with song learning (Slabbekoorn & Smith, 2002). He believed that if the tīeke continue down this path, they may enter the latter stages of this model, potentially leading to an allopatric model of speciation within translocation populations of tīeke (Parker et al., 2010; Slabbekoorn & Smith, 2002). However, many

papers have shown that southern hemisphere songbirds behave differently to northern hemisphere species (Morton, 1996; Odom et al., 2014; Robinson, 1949; Slater & Mann, 2004). The tīeke is a long-lived, non-migratory, site and pair faithful, southern hemisphere passerine (Blackburn, 1964; Jenkins, 1977; Merton, 1965, 1966), and Slabbekoorn & Smith (2002) based their acoustic divergence model largely from short-lived, migratory, sexually promiscuous, northern hemisphere passerines. Further, Parker et al.'s (2010) assessment was determined from a single series of playback experiment conducted on a single population during one field trip. I believe similar playback experiments should be conducted on multiple tīeke populations with varying levels of playback exposure to help corroborate Parker et al.'s (2010) findings and speculation. One must also consider the natural history of the model species for which Slabbekoorn & Smith's (2002) acoustic divergence model was founded, and its applicability to tīeke as a species.

My results indicate that concerns for speciation through cultural contact barriers in tīeke may be unwarranted. Using the population at Shakespear, I demonstrated that MRS is not solely sufficient to act as a pre-mating barrier between tīeke of different cultures. Although assortative paring did occur at Shakespear, the degree of assortative pairing was likely an overestimation, and genetic mixing between two cultural distinct populations occurred just one year after translocation. Cultural neighbourhoods did form representing the dialects of both source populations at Shakespear, which may have the potential to restrict genetic and cultural mixing. However, I found rapid MRS innovation within the first-generation which leads me to believe that the boundaries of these source population neighbourhoods may blur to form new boundaries with each progressive generation. Further, source population MRS dialects of both founder populations were passed onto the next generation, although I could not definitively conclude that this caused an increase in Shakespear's cultural complexity

when compared to the other 16 study-sites. It is possible that not enough time had passed to see the full effects that a mixed founder population can have on maximising a new population's cultural diversity. Based from my findings at Motuihe, I believe many dialects at Shakespear will continue to persist in the population provided adult tutors are distributed across the park, and that further long-term tracking of Shakespear's song culture be conducted to quantify the effects of mixed founder population translocations to tīeke culture.

Limitations exist with my study of Shakespear in the way of being unable to test for learning bias in first-generation males (Braaten & Reynolds, 1999; Laland, 2004; Rendell et al., 2011; Slabbekoorn & Smith, 2002). I was unable to identify potential social song tutors for first-generation male tīeke since I did not band them when they were juveniles and did not track their dispersal. It is possible that young males chose to learn MRSs based on individual male qualities that were beyond the scope of this project. This is an interesting aspect of social song learning in tīeke that, if studied, could illuminate which males are "good" tutors based on a criterion established from potential song learning bias exhibited by young males. Future studies on this could allow for future conservation translocations to favourably select for the best tīeke candidates for increasing the cultural complexity in a founder group. Limitations also exist with my findings of innovation in young males. It is possible that those innovative MRS types identified were a result of unrecorded MRS from adult males who had perished, or simply not sung that variant when I was recording. They could be rare or unusual song types that were not used in territory defence or mate attraction and therefore might not be important from a cultural perspective (Parker, 2011). I was also unable to determine if there was any innovation within the founder group of adult males. Future directions from this study could investigate the rate of change of known MRS types from the founder group of male tīeke post-translocation by pre-recording each founder male's repertoire pre-translocation, then re-recording them post-translocation.

I concluded from my findings at Motuihe that tīeke culture changes rapidly in even the younger, most linear, serially translocated populations. Most of the MRSs in the 2019 population were newly innovated, more MRS types were present, and variability in song increased. This further indicates that future conservation translocations may not need to apply as much emphasis on preserving ancient cultural dialects from a founder population perspective, as tīeke song seems to change irrespectively and cultural complexity seems to increase with time. I believe that the rapid cultural evolution that Motuihe underwent was intensified through the steady improvements in suitable habitat causing an expansion of the population and a patchy distribution of social tutors and naive young males across the island. If conservation prerogatives are to preserve ancestral dialects like, for example, in Shakespear, then my findings at Motuihe would elucidate that an even distribution of adult social tutors across new populations may mitigate the effects of cultural mutations. Further, future conservation efforts could consider possibly teaching young male tīeke bred in captivity complex MRS from ancestral tutors or recordings from Hen Island. Teaching song to social songbirds has been conducted on oscines both bred in captivity (e.g. Derégnaucourt, 2011) and in the wild (e.g. Mennill et al., 2018), and other cultural conservation programmes have advocated the positive effects of teaching captive bred species advantageous social behaviours prior to reintroducing them into an area (Whitehead, 2010). If young male tīeke are taught ancestral MRS, then incorporated into a founder group for a new population, this may provide another method for conserving ancient dialect.

Limitations in the Motuihe site come in the way of my inability to formally quantify the changes to habitat at Motuihe, and to formally assess the distribution and densities of young males and older males on the island in relation to the habitat. Therefore, many of my general conclusions made from my research on Motuihe remain speculative. Further, though I was able to identify fundamental measurable spectral changes to tīeke song between 2008 and 2019, the functional significance of these changes remains unclear as very little research has

been conducted on Mel Frequency Cepstral-derived features and coefficients in relation to birdsong. Like Shakespear, social learning strategies were not tested for at Motuihe and present an avenue for future studies. Future research could explore the MRS types shared across populations and within populations to try and highlight why they may persist, and possibly identify any forms of song learning bias or spectral qualities of these particularly robust MRS types that lends to their cultural endurance (Laland, 2004; Slater, 1989; Wheelwright et al., 2008).

My findings with Tāwharanui and the historic populations indicate that the interplay between cultural drift, cultural mutations, founder effects and cultural bottlenecks have caused distinct, spectrally measurable differences to the song culture of each population (Baker & Jenkins, 1987; Hooson & Jamieson, 2003b; Jenkins, 1977; Lynch, 1996; Mundinger, 1980; Parker et al., 2010; Parker, 2011; Parker et al., 2012; Slabbekoorn & Smith, 2002). Importantly, my findings highlight the simplicity of Tāwharanui's song culture in relation to the ancestral Hen Island dialect despite it having a complex translocation procedure involving a historically large founder group composed of three culturally distinct populations (K. Parker & D. Brunton pers. comm., 2019). Tāwharanui *should* have been more culturally diverse given this translocation initiative (K. Parker & D. Brunton pers. comm., 2019), but during the field season the population had declined to fewer birds than were released during the original translocation. This emphasises the unanticipated impacts that invasive mammals can have on the conservation direction of a species.

Limitations arise from the inability to re-record all study-sites within a similar time frame to give a true indication of the current cultural complexity of tīeke across the study-sites. Since I used historic recordings for 14 study-sites, and I have established that culture changes rapidly in this species, it is plausible that the acoustic relationships in non-metric acoustic space between the study-sites differs from the one that I have demonstrated in this thesis. It

is also possible that the seven discriminate features used to distinguish study-sites based on their spectral signatures may not have any functional significance to tīeke, though this was beyond the scope of the project to investigate.

Indeed, the success of the tīeke is fundamentally underpinned by how successful predator management regimes are. Although genetic diversity, cultural diversity, small founder populations, serial bottlenecks and disease screening are warranted concerns, they do not seem to radically impact the survivability or breeding success of new tīeke populations (Armstrong & Craig, 1995; Lambert et al., 2005; Taylor et al., 2005, 2008; Thorne, 2007). However, the failure to establish tīeke populations on offshore or mainland sites can be directly attributed to the presence of invasive mammalian predators in all cases but one (see *Appendices*) (Hooson & Jamieson, 2003a, 2003b; Lovegrove, 1996; Taylor et al., 2005). Therefore, if one wants to increase the numbers and populations of tīeke, exotic mammals have to be eliminated pre-translocation and the locations must remain free of these animals. If populations are to persist in nature, exotic mammals must be intensively controlled. All other concerns about tīeke have relatively minor impacts in comparison to predation. A reduction in cultural complexity does not affect the breeding choices of tīeke, and cultural complexity seems to increase with time. Specifically, as I have demonstrated with Motuihe, tīeke culture seems to change so rapidly, irrespective of their translocation history, that conservation translocations may not need to be as concerned about its preservation. Further to this, as I have demonstrated with Shakespear, the formation of distinct tīeke cultures does not seem to prevent cross-culture mating; genetic mixing between culturally distinct populations occurs within the first year of being translocated into the same area. Lastly, if the Tāwharanui population was any indication, stable populations of well-established tīeke are as much at risk of failing as new ones are, and can become dramatically altered with but a few incursions of invasive mammals. Indeed, a few invasive mammals have the potential

to undo decades of conservation efforts, and drastically alter the conservation direction of the species.

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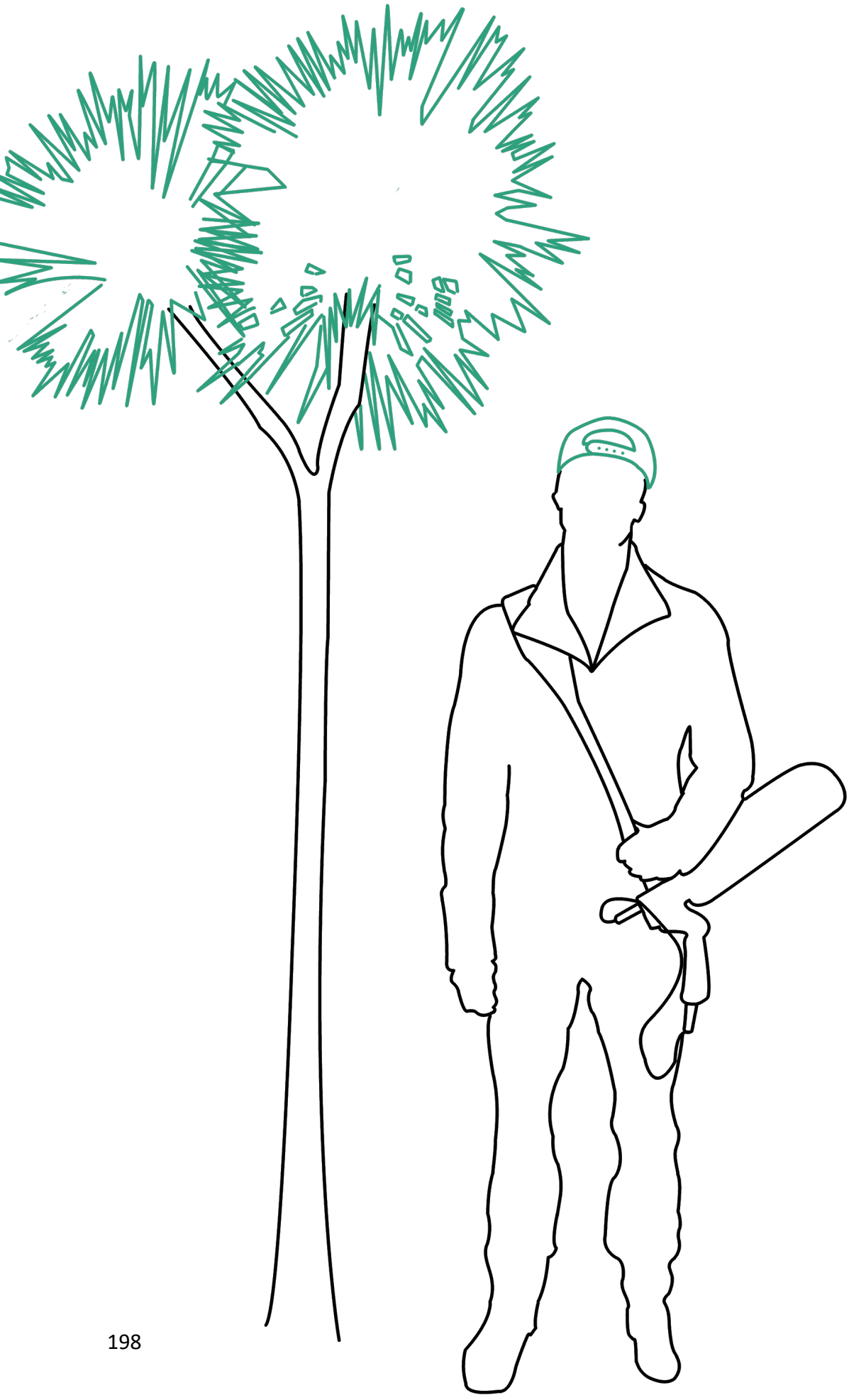
Chapter 6: Appendices



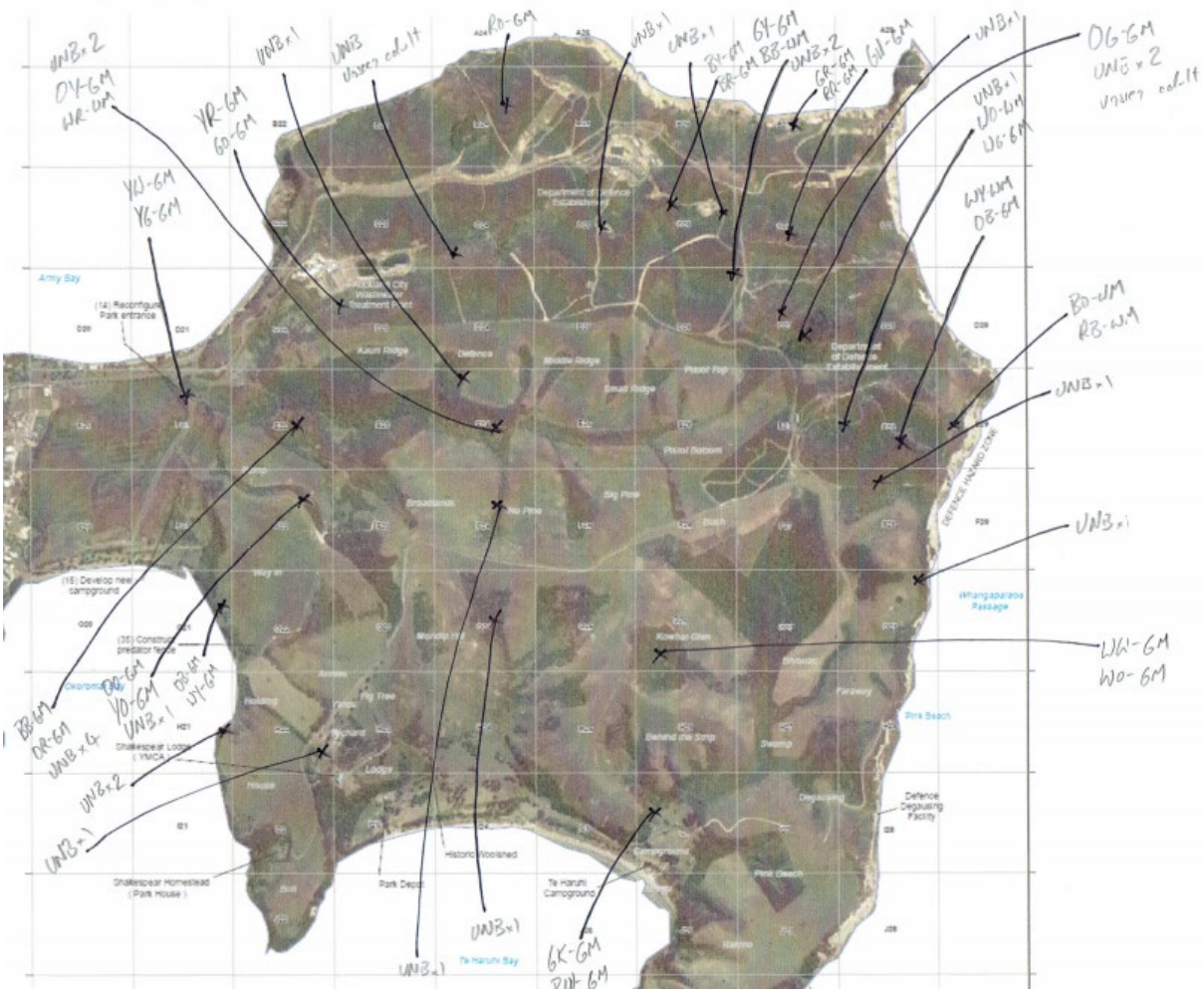


Figure 6.1: March 2019 survey of tīeke at Shakespear conducted by Kevin Parker, Parker Conservation, prior to my field season.

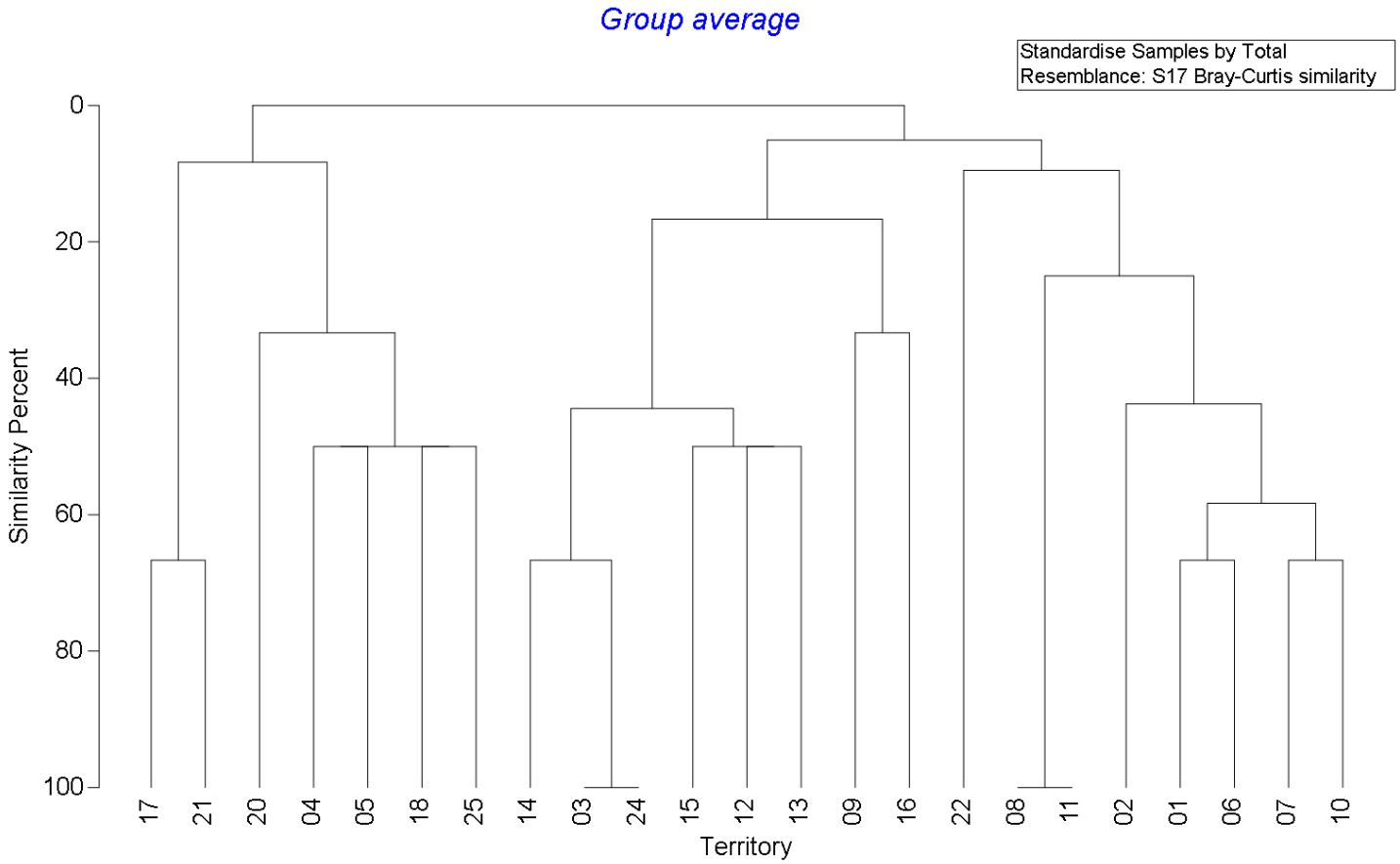
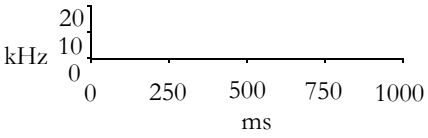
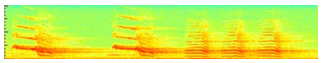
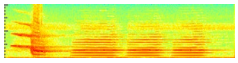
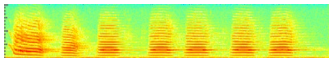
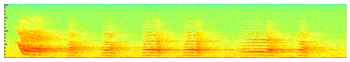
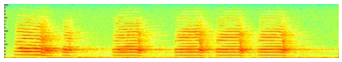
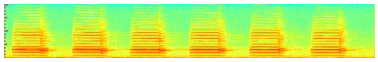
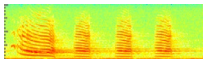
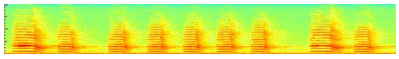
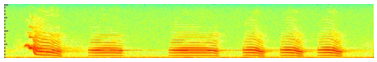
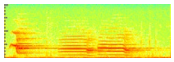
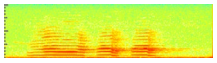
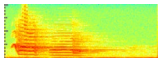
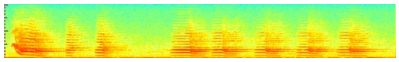
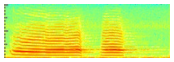
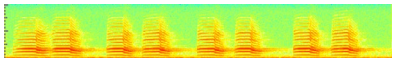
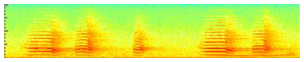
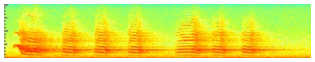
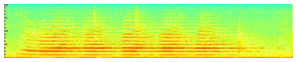
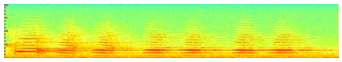
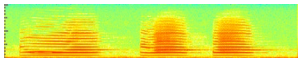


Figure 6.2: A dendrogram illustrating the relationship between individual's song repertoire at Shakespear. Males that are closer together share more MRS types. Y-axis gives a similarity score. X-axis is the name given to each individual male based on their territory number.

Table 6.1: MRS types sang in Shakespear, 2019. A spectrogram of the MRS provides an example of what the repeated phrase within the MRS type looked like. Abundance indicates how many recordings of that type there were.

Shakespear 2019	20 MRS Types 23 Individuals 321 Songs		Proportion of Individuals			
MRS Type	**Abundance**	**Spectrogram**	**Tiri**	**Tawh**	**1st Gen**	**Total**
37	51		4	0	4	8
39	54		3	0	3	6
2	39		0	3	2	5
42	24		3	0	2	5
26	47		2	0	1	3
31	15		2	0	1	3
32	20		0	1	2	3
38	12		3	0	0	3
28	14		0	0	2	2
33	2		1	0	1	2
34	4		2	0	0	2
43	13		1	0	0	1
35	1		1	0	0	1
56	5		0	0	1	1
27	1		0	0	1	1
36	1		0	0	1	1
40	4		0	0	1	1
30	3		0	1	0	1
21	1		0	1	0	1
24	10		0	1	0	1

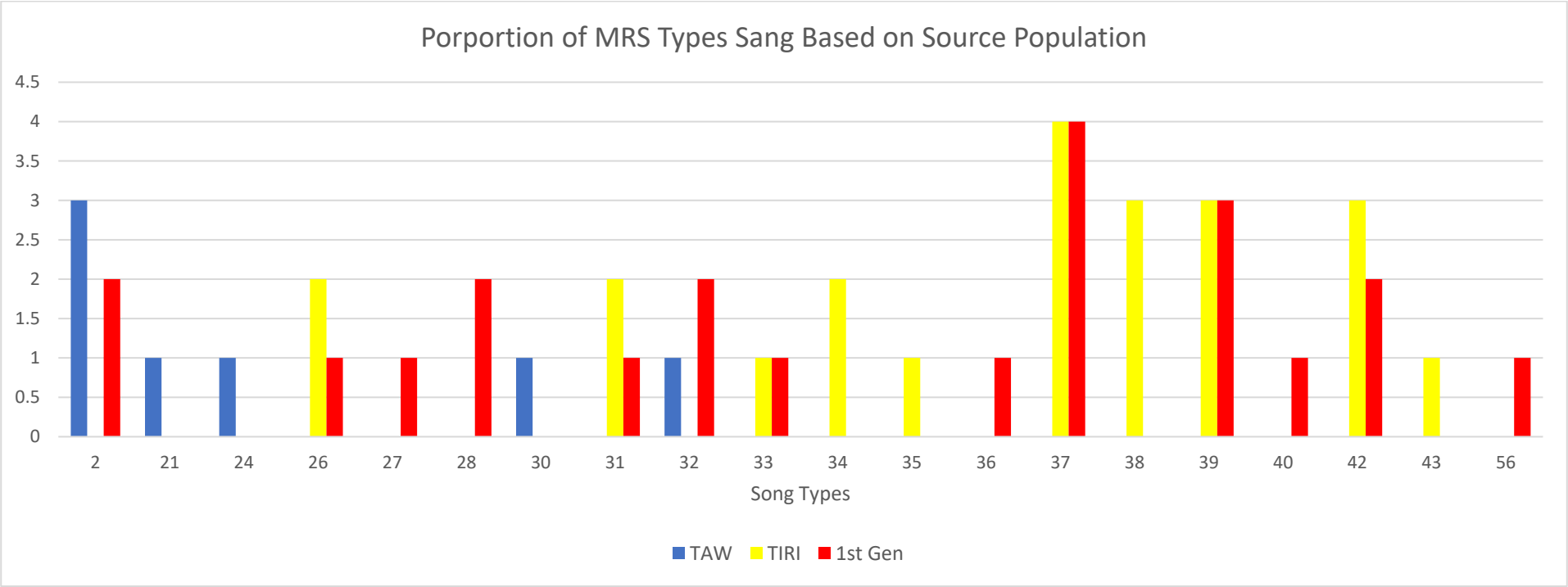


Figure 6.3: A bar chart indicating the proportion of MRS types sang based on where the males came from that sung them. Tāwharanui (TAW) is in blue, Tiritiri Matangi (TIRI) is in yellow, and first-generation males (1st Gen) is in red.

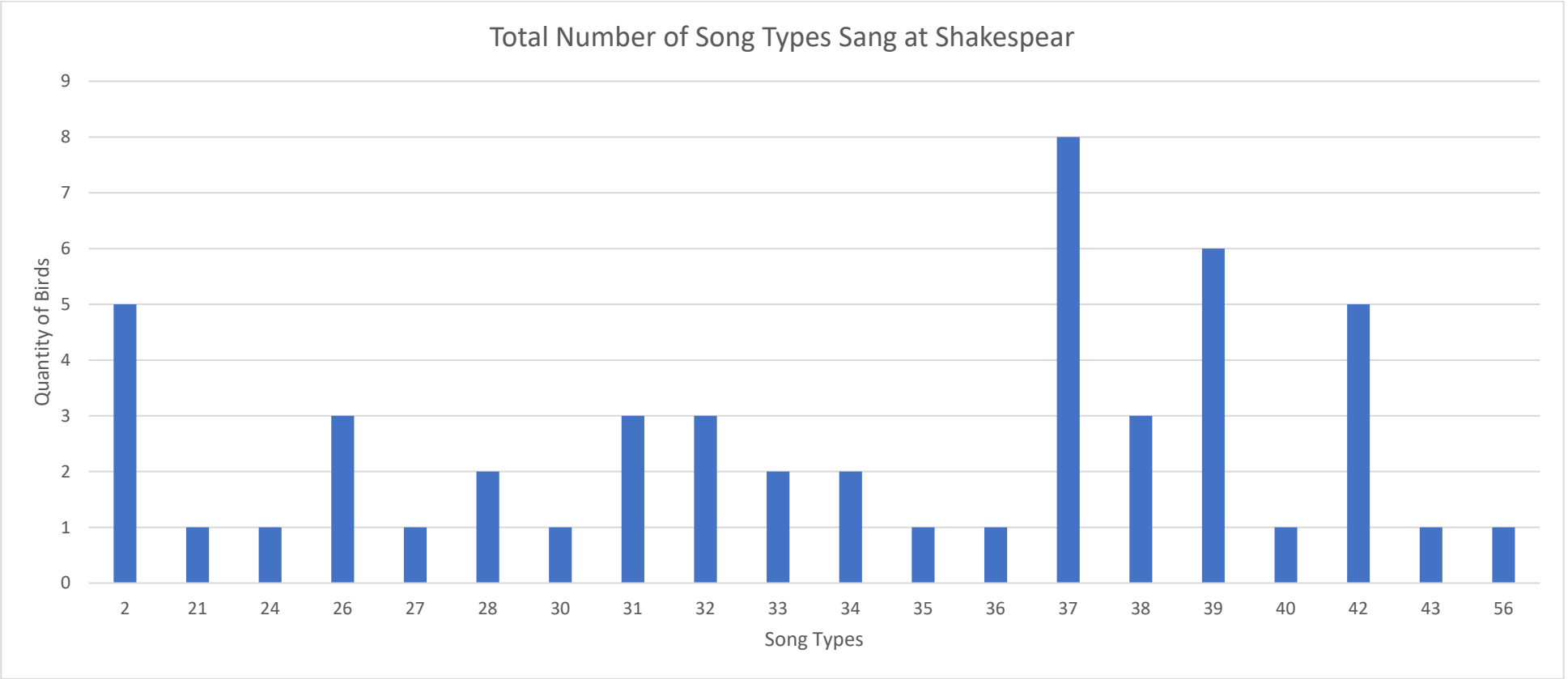


Figure 6.4: A bar chart indicating the total number of MRS types sang at Shakespear.

Table 6.2: Descriptive statistics comparing age (older than first-generation vs first-generation) of male tīeke at Shakespear in relation to the amount of MRS types sung between the two groups.

Older than First - Generation		**First - Generation**	
Mean	2.230769231	Mean	2.2
Standard Error	0.257050483	Standard Error	0.249443826
Median	2	Median	2
Mode	2	Mode	3
Standard Deviation	0.926808696	Standard Deviation	0.788810638
Sample Variance	0.858974359	Sample Variance	0.622222222
Kurtosis	-0.545600356	Kurtosis	-1.074161808
Skewness	0.210816648	Skewness	-0.407485087
Range	3	Range	2
Minimum	1	Minimum	1
Maximum	4	Maximum	3
Sum	29	Sum	22
Count	13	Count	10
Confidence Level(95.0%)	0.56006489	Confidence Level(95.0%)	0.564281137

Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	13	29	2.230769231	0.858974359
Column 2	10	22	2.2	0.622222222

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.00535117	1	0.00535117	0.00706416	0.933813877	4.324793743
Within Groups	15.9076923	21	0.75750915			
Total	15.9130434	22				

Table 6.3: Descriptive statistics comparing location (Tāwharanui, Tiritiri Matangi & first-generation;) of male tīeke at Shakespear in relation to the amount of MRS types sung between the three groups.

Tāwharanui		**Tiritiri Matangi**		**First - Generation**	
Mean	2.3333333	Mean	2.2	Mean	2.2
Standard Error	0.3333333	Standard Error	0.3266	Standard Error	0.24944
Median	2	Median	2	Median	2
Mode	2	Mode	3	Mode	3
Standard Deviation	0.5773503	Standard Deviation	1.0328	Standard Deviation	0.78881
Sample Variance	0.3333333	Sample Variance	1.06667	Sample Variance	0.62222
Kurtosis	#DIV/0!	Kurtosis	-0.8956	Kurtosis	-1.07416
Skewness	1.7320508	Skewness	0.27232	Skewness	-0.40749
Range	1	Range	3	Range	2
Minimum	2	Minimum	1	Minimum	1
Maximum	3	Maximum	4	Maximum	3
Sum	7	Sum	22	Sum	22
Count	3	Count	10	Count	10
Confidence Level(95.0%)	1.4342176	Confidence Level(95.0%)	0.73882	Confidence Level(95.0%)	0.56428

Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	3	7	2.333333333	0.333333333
Column 2	10	22	2.2	1.066666667
Column 3	10	22	2.2	0.622222222

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.0463768	2	0.0231884	0.02922908	0.971235362	3.492828477
Within Groups	15.866666	20	0.7933333			
Total	15.913043	22				

Table 6.4: Descriptive statistics for the 48 spectral features used that are important at discriminating between song types at Shakespear. See https://github.com/fzyukio/koe/wiki for a descriptive list of all features.

Spectral Variables	Mean	Median	S.E.
duration	0.038228	0.03444	0.000655
goodness_of_pitch_median	0.140083	0.139558	0.002453
mfc_max.13	-19.7211	-17.6554	0.575163
mfc_max.20	0.127679	1.533242	0.419564
mfc_max.23	-6.20602	-6.09536	0.547084
mfc_max.24	-10.9334	-10.6986	0.557508
mfc_max.25	-16.0051	-16.0684	0.585775
mfc_max.26	-23.8463	-23.4078	0.471493
mfc_max.32	-31.6857	-30.7687	0.560797
mfc_max.9	-18.6108	-18.2508	0.323159
mfc_mean.21	-26.2963	-26.4989	0.382131
mfc_mean.22	-34.6784	-34.3982	0.563992
mfc_mean.23	-35.9662	-35.7052	0.332102
mfc_median.19	-38.0753	-37.1342	0.408056
mfc_median.22	-35.0246	-34.983	0.600676
mfc_median.23	-36.7611	-36.6878	0.346602
mfcc_delta_variance.8	15.37561	15.2655	0.109476
mfcc_delta2_variance.10	11.72145	11.47504	0.137362
mfcc_delta2_variance.11	13.73354	13.80217	0.152414
mfcc_delta2_variance.16	10.948	10.81201	0.180832
mfcc_delta2_variance.17	10.34048	10.08426	0.165381
mfcc_max.10	24.9114	24.05197	0.411642
mfcc_max.11	29.431	30.1321	0.398199
mfcc_max.16	18.70923	18.88517	0.295627
mfcc_max.19	1632.54	1487.178	50.27156
mfcc_mean.14	4.424246	3.498774	0.284826
mfcc_mean.15	-1.94906	-2.56595	0.253561
mfcc_mean.16	2.364375	2.493122	0.232074
mfcc_mean.17	5.552009	5.571775	0.15922
mfcc_mean.18	3.461755	3.485898	0.149284
mfcc_mean.19	-280.241	-281.091	1.48123
mfcc_median.14	4.860487	3.904933	0.268904
mfcc_median.15	-1.64668	-2.27811	0.257893
mfcc_median.16	2.080816	2.359376	0.230315
mfcc_median.17	5.769909	5.904562	0.170952
mfcc_median.18	3.60773	3.681448	0.143832
mfcc_median.19	38.7867	38.56395	0.634768
mfcc_min.11	-20.8293	-20.9021	0.307646
mfcc_min.13	-20.1355	-21.0706	0.516724
mfcc_min.14	-17.1778	-18.2513	0.434371
mfcc_min.15	-20.4874	-20.4659	0.316287
mfcc_min.19	-209.984	-209.869	1.695604
mfcc_min.8	-22.5251	-22.6308	0.364935
mfcc_std.14	7.524674	7.426242	0.088052
mfcc_std.8	8.387625	8.278725	0.092485
mfcc_variance.14	59.08622	55.14907	1.431157
mfcc_variance.8	73.07226	68.53728	1.610451
spectral_contrast_median.5	29.67839	29.96885	0.198429

Table 6.5: MRS types sang in Motuihe in 2008. A spectrogram of the MRS provides an example of what the repeated phrase within the MRS type looked like. Abundance indicates how many recordings of that type there were. Types highlighted in yellow indicated shared MRS types between 2008 and 2019.

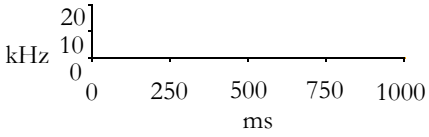
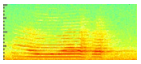
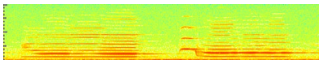
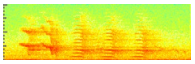
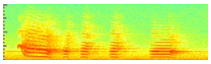
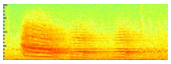
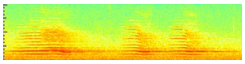
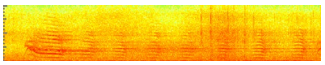
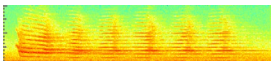
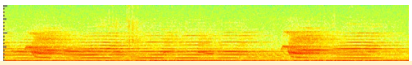
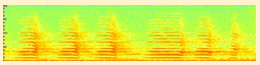
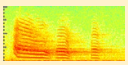
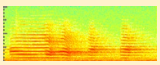
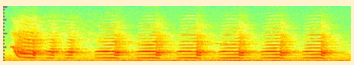
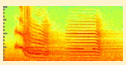
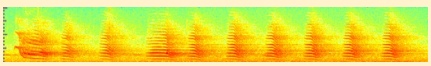
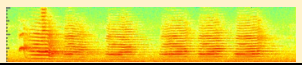
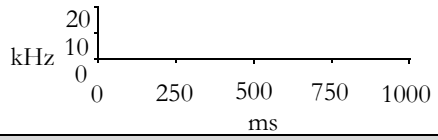
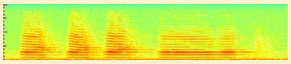
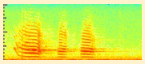
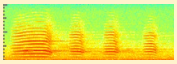
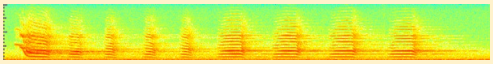
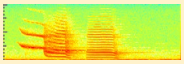
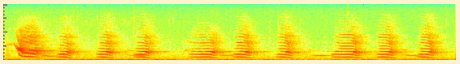
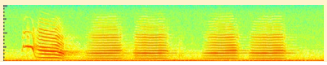
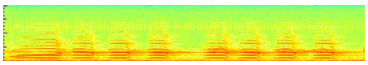
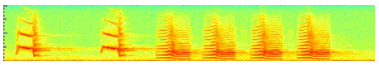
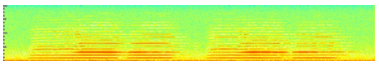
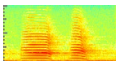
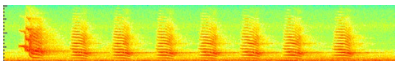
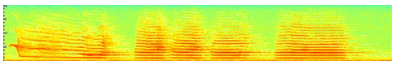
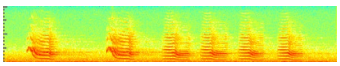
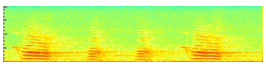
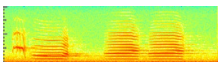
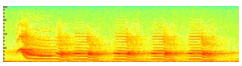
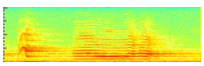
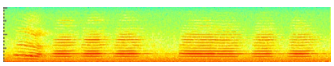
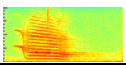
Motuihe 2008	N = 23 males 16 MRS types 58 Songs	
MRS Type	**Abundance**	**Spectrogram**
01	2	
02	8	
03	4	
04	3	
05	1	
07	1	
08	1	
09	1	
10	1	
44	14	
46	2	
47	11	
49	2	
55	1	
68	1	
69	4	

Table 6.6: MRS types sang in Motuihe in 2019. A spectrogram of the MRS provides an example of what the repeated phrase within the MRS type looked like. Abundance indicates how many recordings of that type there were Types highlighted in yellow indicated shared MRS types between 2008 and 2019.

Motuihe 2019	**N = 120 males** **27 MRS types** **235 Songs**	
MRS Type	**Abundance**	**Spectrogram**
44	23	
46	8	
47	21	
49	11	
55	9	
68	1	
69	11	
40	1	
41	19	
42	2	
43	3	
45	9	
48	11	
50	13	
51	1	
52	4	
53	14	
54	4	
58	3	
59	7	

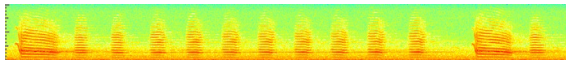
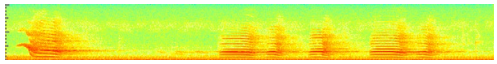
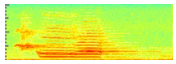
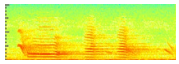
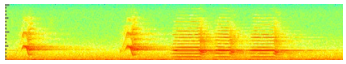
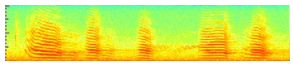
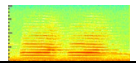
60	20	
61	14	
62	8	
63	4	
64	2	
65	10	
70	2	

Figure 6.5: Satellite imagery of Motuihe Island showing changes in the amount of vegetative cover over 15 years.

Table 6.7: Descriptive statistics for the seven spectral features used that are important at discriminating between the population averaged translocation groups. See https://github.com/fzyukio/koe/wiki for a descriptive list of all features.

LBI Cuv				**LBI Wha**			
Spectral Variables	**Mean**	**Median**	**S.E.**	**Spectral Variables**	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	25.66	25.97	0.18	spectral_contrast_median/6	24.48	24.87	0.30
spectral_contrast_mean/6	25.40	25.60	0.17	spectral_contrast_mean/6	24.32	24.49	0.28
mfcc_min/2	-61.03	-61.40	0.60	mfcc_min/2	-62.83	-63.06	1.02
mfc_max/27	-16.56	-17.37	0.64	mfc_max/27	-17.19	-17.51	0.85
spectral_bandwidth_min	2066.71	2055.12	19.49	spectral_bandwidth_min	2300.13	2309.66	25.28
mfcc_min/4	-20.33	-19.88	0.45	mfcc_min/4	-18.21	-17.90	0.69
mfcc_delta2_median/2	-0.0059	-0.0001	0.0096	mfcc_delta2_median/2	-0.0074	-0.0019	0.0141
Cuvier				**Whatupuke**			
Spectral Variables	**Mean**	**Median**	**S.E.**	**Spectral Variables**	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	25.90	26.52	0.17	spectral_contrast_median/6	24.76	25.37	0.38
spectral_contrast_mean/6	25.45	25.95	0.16	spectral_contrast_mean/6	24.45	24.94	0.35
mfcc_min/2	-61.03	-61.90	0.73	mfcc_min/2	-51.94	-52.88	1.21
mfc_max/27	-20.10	-19.98	0.56	mfc_max/27	-21.23	-20.51	1.14
spectral_bandwidth_min	2348.27	2338.87	18.65	spectral_bandwidth_min	2410.64	2391.13	38.85
mfcc_min/4	-20.20	-20.58	0.42	mfcc_min/4	-19.53	-19.86	0.74
mfcc_delta2_median/2	-0.0030	0.0000	0.0080	mfcc_delta2_median/2	0.0162	0.0000	0.0193
Lady Alice				**Coppermine**			
Spectral Variables	**Mean**	**Median**	**S.E.**	**Spectral Variables**	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	25.27	25.45	0.26	spectral_contrast_median/6	25.60	26.12	0.43
spectral_contrast_mean/6	24.94	25.06	0.23	spectral_contrast_mean/6	25.27	25.93	0.40

mfcc_min/2	-61.84	-61.76	1.38
mfc_max/27	-17.41	-17.18	0.81
spectral_bandwidth_min	2180.27	2128.42	37.84
mfcc_min/4	-24.69	-25.16	0.75
mfcc_delta2_median/2	-0.0028	0.0000	0.0127
Kapiti			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	27.42	27.58	0.16
spectral_contrast_mean/6	26.61	26.74	0.14
mfcc_min/2	-64.26	-63.85	0.64
mfc_max/27	-17.62	-17.70	0.44
spectral_bandwidth_min	2139.42	2145.44	17.21
mfcc_min/4	-24.20	-25.06	0.45
mfcc_delta2_median/2	0.0023	0.0000	0.0086
Motuihe 2008			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	26.87	27.34	0.47
spectral_contrast_mean/6	26.64	27.43	0.44
mfcc_min/2	-59.22	-59.18	1.17
mfc_max/27	-14.06	-14.25	1.19
spectral_bandwidth_min	2087.45	2079.15	54.97
mfcc_min/4	-21.61	-22.28	0.82
mfcc_delta2_median/2	0.0068	0.0061	0.0204
Stanley			

mfcc_min/2	-60.11	-59.03	1.59
mfc_max/27	-18.12	-17.32	1.44
spectral_bandwidth_min	2277.43	2313.80	43.70
mfcc_min/4	-22.14	-23.06	1.03
mfcc_delta2_median/2	0.0067	0.0000	0.0200
Mokoia			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	26.52	26.73	0.20
spectral_contrast_mean/6	25.86	26.15	0.17
mfcc_min/2	-66.94	-68.17	0.87
mfc_max/27	-17.86	-18.15	0.67
spectral_bandwidth_min	2080.84	2048.90	22.60
mfcc_min/4	-21.83	-21.73	0.53
mfcc_delta2_median/2	-0.0067	0.0000	0.0097
Motuihe 2019			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	27.32	27.48	0.23
spectral_contrast_mean/6	27.14	27.66	0.19
mfcc_min/2	-62.13	-62.05	0.89
mfc_max/27	-21.73	-21.31	0.70
spectral_bandwidth_min	2112.04	2149.39	27.32
mfcc_min/4	-17.68	-17.88	0.56
mfcc_delta2_median/2	-0.0173	0.0000	0.0141
Tiritiri Matangi			

Spectral Variables	Mean	Median	S.E.
spectral_contrast_median/6	25.90	26.05	0.24
spectral_contrast_mean/6	25.77	25.89	0.22
mfcc_min/2	-62.47	-62.78	1.05
mfc_max/27	-13.10	-12.44	0.92
spectral_bandwidth_min	2358.25	2323.89	23.45
mfcc_min/4	-22.31	-21.99	0.67
mfcc_delta2_median/2	0.0109	0.0123	0.0130
Moutuhora			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	27.03	27.47	0.16
spectral_contrast_mean/6	26.69	26.98	0.16
mfcc_min/2	-61.66	-60.63	0.56
mfc_max/27	-16.54	-17.21	0.54
spectral_bandwidth_min	2324.12	2349.09	18.24
mfcc_min/4	-22.05	-22.30	0.38
mfcc_delta2_median/2	-0.0080	-0.0003	0.0080
Shakespear			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	25.90	26.05	0.24
spectral_contrast_mean/6	25.77	25.89	0.22
mfcc_min/2	-62.47	-62.78	1.05
mfc_max/27	-13.10	-12.44	0.92
spectral_bandwidth_min	2358.25	2323.89	23.45
mfcc_min/4	-22.31	-21.99	0.67

Spectral Variables	Mean	Median	S.E.
spectral_contrast_median/6	24.68	25.59	0.33
spectral_contrast_mean/6	24.36	24.98	0.30
mfcc_min/2	-61.72	-62.80	1.08
mfc_max/27	-14.57	-13.27	0.87
spectral_bandwidth_min	2276.54	2237.26	37.80
mfcc_min/4	-20.73	-21.90	0.68
mfcc_delta2_median/2	-0.0085	0.0000	0.0126
Red Mercury			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	25.73	25.77	0.13
spectral_contrast_mean/6	25.53	25.64	0.12
mfcc_min/2	-56.47	-56.35	0.62
mfc_max/27	-19.52	-18.71	0.46
spectral_bandwidth_min	2250.23	2196.76	23.19
mfcc_min/4	-18.50	-18.71	0.31
mfcc_delta2_median/2	0.0006	0.0000	0.0059
Tāwharanui			
Spectral Variables	**Mean**	**Median**	**S.E.**
spectral_contrast_median/6	28.91	28.95	0.17
spectral_contrast_mean/6	28.61	28.60	0.17
mfcc_min/2	-69.50	-70.07	0.56
mfc_max/27	-23.86	-23.55	0.48
spectral_bandwidth_min	1939.04	1952.44	16.54
mfcc_min/4	-16.32	-16.73	0.41

mfcc_delta2_median/2	0.0109	0.0123	0.0130	mfcc_delta2_median/2	0.0155	0.0011	0.0077
Hen							
Spectral Variables	**Mean**	**Median**	**S.E.**				
spectral_contrast_median/6	22.81	23.14	0.25				
spectral_contrast_mean/6	22.64	22.67	0.24				
mfcc_min/2	-54.57	-54.91	1.04				
mfc_max/27	-25.12	-25.05	0.65				
spectral_bandwidth_min	2146.88	2130.36	25.99				
mfcc_min/4	-11.87	-11.74	0.57				
mfcc_delta2_median/2	-0.0091	0.0000	0.0098				

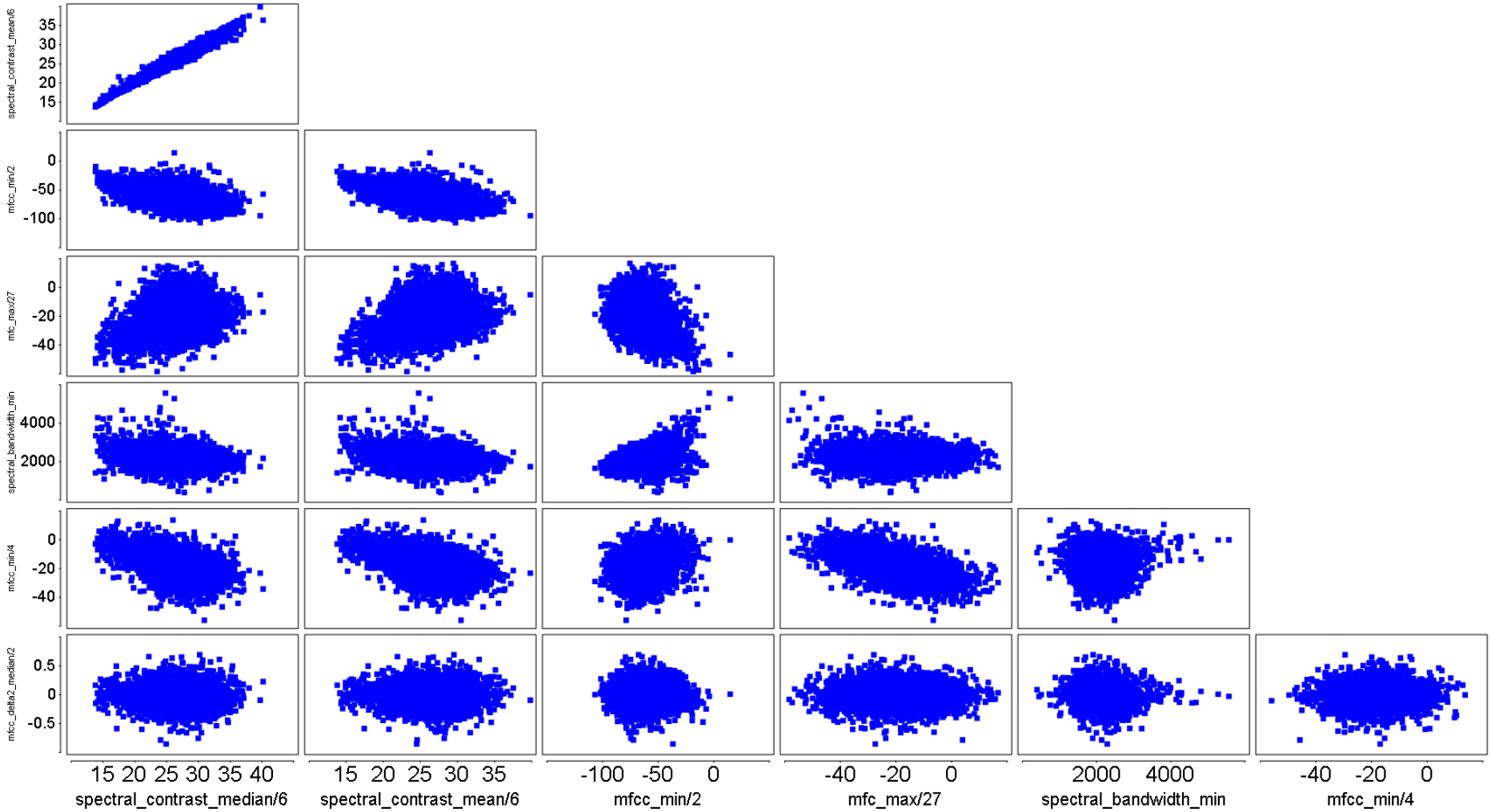


Figure 6.6: A draftman plot run for the seven spectral features that best discriminate between populations to check for normal distribution.

Table 6.8: Summary of tīeke (North Island saddleback; *Philesturnus rufusater*) translocation to offshore and mainland sanctuaries from 1925-2018. Data was collated from Lovegrove (1996) and Hoosen & Jamieson (2003) and updated.

Date of Release	Source Island	Release Island	Possible Predators	Area (ha)	# Released	Result	Notes, Population Size	Post-release Survival	References
Ancestral	Original Population	Original Population	K	484	Original Population	**s**	c.490 (1986)		Lovegrove, 1986
1925-10-18	Hen	Little Barrier	C,K	3083	9	x	Disappeared quickly		Turbott, 1947
1925-10-29	Hen	Kapiti	C,N,P,K,W	1965	9	x	Extinct by March 1931		Wilkinson & Wilkinson, 1952
1950-06-12	Hen	Lady Alice	K	155	6	x	c.3 by December 1952		Champers et al., 1955
1964	Hen	Whatupuke	K	102	23	**s**	c.500 (1996)		Merton, 1965
1966-01-30	Hen	Red Mercury	K	225	29	**s**	c.400 (1996)		Merton, 1975
1966-01-25	Hen	Cuvier	K	170	29	**s**	c.1200 (2004)	41%	Owen, 1998; Sullivan, 2004
1968-02-05	Hen	Fanal	K	75	25	x	c.3 by 1973		Jenkins, pers. comm.
1971	Whatupuke	Lady Alice	K	155	21	**s**	c.300 in 1986		Lovegrove, 1996
1977-01-23	Cuvier	Stanley	K	100	24	**s**	c.250 (1989)	46%	Lovegrove, 1996

1970s	Whatupuke	Coppermine	K	75	Natural Colonisation	**s**	c.20 (1979)		Newman, 1980
1981-01-20	Hen	Kapiti	N,K,P,W	1965	25	x	c.4 by 1986		Lovegrove, 1996
1981-02-06	Cuvier	Kapiti	N,K,P,W	1965	50	x	c.4 by 1986		Lovegrove, 1996
1981-02-12	Lady Alice	Kapiti	N,K,P,W	1965	25	x	c.4 by 1986		Lovegrove, 1996
1982-02-19	Hen	Kapiti	N,K,P,W	1965	22	x	c.4 by 1986		Lovegrove, 1996
1982-03-03	Cuvier	Kapiti	N,K,P,W	1965	50	x	c.4 by 1986		Lovegrove, 1996
1982-03-10	Lady Alice	Kapiti	N,K,P,W	1965	22	x	c.4 by 1986		Lovegrove, 1996
1983	Hen	Motukawanui	S,K	380	16	x	Extinct by 1986		Lovegrove, 1996
1983-03-19	Cuvier	Kapiti	N,K,P,W	1965	50	x	c.4 by 1986		Lovegrove, 1996
1984-02-25	Cuvier	Little Barrier	K	3083	50	**s**	c.2500 (2000)	44%	Lovegrove, 1996
1984-02-26	Cuvier	Tiritiri Matangi	K	197	24	**s**	c.600 (2002)	79%	Craig, 1990; Hoosen & Jamieson, 2003
1984-03-17	Hen	Motukawanui	K	380	12	x	Extinct by 1986		Lovegrove, 1996
1985-03-03	Cuvier	Fanal	K	75	29	x	c.5 by 1987		Hodsell, pers. comm.
1986-10-10	Lady Alice	Little Barrier	K	3083	42	**s**	c.2500 (2000)		Lovegrove, 1996
1987-03-06	Cuvier	Little Barrier	K	3083	47	**s**	c.2500 (2000)		Lovegrove, 1996
1988-04-18	Cuvier	Little Barrier	K	3083	49	**s**	c.2500 (2000)		Lovegrove, 1996
1987-09-26	Stanley	Kapiti	N,K,W	1965	43	**s**	c.97 (2000)		Lovegrove, 1996
1988-08-24	Stanley	Kapiti	N,K,W	1965	39	**s**	c.97 (2000)		Lovegrove, 1996
1989-08-26	Stanley	Kapiti	W (1996)	1965	40	**s**	c.97 (2000)		Lovegrove, 1996

1992-04-12	Tiritiri Matangi	Mokoia	M,W	135	36	**s**	c.200. First inland island population	81%	Davidson, 1999
1997-08-15	Tiritiri Matangi	Moturoa	S	150	26	x	Extinct by 1999		Asquith, pers. comm.
1999-03-15	Cuvier	Moutohora	M	143	40	**s**		55%	Brunton, 2000
2002-06-16	Tiritiri Matangi	Zealandia	M	225	39	**s**	First mainland population	49%	Campbell-Hunt, 2002
2004-09-10	Cuvier	Boundary Stream	N,S,P	800	37	x	First unfenced mainland population		Armstrong & Davidson, 2006; Sullivan 2006
2005-08-13	Tiritiri Matangi	Motuihe		179	20	**s**	c.300	70%	Armstrong, 1999; Parker & Laurence, 2008
2006-06-19	Mokoia	Bushy Park		87	34	**s**		55%	Gedir et al., 2013
2006-12-07	Mokoia	Bushy Park		87	4	**s**			Gedir et al., 2013
2011-08-27	Tiritiri Matangi	Motutapu		1510	20	**s**			https://www.doc.govt.nz/news/media-releases/2011/tieke-released-on-rangitoto-and-motutapu-islands-hatching-chicks/
2011-08-28	Tiritiri Matangi	Rangitito		2311	20	**s**			https://www.doc.govt.nz/news/media-releases/2011/tieke-released-on-rangitoto-and-motutapu-islands-hatching-chicks/

2012-03-10	Lady Alice	Tāwharanui	M, *C, *N, *S, *P	558	30	**s**	c.65 (2019). First multi-sourced founder group		http://www.tossi.org.nz/assets/pdf/newsletters/newsletter-march-2012.pdf
2012-03-20	Mokoia	Tāwharanui	M, *C, *N, *S, *P	558	30	**s**	c.65 (2019). First multi-sourced founder group		http://www.tossi.org.nz/assets/pdf/newsletters/newsletter-march-2012.pdf
2012-03-26	Red Mercury	Tāwharanui	M, *C, *N, *S, *P	558	30	**s**	c.65 (2019). First multi-sourced founder group		http://www.tossi.org.nz/assets/pdf/newsletters/newsletter-march-2012.pdf
2013-03-15	Cuvier	Cape Sanctuary	M,S,P	2500	120	x			http://www.lowecorp.co.nz/conservation/index.htm
2013-05-10	Tiritiri Matangi	Maungatautari	M, *C, *N, *S, *P	3400	40	**s**	c.65 (2017)		Parker & Smuts, 2013
2014-05-13	Little Barrier	Rotoroa		82	40	**s**			https://www.nzherald.co.nz/aucklander/news/article.cfm?c_id=1503378&objectid=11254155
2014-05-15	Little Barrier	Rotokare		230	19	**s**	c.400 (2018)		https://predatorfreenz.org/rotokare-scenic-reserve-valued-and-thriving-once-more/
2014-06-01	Bushy Park	Rotokare		230	40	**s**	c.400 (2018)		https://predatorfreenz.org/rotokare-scenic-reserve-valued-and-thriving-once-more/

2015-03-29	Lady Alice	Urupukapuka		208	20	**s**			http://www.terawhitimarae.maori.nz/tieke-saddleback-release/
2015-03-29	Lady Alice	Moturua		136	20	**s**			http://www.terawhitimarae.maori.nz/tieke-saddleback-release/
2015-05-30	Tiritiri Matangi	Urupukapuka		208	20	**s**			http://www.terawhitimarae.maori.nz/tieke-saddleback-release/
2015-05-30	Tiritiri Matangi	Moturua		136	20	**s**			http://www.terawhitimarae.maori.nz/tieke-saddleback-release/
2018-05-26	Tiritiri Matangi	Shakespear	M	377	40	**s**	c.57(2019)	46%	http://www.sossi.org.nz/tieke-arrive/
2018-06-15	Tāwharanui	Shakespear	M	377	10	**s**	c.57(2019)	46%	http://www.sossi.org.nz/tieke-arrive/

S = Stoats (*Mustela erminea*); K = Kiore (*Rattus exulans*); C = Feral Cats (*Felis catus*); N= Norway Rats (*Rattus norvegicus*); P= Common Brushtail Possums (*Trichosurus vulpecula*); W = Weka (*Gallirallus australis*); M= Mice (*Mus musculus*).

* = incursions

x = failed translocation

s = successful translocation