Dialect formation in fragmented populations of the endangered North Island kōkako (*Callaeas wilsoni*)

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SANDRA VIVIANA VALDERRAMA ORTIZ

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Abstract

The role of behavioural ecology in the conservation of species and biodiversity remains poorly understood. Observational and experimental studies of bird song, using a biogeographic approach, provide an opportunity to address this issue. Here I test hypotheses on the emergence and divergence of song cultures related to historical as well as more recent population fragmentation events. The North Island kōkako (*Callaeas wilsoni*) is a duetting songbird endemic to New Zealand that was once widespread but, due to habitat loss and introduced predators, has become endangered. These birds are sedentary and monogamous with poor flying abilities. Therefore, all of the c. 1500 surviving individuals are marooned in 13 scattered surviving populations and 11 translocated populations. The historical fragmentation of populations, the kōkako's territorial nature and capacity to learn songs, and the establishment of new populations through translocation make this species a good candidate for studies on the emergence of song cultures, social divergence and landscape effects on conservation from a behavioural perspective.

Song sharing and comparisons of acoustic characteristics were used to reconstruct associations of song traditions and acoustic traits at both macrogeographic and microgeographic levels in the six largest surviving populations of kōkako (Chapter 2 and 3). Distinct song cultures or dialects were discovered in all populations examined. However, patterns of vocal similarity observed were not correlated with historical fragmentation patterns or linear geographical distance (Chapter 2). Instead, rapid vocal drift following fragmentation and isolation as well as founder effects linked to population contraction may explain current macrogeographic song variation (Chapter 3). Nevertheless, a fragmentation effect on song similarity, generating song repertoire divergence, was observed at a microgeographic scale within discontinuous populations (Chapter 2). In addition, juvenile dispersal across portions of

tenuously connected habitat, which have strikingly different song cultures, suggests that kōkako learn songs after dispersal (Chapter 2). Post-dispersal learning may explain the lack of consistency between dialect membership and genetic relatedness among surviving populations. Dialect formation may occur as different cultural trajectories are forged by fragmentation and isolation; subsequent song convergence may then occur due to social selection or chance events.

The effects of population size on song attributes, repertoires and sharing, vocal versatility and syntactical structure were examined within the six largest natural populations, as well as two translocated populations of kōkako (Chapter 3). Repertoire size, song diversity and the predictability of syntactical structure were positively correlated with population size. Song traditions and the rate of cultural evolution may depend on social interaction and population size, as the neutral model of song microevolution predicts. Smaller populations of kōkako, with reduced social stability under relaxed selection pressures, may resemble small colonizing groups undergoing founder effects and vocal drift leading to loose syntax, consistent with the 'withdrawal of learning' hypothesis. Furthermore, social modulation of vocal behaviour and song traditions are discussed in the context of reproductive success and adaptation to differing social conditions as in the case of translocation events (Chapter 3).

Recently isolated translocated populations exhibit remarkable acoustic divergence and reduced song sharing with the corresponding source population (Chapter 4). Translocated populations showed relatively low song diversity and increased song sharing as well as acoustically distinct song features. To investigate how meaningful this vocal divergence was for individuals in source and translocated populations, a reciprocal playback experiment was performed to examine vocal and approach responses to simulated local and non-local intruders. Responses to simulated intruders differed among populations but there was little evidence of discrimination based on stimulus type. The degree of song divergence (i.e., repertoire and acoustic features) and vocal response to playback relative to the source population was greater in an older translocated population than a more recently translocated population (Chapter 4). Consistent with the consequences of founder effects and vocal drift, these results demonstrate that kōkako populations vocally diverge in isolation following the establishment of a population with a

vocal subset and subsequently a different cultural trajectory (in accordance with the 'withdrawal of learning' hypothesis). Cultural erosion in small translocated populations may affect their viability as reduced vocal virtuosity can be associated with a reduced capacity for territory defense and mate attraction, and consequently low reproductive success. Song divergence can ultimately have important implications for our understanding of the evolution of animal societies and our ability to conserve animal populations.

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Chapter 1

Introduction

North Island kōkako (above) and the South Island kōkako (extinct), by George Lodge (1913-1914, Museum of New Zealand Te Papa Tongarewa. (Used with permission).

Habitat destruction has been identified as the major cause of species extinction in the world (i.e. Tilman et al. 1994; Brooks at al. 2002; Pimm & Raven 2000). Rapid anthropogenic transformation of natural habitats, mainly for agriculture, has resulted in habitat loss (Launders 2010). During the process, habitats often undergo reduction and fragmentation with consequent declines in populations and species (Henle et al. 2004; Şekercioğlu & Sodhi 2007; Bennet & Saunders 2010). According to the theory of island biogeography (MacArthur & Wilson 1967), smaller populations are more vulnerable to isolation, as there is restricted dispersal; they are also vulnerable to stochastic events such as loss of genetic variability, changing environmental conditions and catastrophic events (e.g. hurricanes, floods, and fire). The introduction of alien species, for instance, can represent a catastrophic event in vulnerable environments such as fragments of habitat and islands. On islands, where many species have limited dispersal abilities, inhabit a limited range of habitat types, and are endemic to small areas (Long et al. 1996), population depletion and extinction occurs rapidly when natural habitats are disrupted or disappear, and when introduced predators become invasive (Newton, 2003; Steadman, 1997).

New Zealand represents a well-known extreme scenario in conservation biology. Because of its high endemism and level of threats to native species, New Zealand is one of the 25 biodiversity hotspots in the world (Myers et al. 2000). It is one of the places most dramatically affected by habitat destruction and, more recently, by the introduction of alien herbivores and predators, among others, that have become widespread (i.e. Allen & Lee 2006; Saunders & Norton 2001, Kelly & Sullivan 2010). Only 22% of the original primary vegetation remains (Myers et al. 2000) and 30 species of mammals have been introduced. Australian brushtail possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*) and rats (*Rattus rattus, R. norvegicus and R. exulans*) have severely affected bird populations, often to the extent of local extinction (Allen & Lee 2006). Although conservation efforts have been focused on the protection of areas with undisturbed habitat since the 1970's, ongoing decline and extinction of bird populations and species indicates that management of invasive species remains crucial (Saunders & Norton 2001).

Surviving populations of many native species in New Zealand are marooned on isolated areas with preserved habitat under strict conservation management.

However, it has been recently recognized that historical land use, habitat loss and connectivity may play an important role in current species assemblages, extinction thresholds and the dynamics of invasive species populations; hence past forest loss continues to be relevant to present conservation (e.g. Tilman et al. 1994; Harding et al. 1998; Didham et al. 2005; Ewers et al. 2006).

An initial strategy for preventing further extinctions involved the translocation of birds to New Zealand offshore predator-free islands. Subsequently, intensive pest control established on mainland reserves over the last 20 years has made feasible numerous translocations of threatened species to remnants of mainland habitat from which they had disappeared (Armstrong & McLean 1995; Clout 2001; Saunders & Norton 2001). Translocation to both island and mainland reserves has been a successful conservation tool in New Zealand and it has served as a model implemented worldwide (Jamieson et al. 2006; Taylor et al. 2005). However, the overall impacts of translocation have been focused on management (e.g. Scott & Carpenter 1987, Bright & Morris 1994; Lovegrove 1996; Wolf et al. 1996) and ecological aspects (e.g. Kurzejeski & Root 1988, Musil et. al.1993, Cunningham 1996, Armstrong et al. 1999, Armstrong & Ewen 2001; Jamieson & Wilson 2003). More recently, genetic inbreeding effects on translocated animal populations have been studied (Stockwell et al. 1996, Storfer 1999; Cardoso et al. 2009; Bronwyn et al. 2010).

As on islands (Frankham et al. 2002) and fragmented habitats (Segelbacher 2008), translocated populations may present reduced genetic diversity and genetic divergence due to founder effects and genetic bottlenecks, which may threaten the survival of reintroduced populations (Cardoso et al. 2009). However, biological diversity includes behavioural diversity, which may be crucial in the evolution, survival and persistence of populations and species. Despite the potential importance of behavioural diversity, the effects of past habitat loss, translocation and isolation on behaviour and cultural transmission remain poorly understood (Clemmons & Buchholz 1997).

One key aspect of behavioural diversity likely to be affected by and relevant to conservation work is song. Birdsong is a well-studied paradigm in behavioural ecology with a wide spectrum of developmental plasticity that has resulted in outstanding intraspecific and heterospecific singing diversity. Song development ranges from species with no apparent imitative learning (e.g., Suboscines),

demonstrating a genetically encoded ability to produce normal song, to species in which vocal learning is necessary to develop normal song. Vocal learning appears to have independently evolved in hummingbirds (e.g., Wiley 1971; Baptista & Schuchmann 1990; Gaunt et al. 1994), parrots (e.g., Farabaugh & Dooling 1996; Bradbury et al. 2001; Wright & Wilkinson 2001), and songbirds (e.g., Nottebohm1972). Like other learned behaviours, song learning occurs by imitation and through social interaction mainly with conspecifics. The modification of vocal behaviour through social learning means that birds acquire singing skills and, therefore, how fast or how well they sing may also depend on experience and social exposure to conspecifics. The ability to modify behaviour may have evolved for its advantages to adapt to environmental changes, which can modify the trajectory of behavioural development (van Shaik 2010). For example, when young birds disperse, flexibility to learn the local song may be important to obtain a territory, through counter-singing, and for effective communication using local, familiar song in neighbour interactions (Beecher & Brenowitz 2005).

Learned vocalizations constitute communication systems underlain by mechanisms of biological evolution, individual learning and cultural evolution (Kirby 2007; Fig. 1.1). Similar to human language, song learning is a derived character affected by a large number of genes involved in the mechanics of vocal production and complex traits of social behavior. Therefore, intraspecific heritability of song is likely to be low; dispersing individuals, for instance, can learn their songs from neighbours and vocally adapt to new neighbourhoods (e.g. Nordby et al. 2001). In consequence, vocal patterns reflect past habitat connectivity, much as human language variation between islands can be used to reconstruct historical migration and colonization patterns (Williamson 1981). Vocal patterns may also influence inter-population differentiation and interaction in the case of translocated populations from multiple sources.

The importance of variation in song traditions has only recently been considered in conservation biology (Gaunt & McCallum 2004; Laiolo 2010). Song can be affected by habitat fragmentation (Laiolo & Tella 2005; Laiolo & Jovani 2006; Laiolo & Tella 2006), and can predict population viability (Laiolo et al. 2008). However, the social significance of song variation as a consequence of population structure, habitat fragmentation and isolation is still poorly understood.

Hence, it is imperative to collect information on patterns of song divergence in isolation, ecological factors involved in vocal differentiation, and behavioural outcomes of translocation.
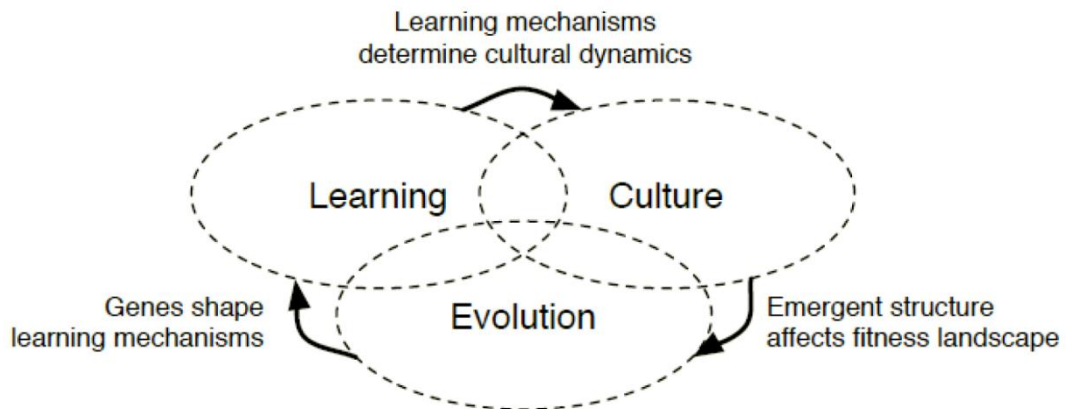
Figure. 1.1. Spatio-temporal variation of learned vocalizations emerges from the interaction of individual learning, cultural transmission and biological evolution (from Kirby 2007).

1.1 Geographic variation of birdsong

The evolution of vocal diversity is a major area of interest in the study of birdsong and animal behaviour. This process of vocal divergence is an example of rapid diversification (Podos et al. 2004) whereby song can play a role as an isolating mechanism (Grant & Grant 1996, Slabbekoorn & Smith 2002, Remsen 2005). Patterns of song variation provide insight into the processes by which song traits may evolve and persist, as well as vocal mechanisms involved in those evolutionary processes.

Song variation occurs within and between individuals as well as populations at a species level (Searcy & Nowicki 1999) and it has been widely documented in birds (Baker & Cunningham 1985, Mundinger 1982, Podos & Warren 2007). Cultural transmission by imitation during song learning can both favour and constrain song divergence (Podos et al. 2004, Slabbekoorn & Smith 2002, Slater 1989), which results in complex variation. Microgeographic variation occurs where differences from individual to individual or among neighbouring

populations are reduced by vocal imitation; macrogeographic variation refers to differences between populations separated by a geographic barrier (Mundinger 1982). Vocal geographic variation by song learning results in dialect formation when individuals breed and sing where they learned their songs (Kroodsma 2004), which in turn results in sharp boundaries within populations (Rothstein & Fleischer 1987, Slater 1989).

1.1.1   Imitative learning and cultural transmission

The process of vocal learning involves a stage of memorization and a stage of practicing in which the birds learn to match songs with sounds in their memory; they modify their songs based on auditory feedback (Hultsch & Todt 2004, Konishi 2004).

During song memorization, sensitive phases take place in which birds are not capable of singing yet but hear and receive song stimuli. These phases have been demonstrated to be fundamental in the development of song. For example, some experiments, in which hearing was prevented during this phase, showed an extension of this period to incorporate songs heard later (Nelson et al. 1997, Slater at al 1988). Thus, experience plays a crucial role in song acquisition (Brainard & Doupe 2002). Furthermore, sensitive phases vary in song birds; as a result, there are 'closed-ended' learners that apparently do not modify their song as adults, whereas 'open-ended' learners can incorporate new sounds later or during adulthood (Hultsch & Todt 2004, Nottebohm 2004). However, there is a continuum in the variation of birdsong plasticity, from 'closed' to 'open' learning; studies of this variation might shed light on our understanding of neural mechanisms involved in learning (Brainard & Doupe 2002, Brenowitz & Beecher 2005).

The sensory motor stage follows the sensitive phase through progressive steps in order to develop song (Marler & Peters 1977, Hultsch & Todt 2004). From subsong to plastic song and finally 'crystallized' full song, birds establish a neural connection between stimuli from hearing tutors and song production through imitating and practicing. As song patterns begin to stabilize, characteristics such as loudness, repertoire size and stereotypy appear (Marler & Peters 1981, Podos et al 1999, Brumm & Hultsch 2001, Hultsch & Todt 2004). Finally, birds select

sounds heard when they socially interact with conspecifics to complete normal song development (Brainard & Doupe 2002).

1.1.2   Song dialects

Dialects are a result of imitative learning, a process in which song structure plasticity is a decisive feature. Although genetic constraints related to mechanical design may stabilize directional evolution, song traits may evolve through selection and drift during cultural transmission (Konishi 1985). Changes of song traits and acoustic structure occur during information processing in song learning. Causes of variation in songs may include copying errors, rearrangement of copied elements, and the invention of novel elements (e.g. Baptista 1977, Grant & Grant 1996, Ince et al. 1980, Lemon 1975, Podos et al. 2004, Slabbekoorn et al. 2003, Slater 1989).

There have been numerous studies on song dialects in different species including hummingbirds (Gaunt et al 1994), parrots (Wright 1996, Baker 2000, Wright et al 2008) and mainly songbirds (Kroodsma 2004). Some examples of songbirds with dialects are sunbirds (e.g., *Cinnyris coccinigastrus*, Grimes 1974; *Nectarinia osea*, Payne 1978), the European wren (*Troglodytes troglodytes*, Catchpole & Rowell 1993), redwings (*Turdus iliacus*, Bjerke & Bjerke 1981), corn buntings (*Miliaria calandra*, McGregor and Thompson 1988), house finches (*Carpodacus mexicanus*, Mundinger 1975) and saddlebacks (*Philesturnus carunculatus*, Jenkins 1978).

Origin and temporal stability of birdsong dialects

Song diversity is a consequence of cultural evolution as differential transmission results in variability of song traits across generations. How those cultural changes occur may be better understood by comparison with processes of biological evolution that involve well known forces at a genetic scale such as mutation, drift, migration and selection (Lynch 1996). Therefore, evolutionary forces are considered to act on song traits. Podos et al. (2004) have recognized two substrates in song evolution which are memes and mechanisms (e.g., vocal control, production and ontogeny).

Memes are units of information culturally transmitted between individuals by imitative learning (Dawkins 1976). In birdsong, memes may refer to song patterns that range from syllables to phrases and complete songs (Lynch 1996, Lynch et al. 1989) whose changes are governed by neural mechanisms of song perception and memorization (Podos et al. 2004).

Moreover, the processes or mechanisms directly involved in song evolution allow us to explain how changes occur. Mutation is the most extreme source of variation and occurs as a result of inaccurate reproduction of model songs such as errors in copying and invention of new elements (e.g., Nottebohm 1970, Marler & Mundinger 1971, Baptista 1977, Lemon 1975, Kroodsma 1982). Drift occurs when changes by chance (mutation) are transmitted across generations during learning (e.g., Jenkins 1978, Payne 1981) or if allopatric populations arise (e.g., Thielcke 1973, Baker 1975, Mundinger 1975, Baker & Cunningham 1985, Thielcke & Wüstenberg 1985). However, memes are differentially transmitted from one to another generation due to selection. As a result, the persistence of memes depends on their effectiveness as communication signals, which in turn reduces variability within populations (Lynch 1996, Podos 2004). Between populations, migration or contact will generate the possibility of an interchange of memes and it may consequently reduce divergence (Lynch 1996); however, isolated populations may be exposed to differing ecological factors such as population reduction and habitat fragmentation that can result in differing cultural trajectories and song divergence leading ultimately to the emergence of a reproductive barrier (Slabbekoorn & Smith 2002).

Models to explain dialect formation

In the light of significant ecological factors such as historical events of colonization, dispersal, isolation, and changes in habitat structure and population size, three models of dialect formation have been proposed with corresponding predictions (Payne 1981; discussed in Baker & Cunningham 1985; Table 1.1):

1.   **Historical model**. Cultural song divergence can emerge due to random founding events that occur by dispersal, invasion and colonization by a reduced number of individuals. Similarly, habitat loss and fragmentation as well as

dramatic population contractions may result in founder effects and subsequent independent evolution of local song traditions (Baker 1975). Fewer tutors in a population may lead to the appearance of new song variants by 'withdrawal of learning' (Thielcke 1973, 1985).

2. **Genetic adaptation model.** Local specialization to geographically differing environmental conditions may ensue behavioural differences and consequently vocal divergence. Natural selection may favour locally adaptive features and birds may be attracted to and learn local songs. For example, the evolution of morphological and physiological features involved in song production may cause geographic song variation by local adaptation (e.g., Tubaro & Mahler 1998; Slabbekoorn & Smith 2000; Podos 2001). However, selective pressures on acoustic signals for optimal sound transmission in different habitats may also result in song differentiation between populations (Handford 1988; Searcy & Nowicki 1999; Podos 2004; Nicholls & Goldizen 2007).

3. **Social adaptation model.** Local song sharing may confer advantages (e.g., holding a territory and attracting a mate) to newly-established birds that are able to learn songs after dispersal. In that way, song divergence can arise when social interaction is disrupted, but dispersal is maintained between dialectal areas, and post-dispersal learning occurs (Rothstein & Fleischer 1987; Warren 2002).

Table 1.1. The predictions of the three models of dialect formation from Payne (1981).

Variable	Model		
	Historical	Genetic adaptation	Social adaptation
Genetic differentiation	Sometimes	Yes	Usually no
Habitat	No relation	Patchy, matches dialect	No relation
Population structure			
Dispersal	Little	No	Yes
Variation in population size	High	High	Low
Variation in area	High	High	Low
Stability	Yes	Yes	No
Social behaviour	(no prediction)	(no prediction)	Song sharers interact
Behaviour function of song	(no prediction)	Intersexual	Intrasexual > intersexual
Behaviour development	(no prediction)	Closed	Open and socially conditional

Evidence for temporal variation of song dialects

Studies on temporal variation in songs have been conducted at a population scale considering a few generations. Fine structure of notes (Jenkins 1977, Grant & Grant 1996), reordering, deletion or incorporation of notes (Baker & Gammon 2006, Ince et al. 1980, Payne 1996,) and recombination of notes from models (Payne 1996) have been studied.

Jenkins (1977) studied in great detail song change in a population of saddlebacks (*Philesturnus carunculatus*) over a period of five years. He documented small changes in the tone of notes as well as the formation of hybrid songs which combined elements from different neighbourhoods. Grant & Grant (1996) studied song transmission and stability of song in two species of Darwin's finches (*Geospiza fortis and G. scandens*) during periods of three and nine years. They did not find major changes but small changes in structure. These changes apparently appeared as innovations from defective copying. Ince et al. (1980) compared songs from two years, 18 years apart, in a population of chaffinches (*Fringilla coelebs*). They found some syllables that did not change but also syllables that showed substantial changes as well as reassortment between song

types. They concluded that changes over time depend on mortality rates, accuracy of copying and frequency of particular song types in the population. Payne (1996) documents 17 years of observations on song change over time in a population of the migratory indigo bunting (*Passerina cyanea*). Overall song changes occurred when male yearlings improvised songs during interactions with neighbours, when birds learned themes in one neighbourhood but established territories in a different neighbourhood, and also when adults modified their songs. Furthermore, song changes and persistence of songs were strongly influenced by the survival of individuals after migration. Birds that never returned from their winter locations did not transmit their songs. For example, certain songs appeared but were never copied as the original singers did not survive.

In addition, Lynch (1996) documented a transfer experiment of chaffinches, from the North Island to the South Island of New Zealand, to investigate the neutrality of songs. In this study, transferred birds that maintained their songs were able to establish territories and males that also incorporated a particular local call were able to get a mate. Thus, the study suggests that songs from different populations may be equivalent, although different selective pressures may underlie different song elements (Lynch 1996, Nelson & Soha 2004). Therefore, it is of crucial importance to study aspects of cultural evolution of birdsong such as the significance and diffusion of song variants, patterns of song transmission and conformation of song elements. An experimental scenario, in particular a transfer of individuals from one population to another, offers an opportunity to investigate the evolution of cultural vocal traditions.

1.2   Bird song perception

The complexity of birdsong goes beyond the mere production of sound. Perceptual mechanisms are an integral part of the study of avian acoustic communication. During the process of perception, detection and discrimination are crucial mechanisms for birds to resolve which signal, from where and by whom (Klump 1996). As signals of interest are unpredictable in time, birds continuously survey the acoustic environment to be able to detect signals opportunistically (Klump 1996). How do they do it in a noisy background? Signal amplitude and energy allow the birds to decode the information received by using

a "signal-to-noise ratio" which is apparently also important in recognition (Klump 1996).

Recognition is then the next stage in perception, an often-investigated mechanism as it elicits responses from receivers. More detailed information including species, sex and individual identity is conveyed in acoustic signals, which birds are able to distinguish based on certain song cues (Emlen 1972). Thus, variation in song parameters allows birds to discern the identity of acoustic signallers (Falls 1982). In order to identify potential cues that birds might use for recognition, geographical song variation has been studied qualitatively and quantitatively by using sonograms. Songs have been categorized into discrete sounds such as elements, syllables, phrases and song types, and quantitative methods have been used to analyse variation within these categories (e.g., Catchpole and Slater 1995, Searcy et al. 1995). Some cues such as fine structure (e.g., Emlen 1972, Falls 1982), song types (e.g., Emlen 1972, Searcy et al. 1995) and syntax-ordering differences (e.g. Emlen 1972, Nelson & Soha 2004, Nowicki et al. 2001) have been shown to be important in song recognition.

1.3   The North Island kōkako

The North Island kōkako (*Callaeas wilsoni*) is an endangered songbird of the New Zealand endemic family Callaeidae (BirdLife International 2011). Kōkako were widespread in the North Island but currently only scattered remaining populations survive in a few isolated areas (Innes et al. 1999; Lavers 1978; O'Donnell 1984) and are declining in unmanaged areas (Innes et al. 1999). Historical decline was due to massive habitat loss and fragmentation, and more recently introduced taxa (e.g. rats – *Rattus rattus*, *R. norvegicus* and *R. exulans*, common brushtail possums –*Trichosurus vulpecula*, stoats –*Mustela erminea*) have caused their dramatic decline (Innes & Flux 1999). However, in its effort to recover kōkako populations, the Department of Conservation has implemented predator control programs since the 1980's, and also it has launched translocations of kōkako to areas with suitable habitat and pest control since the 1990's (Molles et al. 2008). Kōkako have been translocated to both islands and mainland reserves. A total of 71 individuals were transferred to different islands, between 1981 and 2005, to assure the survival of the species and also to gather

and maintain genetic reservoirs (Molles et al. 2008). Mainland translocations have been intended to re-establish kōkako populations where habitat is available. Between 1996 and 2010, 117 individuals have been transferred to mainland management areas from the largest populations in the central and eastern North Island.To date 13 surviving populations, 8 reintroduced populations on the mainland and 4 translocated island populations comprise all extant kōkako (Fig. 1.2).

Kōkako is one of New Zealand's iconic species for its island typical features, conservation status, attractiveness, and haunting voice. Kōkako are long-lived birds with limited dispersal abilities, and are territorial and monogamous. Both members of a pair duet and defend their territory. There have been some studies on the voice of kōkako that include early descriptions of their songs, vocal dynamics, territorial behaviour, duetting, and influence of song variation in pair formation. Early notes by Maning (1960) about the songs distinguished five types of vocalizations. The full song was described as organ-like notes that can be heard 1.6 km away. Calls were described as "mewing" (contact call), "double bell-like call" (distant call between mates), "alarm or curiosity pt-pt-pt-pt or took-took-took-took call" (short distance call), "bell-like cowbell call" and "fragmentary calls" or elements from other calls (Maning 1960). McLeod (1998) studied song and territorial behaviour in male-male pairs and male-female pairs. His study showed that males contribute more than females during duetting bouts and also they are able to do female-typical contributions (McLeod 1998); as a result, kōkako males and females adopt singing roles that are sex-typical but not strictly sex-specific (see male and female examples in Appendix D, CD #7). More detailed evidence on duetting behaviour has confirmed a higher contribution from males as well as non-specific sex repertoires (Molles et al. 2006); also, Molles et al. (2006) studied phrase type sharing among neighbours and countersinging behaviour; they reported high song similarity among neighbouring kōkako. In addition, a playback study provided evidence on the role of duetting in territorial defence as simulated duets elicit more aggressive responses, as well as "phrase matching" and "anticipating", than do solo songs (Molles & Waas 2006).

Geographic variation of kōkako songs has been recognized as distinctive dialects with defined boundaries (Hudson 2001, Innes et al. 2006). Variation in phrase types but similar song structure between populations has been noted as

well as different dialects within populations with continuous habitat (Innes et al. 2006, McLeod 1998). A recent study on pair formation following translocation from different locations (dialects) suggested assortative mating in the original transferred pairs but not in subsequent generations (Rowe & Bell 2007). Nevertheless, the existence of bi- or tri-lingual adult kōkako (Innes et al. 2006), and reports of song change in natural populations from year to year (Innes et al. 2006) suggest that adult birds might alter their repertoires following dispersal from natal territories.
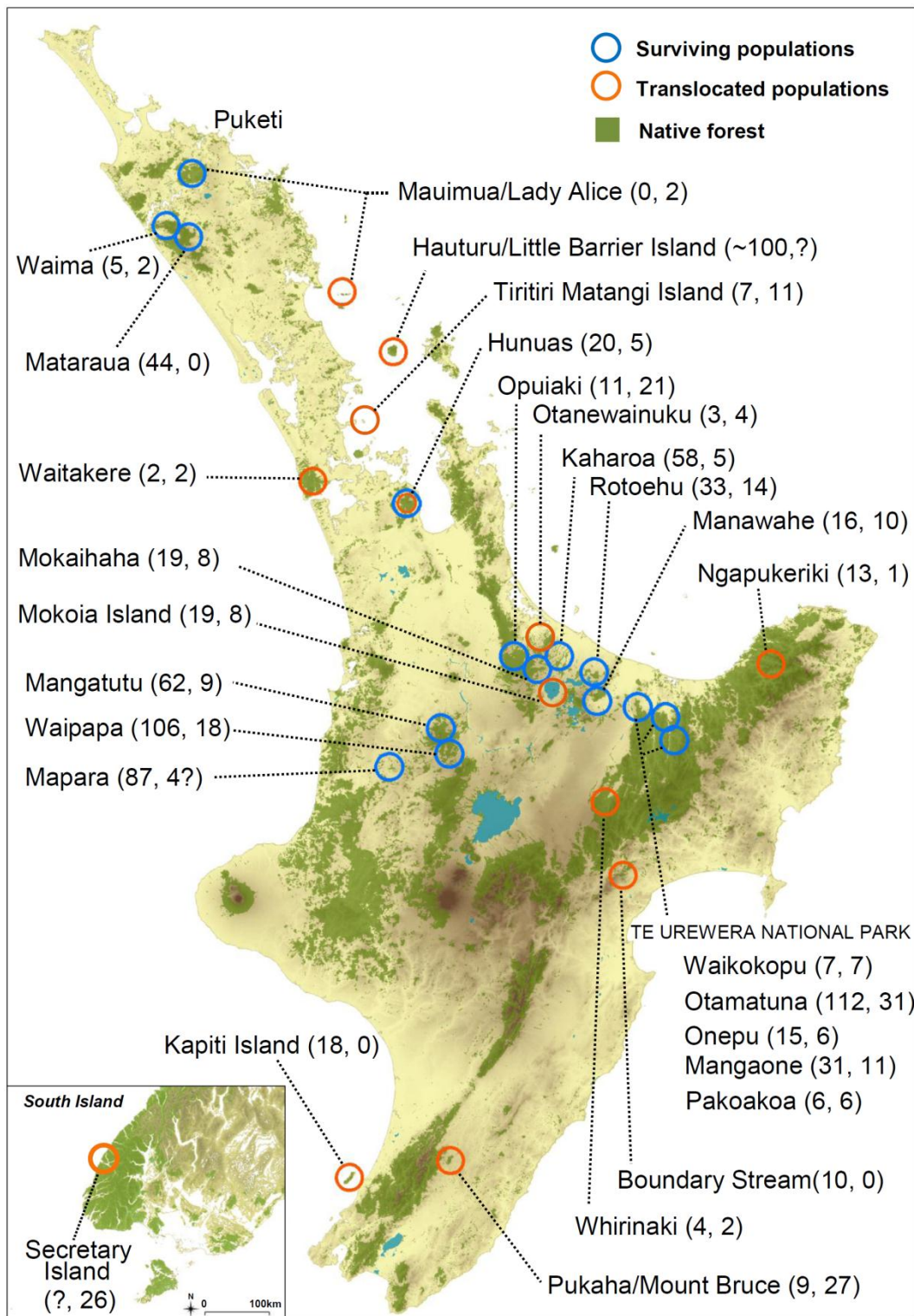
Figure 1.2. Map of distribution of the North Island kōkako with surviving and translocated populations updated until 2011 (Kōkako Recovery Group, Department of Conservation; pers. comm.). Total population size (pairs, singles) and uncertain data (?) are indicated.

1.4   Goals of this thesis

Vocal divergence and dialect formation are intriguing issues in the science of birdsong, evolution and ecology. There is special interest in geographic variation as it provides insights into the processes of speciation and song learning as well as the mechanisms of vocal production. Moreover, proximate consequences of dialects may be of special concern in conservation biology for the purpose of sustaining viable populations and both genetic and cultural variability. Song dialects, viewed as cultural traditions, are considered to be threatened where cultural transmission is prevented because of habitat fragmentation and decreases in population size (Laiolo & Jovani 2006, Laiolo & Tella 2005, Laiolo & Tella 2006). However, studies involving macrogeographic and microgeographic dialect patterns in historically and recently fragmented populations of songbirds of conservation concern are scarce.

This thesis explores patterns of song variation among surviving populations of the North Island kōkako, dialect formation in surviving as well as translocated populations, and finally discrimination of diverging song variants in translocated populations. New populations of translocated kōkako created as birds are moved from source populations to multiple release sites have allowed me to study the formation of incipient dialects as it occurs. I used a combination of observational and experimental approaches to address the general question of how kōkako dialects vary and form and to explore the historical and social adaptation models. I uncover evidence of the importance of ecological processes in cultural and behavioural divergence, in an evolutionary context, and emphasise the implications for conservation efforts.

1.5   Structure of the thesis*

This thesis is organized into five chapters. In Chapter 1, I have provided the general introduction. In Chapter 2, I explore patterns of song diversity and variation among six isolated surviving populations of kōkako, at a macrogeographic scale, and examine a historical model to explain dialect formation based on local change, driven by population fragmentation, at a microgeographic scale. In Chapter 3, I examine the effect of population size on

singing behaviour including song repertoires and sharing, vocal performance, song sharing and syntactical characteristics within six surviving and two translocated populations. In Chapter 4, I investigate incipient song divergence and behavioural responses in two translocated populations and their source population. I present an experimental field study in which I tested whether birds detect and behaviourally discriminate vocal drift. The final chapter (Chapter 5) provides an overview of my contributions to behavioural ecology linked to conservation and management. I stress the importance of considering behaviour in biodiversity conservation.

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[*] The work reported in this thesis is my own. However, in the three core research Chapters (2, 3 and 4) I list collaborators who will be included in papers submitted to academic journals for publication; these Chapters are formatted as multi- rather than solo-authored contributions.

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Chapter 2

On vocal biogeography and conservation: patterns of song traditions and landscape fragmentation in the endangered North Island kōkako*

By Sandra V. Valderrama

I collected 60 % of the recordings and carried out 100% of the sound analysis, data analysis, and write-up. DB and CN collected a large proportion of recordings in the field. Complementary data on dispersal was provided by JI. Comments and advice were provided by LEM and JRW.

Abstract

Geographic barriers can lead to disruption of culturally transmitted vocalizations, favouring divergence and the evolution of differing song cultures (i.e., dialects). Macrogeographic and microgeographic studies on song variation of fragmented populations may reveal recent cultural changes and the influence of landscape fragmentation. We explored patterns of song diversity and variation among isolated surviving populations of the endangered North Island kōkako (*Callaeas wilsoni*). We examined two macrogeographic scenarios for song divergence between isolated populations based on geographic distance and historical population connectivity, and an alternative scenario of rapid vocal drift triggered and enhanced by fragmentation. We intensively recorded the six largest kōkako populations and generated pair and population repertoires. We then compared song repertoires and measured spectral song characteristics to quantify song sharing and 'acoustic distance' within and among populations. At a macrogeographic scale, we found that distinct dialects have formed in isolated surviving populations. Overall song similarity between populations was not related to geographic distance or past connectivity. At a microgeographic scale, we found that low within-population connectivity has resulted in song repertoire differentiation across patches of tenuously connected habitat. Our findings suggest that isolation has resulted in strong and rapid cultural drift at a macrogeographic scale and that fragmentation on a microgeographic scale triggers the emergence of distinct vocal cultures.

Key-words: cultural transmission, fragmentation, isolation, macrogeographic song variation, microgeographic song variation, North Island kōkako

2.1   Introduction

Habitat loss and fragmentation of formerly contiguous areas results in the emergence of gaps between fragments. These gaps can exceed the dispersal abilities of a species and, therefore, lead to population isolation (e.g., Mills & Tallmon 1999; Whittaker & Fernandez-Palacios 2007). In consequence, populations may diverge as microevolutionary processes take place in isolates (e.g., Carson 1992). Behavioural differences, for instance, can evolve in isolation and could potentially prevent interbreeding between individuals where secondary contact between isolated populations occurs (Kaneshiro 1980; Duckworth 2009), or when conservation management involves reintroductions from different populations to create new populations or boost existing ones.

Island species are particularly vulnerable to extinction and effects of habitat disturbance by human action (e.g., Johnson & Stattersfield 1990; Steadman 1997). Because of their high endemism, habitat restrictions, low population sizes and limited long-distance dispersal abilities, fragmented populations on islands are especially sensitive to isolation and may undergo rapid changes and decline in formerly connected remnants of habitat (e.g., Whittaker & Fernandez-Palacios 2007). Therefore, fragmented populations of island passerines may exhibit behavioural divergence more quickly than mainland populations and represent an scenario that is also becoming more common on 'islands' of suitable habitat positioned within landscapes of unusable habitat. As the greatest proportion of threatened bird species is restricted to islands (e.g., Johnson & Stattersfield 1990), island species are especially likely to be subject to conservation actions – such as reintroductions – where behavioural divergence may impact population viability.

Changes in isolation can occur in behavioural traits involved in sexual activities and territorial conflict resolution such as vocal signaling (e.g., Slater 1989; Nowicki et al. 2002; Catchpole & Slater 1995; Todt & Naguib 2000). For example, birdsong is essential for modulating social interactions in Oscines (e.g., species recognition and mate choice) and is especially susceptible to variation when learned by imitation, whereby cultural transmission occurs and, as a result, innovations appear locally and spread within a population (e.g., Payne 1996; Slabbekoorn & Smith 2002). Therefore, vocal behaviour may reflect incipient divergence among geographically isolated populations that can lead to assortative

mating and prevent interbreeding (e.g., Irwin et al. 2001; Slabbekoorn & Smith 2002; Lachlan & Servedio 2004; Price 2007). Numerous studies have found no evidence that intraspecific song variation enhances assortative mating and could therefore eventually lead to speciation, as shown by a lack of association between dialects and discrete genetic boundaries (Handford & Nottebohm 1976; Lougheed & Handford 1992; Lougheed et al. 1993; Zink & Barrowclough 1984; Hafner & Petersen 1985; Fleischer & Rothstein 1988; Payne & Westneat 1988; Wright & Wilkinson 2001; Soha et al. 2004; Wright et al. 2005). However, other studies suggest that song may represent a barrier to gene flow through divergence between groups and mating preferences for local song (Baker 1982; MacDougall-Shackleton & MacDougall-Shackleton 2001; Patten et al. 2004). Studies on brood-parasitic birds show a clear link between acoustic variation and reproductive divergence and how it can lead to speciation. As indigobirds (*Vidua chalybeate*) vary in the host species they parasitise, males have to learn the specific foster parent song whereas females imprint on it, leading to reproductively isolated subpopulations according to host species (Klein & Payne 1998; Payne et al. 1998, 2000; ten Cate 2000). This unveils additional concerns critical for the conservation of rare species and cultural diversity.

Song variation occurs within and between individuals as well as populations (Searcy & Nowicki 1999). This variation, discrete in birds that inherit their songs (e.g., Suboscine Passerines), is graded over a continuous distribution in song learners (e.g., Oscine Passerines; Marler & Peters 1977). Cultural transmission during song learning favours and constrains song divergence, and this double-edged effect can result in complex variation at small and large scales (Podos et al. 2004, Slabbekoorn & Smith 2002, Slater 1989). Accordingly, microgeographic variation occurs from individual to individual within a population and is reduced by widespread cultural transmission through vocal imitation. Macrogeographic variation, in contrast, refers to differences between populations separated by a barrier (e.g., geographic barriers or bands of unsuitable habitat; Mundinger 1982). Thus, vocal geographic variation by song learning can result in dialect formation when individuals breed and sing where they learned their songs (e.g., Marler & Tamura 1962; Baker & Cunningham; Kroodsma 2004). Moreover, founder effects in isolates may result in an initial loss of cultural diversity (e.g., song traditions) exhibited by a reduced behavioural repertoire; this may initiate divergent

evolutionary trajectories in founding populations (Grant et al. 2001) which are then amplified by cultural transmission within the isolates. Therefore, both founder effects by isolation through habitat loss, and also learning and cultural transmission of locally divergent songs in fragmented habitats, may influence spatial variation of song traditions that reflect past habitat connectivity between populations.

New Zealand is an extreme island scenario of habitat loss, fragmentation and invasive predators (Allen & Lee 2006; Saunders & Norton 2001, Kelly & Sullivan 2010). Forest songbirds as well as many other species have been dramatically affected by historical habitat decline since human arrival on the islands in addition to natural environmental changes like climatic shifts, earthquakes, natural fires, and volcanic eruptions (Fig 2.1). Before human arrival, New Zealand was mostly covered with forest below the treeline (82%), especially the North Island (96%), but severe deforestation and reduction of the avifauna began when Polynesian peoples arrived and established on the islands about 1000 BP (e.g., McGlone 1989; Ewers et al. 2006). Subsequently, the human population increased and lowland forests were burnt for food crops, travelling and facilitating hunting of native species like moa (Aves: Dinornithiformes). At the time of European arrival, forest cover had been reduced to about 68% in total and c. 50% of the lowland forests had disappeared. Subsequently, European settlement resulted in forest clearance over extensive areas for farmland with an additional 60% forest reduction; by the 1950's, only 23% of New Zealand's total area was covered with forest (e.g., Leathwick et al. 2004). On the North Island, remaining native forests have been more intensely affected by fragmentation than South Island forests (Ewers et al. 2006). Despite the enormous influence of historical deforestation on the present species assemblage in New Zealand, more management attention has focused on invasive species control than on habitat loss, as recent rates of forest clearance have been very low. However, historical changes in forest cover and fragmentation may be critically relevant to current species conservation (Harding et al. 1998; Ewers et al. 2005; Ewers et al. 2006; Richard & Armstrong 2010) and especially to conservation of endangered species with restricted dispersal abilities, geographic ranges and habitat requirements (e.g., Fahrig & Merriam 1994).
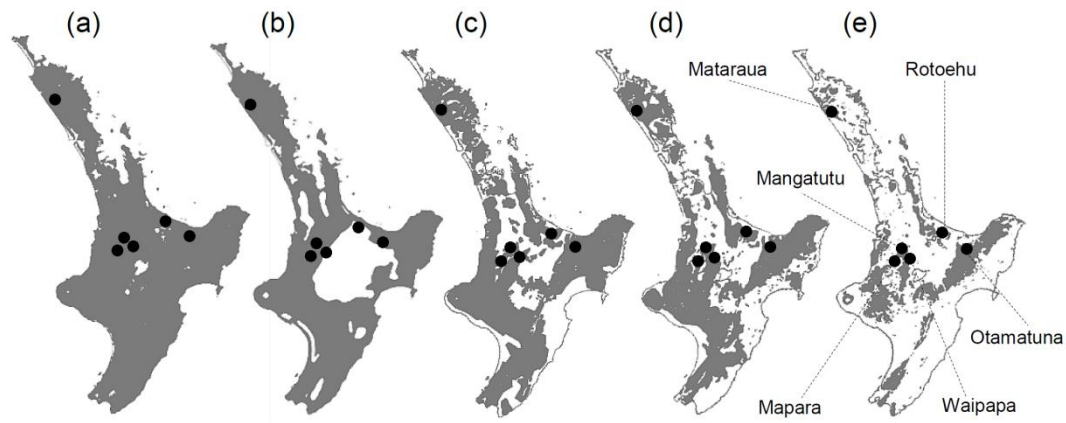
Figure 2.1. Six kōkako populations investigated in this study and forest cover change in the North Island of New Zealand from: (a) pre-human time (Leathwick et al. 2004), (b) 700 AD and (c) 1800 AD (Newsome 1987), (d) 1880 AD (McGlone 1989), (e) 1980 (Thompson 1995).

In this paper, we explore patterns of song diversity and variation among isolated surviving populations of the endangered North Island kōkako (*Callaeas wilsoni*), a territorial and duetting songbird endemic to New Zealand. This is a rare species that was once widespread throughout the North Island, yet it currently survives only on a mosaic of habitat 'islands' under strict predator control (e.g., Lavers 1978; Innes et al. 1999). Only 13 sites with original local kōkako remain but other populations have been established by translocation. Previous studies on kōkako vocalizations have addressed duetting behaviour (McLeod 1998; Molles & Waas 2006) and within-population acoustic variation (Molles et al. 2006); qualitative dialectal variation within and between populations also has been long-recognized (McLeod 1998; Hudson 2001; Innes et al. 2006). However, song variation among populations remains poorly understood despite that cultural variation of song traits may provide insight into recent evolutionary changes and the influence of landscape fragmentation across populations, as well as impacting on the success of species conservation efforts (e.g., the creation of multi-sourced translocated populations).

Given the current isolation among populations, we examined geographically close and distant surviving populations to test a historical model that hypothesises local change, driven by processes like fragmentation and population contraction,

explains current social behaviour (e.g., dialectal and acoustic patterns among bird populations; Thielcke 1985, Payne 1981). Due to the limited dispersal abilities of kōkako, isolation may be drastic between fragments of habitat, such that historical landscape fragmentation has determined the pattern of current kōkako dialects. However, as the precise times of spatial separation between surviving populations is unclear, and patterns of connectivity may be complicated by historical re-connection and habitat loss events, we first provide and discuss scenarios of song divergence patterns by isolation distance (linear distance) and historical habitat connectivity in the light of available historical information; secondly, we directly test for connectivity effects on song similarity within populations.

We incorporated two levels of song variation in our analyses that include differences in song type sharing and spectral song characteristics, within and among populations. We examined two macrogeographic scenarios, and corresponding predictions, for song divergence between isolated populations of kōkako. (1) Song similarity would simply reflect separation by linear geographic distance between populations if time of separation (i.e., dispersal connectivity) has not had an effect; this is our baseline scenario and is quantitatively evaluated. (2) Past patterns of connectivity (i.e., time combined with distance of separation) could be reflected on vocal similarity between formerly continuous areas if vocal drift is gradual enough to preserve patterns of historical dispersion among surviving populations; we predict patterns of song similarity and discuss this scenario on the basis of qualitative data on historical forest cover over time (Fig. 2.1, 2.2). As an alternative to these scenarios, vocal drift associated with fragmentation may occur too rapidly to reflect linear or temporal distances at the resolution currently available. We also take a closer quantitative look at variation within a population with (i) low within-population habitat connectivity, and a population with (ii) high rates of predation in areas separating patches of kōkako habitat in order to test for fragmentation effects on traditional song patterns on a finer microgeographic scale. Our study highlights the importance of considering cultural variation in fragmented populations of songbirds and the ecological significance of song dialects for conservation.

Song similarity association by time of separation (year)
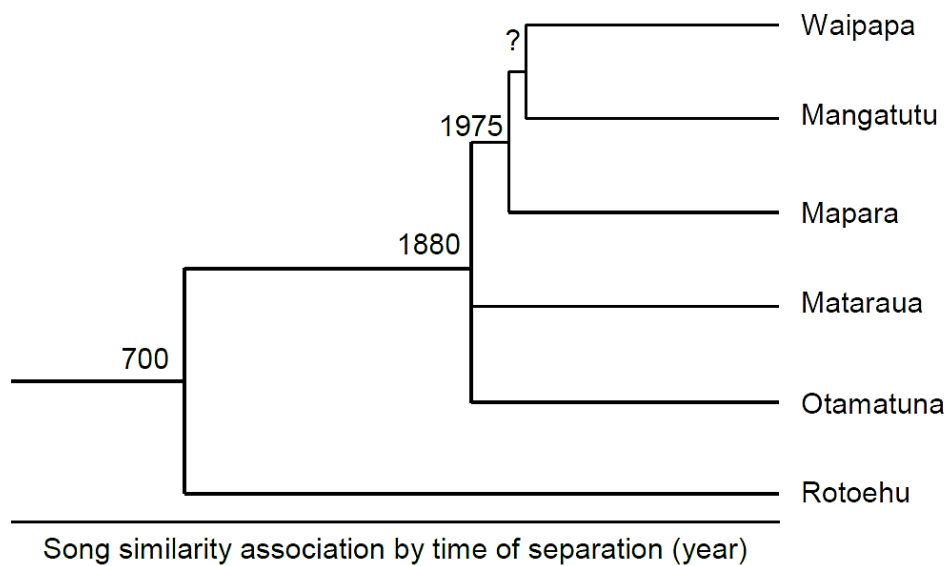
Figure 2.2. Diagram showing predicted song similarity relationships according to historical time of separation, based on forest fragmentation (Figure 2.1), among surviving populations.

2.2 Methods

2.2.1 Study areas

We focused our study on six scattered surviving populations in forest fragments, under intense management, in the North Island (Fig. 2.1). Our six study populations were located in the four remaining regions where kōkako have persisted (Table 2.1). Mataraua Forest sustains the only Northland region population (a few scattered individuals remain in the small nearby Waima Forest Reserve). In the volcanic Mamaku Plateau in the Bay of Plenty region, six populations persist; we studied the songs of kōkako in the Rotoehu Forest. In the Urewera region, the Te Urewera National park sustains the largest population of kōkako (>360 territorial individuals) mainly in five core areas under intense control of invasive species; we included two core areas in this study (Otamatuna

and Onepu). In the Central Plateau region, a fragmented large area of forest (Pureora Forest Park with 78000 ha) includes three isolated areas with kōkako, one of which is the discontinuous Mapara Wildlife Reserve that comprises three larger portions with two connected by a narrow forested boundary and a third separated from the adjacent central portion by 200 m of pasture (Flux et al. 1992). All areas comprise lowland conifer-broadleaf temperate rain forest dominated by tawa (*Beilschmiedia tawa*), with abundant species such as hinau (*Elaeocarpus dentatus*), rewarewa (*Knightia excelsa*), tawari (*Ixerba brexioides*) and kāmahi (*Weinmannia racemosa*) as well as scattered emergent northern rata (*Metrosideros robusta*) and podocarps like rimu (*Dacrydium cupressinum*) and miro (*Prumnopitys ferruginea*).

Table 2.1. Description of the six largest surviving populations of kōkako recorded.

Site	Region	Coordinates	Area (ha)	Population size*	Number of pairs recorded
Mataraua Forest	Northland	35°36'17''S 173°37'47''E	650	84	6
Rotoehu Forest	Mamaku Plateau, Bay of Plenty	37°57'34''S 176°32'7''E	440	62	6
Te Urewera National Park					
Otamatuna core area	Ureweras, Bay of Plenty and Hawke's Bay	38°20'3''S 177°8'38''E	2500	250	11
Onepu core area	Ureweras, Bay of Plenty and Hawke's Bay	38°20'53''S 177°6'8''E	1232	20	5
Mangatutu Ecological Area	Central Plateau, Waikato	38°20'8''S 175°27'30''E	1400	139	6
Waipapa Ecological Reserve	Central Plateau, Waikato	38°26'15''S 175°33'8''E	2532	230	6
Mapara Wildlife Reserve	Central Plateau, Waikato	38°33'3''S 175°15'36''E	1312	174	12

Territorial individuals surveyed by the New Zealand Department of Conservation

2.2.1 Song recording and analysis

We collected recordings from a total of 52 pairs of kōkako from the six surviving populations (Table 2.1; Fig. 2.1) between 2009 and 2010 during non-breeding seasons (i.e. March to November). Complete phrase repertoires from at least six focal pairs were obtained from each population for comparisons within and across populations. A total of four pairs from each of three forest portions within Mapara Wildlife Reserve, eleven pairs in Otamatuna core area and five pairs in Onepu core area (Te Urewera National Park) were recorded for within-population microgeographic analyses. All recordings were made between 0500 and 1000 hours from each pair's territory. Most songs were recorded during spontaneous singing that included countersinging with neighbours, but additional singing was stimulated by using up to three minutes of playback comprising contact calls and local song. We selected pairs with a minimum total of 100 phrases recorded, after which all pairs showed very few new phrase types (not previously recorded). Field recordings were made using Marantz portable PC card recorders (PMD660) with Sennheiser directional microphones (ME66, ME67 and MKH416). All recordings were collected in a Wave file format using a sampling rate of 44.1 kHz and 16 bits per sample.

We visually inspected all recordings as sonograms from which we classified and catalogued all phrases sung by each pair recorded. We first compared all phrases across pairs within populations and generated pair and population repertoires of phrases. We used SYRINX (J. Burt, Seattle, Washington) to visually compare phrases based on absolute frequency characteristics, frequency modulation, shape, and silent intervals as shown on Figure 2.3. Within each population, we first examined between-pair song sharing and from one example of each phrase type per pair we measured twelve acoustic parameters including temporal and frequency characteristics. We subsequently performed comparisons across all populations (see below for details).

Dialect song sharing

We compared all pair repertoires within and between populations in order to calculate pair-wise similarity scores of song repertoire. We used a modified

Jaccard index ($s_{ij}/[s_{ij}+s_i+s_j-c_{ij}]$) to calculate repertoire sharing between pairs, where s_{ij} is the number of phrases common to pairs i and j; s_i is the number of phrases in the repertoire of j but absent from the repertoire of i (s_j is the reciprocal); c incorporates the difference in repertoire size between pairs i and j (Tracy and Baker 1999; Stewart and MacDougall-Shackleton 2008; MacDougall-Shackleton et al. 2009). The Jaccard index, as a measure of song sharing, is an appropriate measure because it is based on the presence of phrase types instead of their absences (Legendre & Legendre 1998). Phrases were visually compared based on absolute frequency characteristics and shape, as represented on sonograms, based on frequency modulation as well as silent intervals between syllables and syllable notes. All syllables and phrases were classified by one trained observer.

Song structure measurements

We analysed spectral and temporal characteristics of one example of each phrase type for the six pairs recorded in each of the six populations for the macrogeographic analysis (Fig. 2.3). For all measurements, we only selected phrases that birds produced as components of themes, defined as sequences of phrases which they repeated and cycled through during singing bouts (see Chapter 3). For each phrase we counted the number of syllables, and used Avisoft-SASLab Pro v 5.1 (Specht 2006) to measure syllable duration (s), minimum and maximum frequency (kHz), and overall peak frequency, as well as peak frequency of the loudest harmonic (kHz). A Hamming window was used with FFT size of 1024 points, 50% frame size, 43 Hz frequency resolution, and 87.5% overlap. We also obtained additional time amplitude and frequency derivatives of phrases using Sound Analysis Pro v1.3 (Tchernichovski et al. 2000; Tchernichovski & Mitra 2004). These measurements were performed by using spectral derivatives that represent the change in power and give higher spectral resolution, which makes it possible to detect and quantify frequency characteristics of more complex sounds (e.g., harmonics). Spectral measurements using this method included: mean amplitude modulation (i.e., changes in amplitude envelope of sounds), mean frequency modulation (i.e., mean slope of frequency contours),

Wiener entropy (i.e., measure of randomness or uniformity) and goodness pitch (i.e., periodicity of sounds; see Fig. 2. 3).
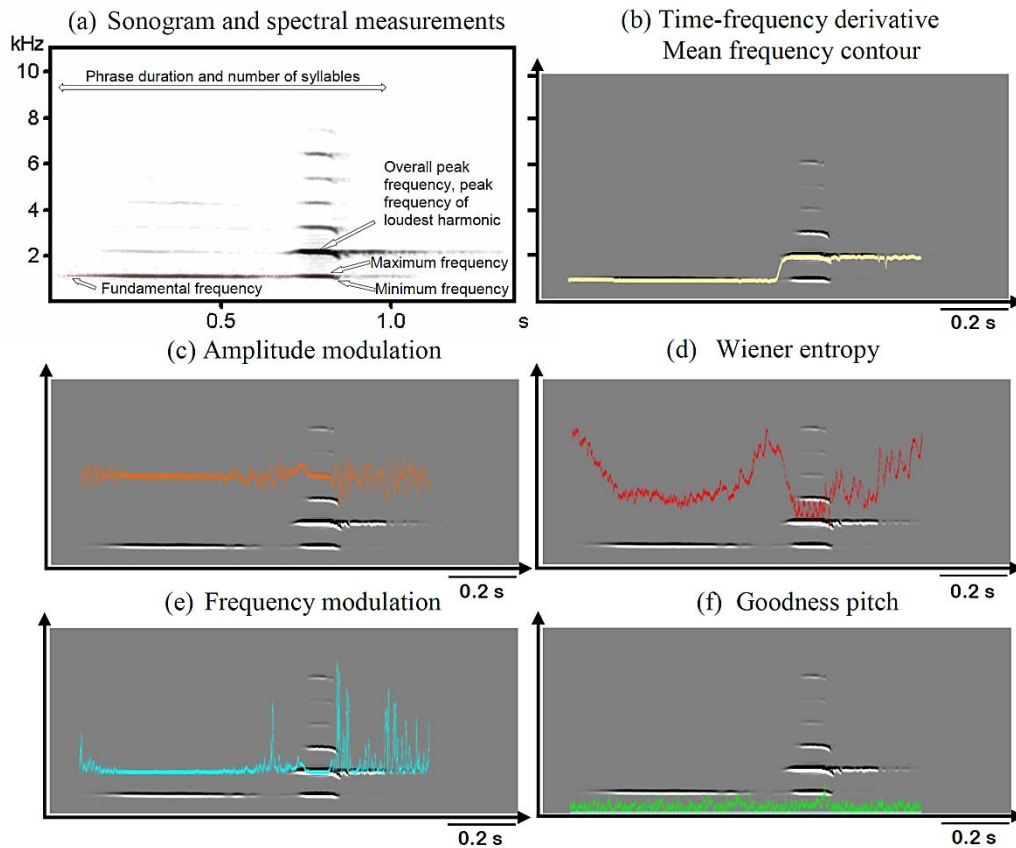
Figure 2.3. Sonogram and spectral derivatives of a kōkako phrase type with two syllables (CD #3) showing twelve fine structure measurements. Song structure parameters were quantified using on-screen cursors in Avisoft to measure seven time (s) and frequency (Hz) traits indicated on the sonogram (a). Five derivative spectral measurements were performed by automatic detection procedures using Sound Analysis Pro (b-f).

2.2.1 Statistical analyses

Song sharing and dialect similarity

Song traditions and dialectal variations were analysed using pairwise comparisons of Jaccard vocal similarity scores. We analysed differences in vocal similarity and association within and among populations using an Analysis of Similarities (ANOSIM). This non-parametric statistic test uses the ranks of all elements in the song similarity matrices to perform a permutation test that evaluates the significance of the difference between within-population similarity and between-population similarity (Legendre & Legendre 1998). We also represented song variation by using vocal similarity scores to construct a dendrogram with the "unweighted pair group method" (UPGMA; Sneath & Sokal 1973). Analyses of association were performed using PRIMER Software package (Clarke & Gorley 2006).

To test for an association between song sharing and geographical distance within and across populations, we first generated matrices of pairwise song similarity scores and geographic distance between all pairs for each population. Similarly, we also generated matrices for pairwise comparisons between populations. Subsequently, we performed Mantel tests using 999 permutations to examine whether pairwise vocal similarity was correlated with geographic distance within and/or among populations. For each population, we used the geographic distance matrix and the vocal similarity matrix to implement a Mantel test with Poptools v 2.7.5 (Hood 2010). Similarly, matrices of: 1) between-population similarity and geographic distance, 2) between-fragment similarity and geographic distance, and 3) vocal similarity within portions versus between portions of managed habitat, were tested with separate Mantel tests.

Acoustic divergence

To examine whether fine song structure parameters differ between six surviving populations, we used SPSS v 15.0 (SPSS, Chicago, Illinois) to conduct a Discriminant Function Analysis (DFA) with the averages of twelve acoustic parameters measured from all selected phrases per pair. We cross-validated the

DFA by using 'leave-one-out' classification, in which each pair is removed from the data set, the classification rules are determined, and the left-out pair is then classified.

We also tested for an effect of geographic distance on acoustic distance between populations. A matrix of acoustic distance was generated using the Mahalanobis generalized distance which takes into account the correlations among our acoustic parameters while being independent of the scales of the various descriptors. Thus, we used this statistic to represent the acoustic variation between groups to test a scenario of acoustic divergence by isolation distance in which the Mahalanobis distance matrix was compared to a geographic distance matrix also using a Mantel test. P values ≤ 0.05 were considered statistically significant.

2.3   Results

We identified 20,562 phrases and classified 309 phrase types for all six populations (see examples in Appendix B, CD #6), with a total number of phrase types (and pair average $\pm$ SE) of 65 in Otamatuna (26.27 $\pm$ 086), 48 in Waipapa (23.5 $\pm$ 2.46), 58 in Mapara (21.26 $\pm$ 1.14), 40 in Mangatutu (23.83 $\pm$ 1.35), 50 in Mataraua (31.67 $\pm$ 1.48), and 40 in Rotoehu (22 $\pm$ 1.97).

2.3.1 Macrogeographic song variation

Scenario 1: Song similarity simply reflects linear geographic distance

Pairwise song similarity values based on song sharing indicated that kōkako pairs within populations shared an average of 57 $\pm$ 17 % of phrases locally while only 19 $\pm$ 3 % are shared between populations (Mantel test: r = -0.80, p < 0.001; Fig. 2.4). Furthermore, the test statistic ANOSIM showed that the six populations significantly differed in phrase types based on 999 permutations (r = 0.97, p < 0.001).

In assessing the relationship between song repertoire similarity and the linear geographic distances between the six reserves, we found no significant correlation (Mantel test: r = -0.61, p = 0.98).
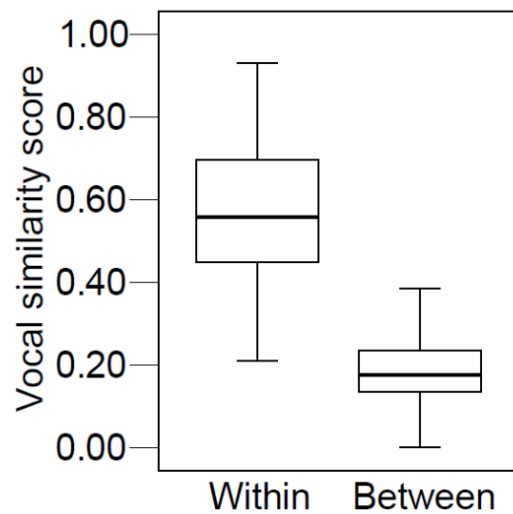
Figure 2.4. Box plot of pair-wise Jaccard values for pair-wise comparisons within and between six surviving kōkako populations.

With regard to acoustic variation among populations, the DFA revealed that the six populations are distinguished based on the twelve song structure parameters. Fundamental frequency was highly correlated with minimum frequency. Pairs from each population were grouped and differentiated from the other populations (Fig. 2.5). The analysis assigned pair average acoustic characteristics to the correct population with 97.2 % accuracy, and 69.4 % of cross-validated pairs were assigned to the correct population. Discrimination was mainly explained by the first two canonical functions (for details see Appendix A). However, the Mantel test to evaluate acoustic divergence by linear distance between populations showed no correlation (r = 0.12, p = 0.55). Mataraua and Rotoehu are acoustically more similar than other populations (Fig. 2.5).
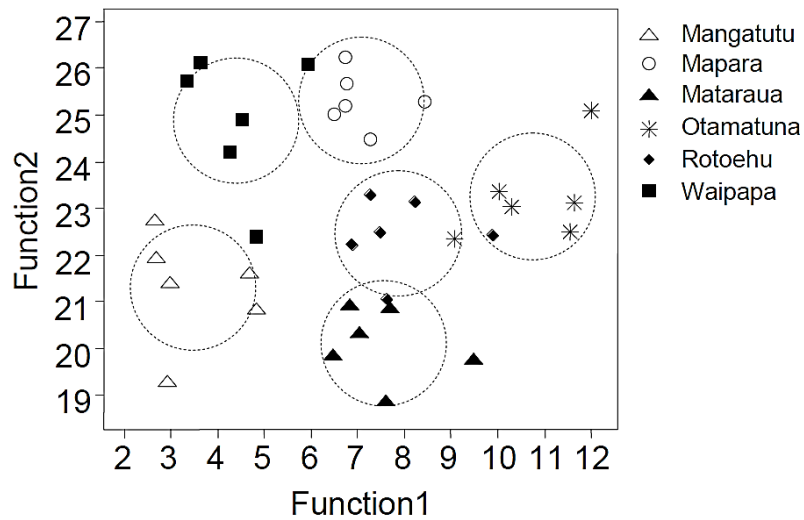
Figure 2.5. Scatterplot of the first discriminant function versus the second. Average observations per pair are represented for each of six populations.

Within-population Mantel tests for all areas with continuous habitat and consistent connectivity (i.e., Mangatutu, Mataraua, Otamatuna, Rotoehu and Waipapa) showed no relationship between pairwise vocal similarity and geographical distance, whilst pairs in the low-connectivity population of Mapara exhibited a significantly negative spatial distance effect on their pairwise song similarity scores (Table 2.2).

Table 2.2. Results of the Mantel tests for vocal similarity and geographical distance within surviving kōkako populations.

| Population | n | VS[a] | | GD[b] | | r | p |
		Mean	SE	Mean	SE		
Mapara	91	0.36	0.02	2462.86	148.5	-0.54	<0.001*
Otamatuna	55	0.44	0.01	1288.55	85.25	-0.37	0.99
Mangatutu	15	0.67	0.03	952.83	133.66	-0.68	0.99
Rotoehu	15	0.62	0.04	1028.82	131.87	-0.40	0.86
Mataraua	15	0.72	0.02	1058.56	114.77	0.08	0.39
Waipapa	15	0.59	0.04	2653.29	419.24	-0.13	0.68

[a]Vocal similarity represented by the Jaccard index
[b]Geographical distance (m)

Scenario 2: Song similarity reflects historical habitat connectivity

The clustering correlation of the dendrogram indicated that UPGMA was effective in representing inter-population song similarities (Fig. 2.6). For our collection of song phrases, the fusion of clusters when the similarity reached the mean inter-cluster similarity value distinguished each population as a group and also identified song similarity affiliations among populations. One derived cluster contains Rotoehu and Mataraua with Mangatutu as an external cluster. Subsequently, clusters are nested within other populations as similarity decreases, with Otamatuna and Waipapa as external groups (Fig. 2.6). The dendrogram for song similarity does not match the hypothetical association according to time of separation between populations (Fig. 2.2).
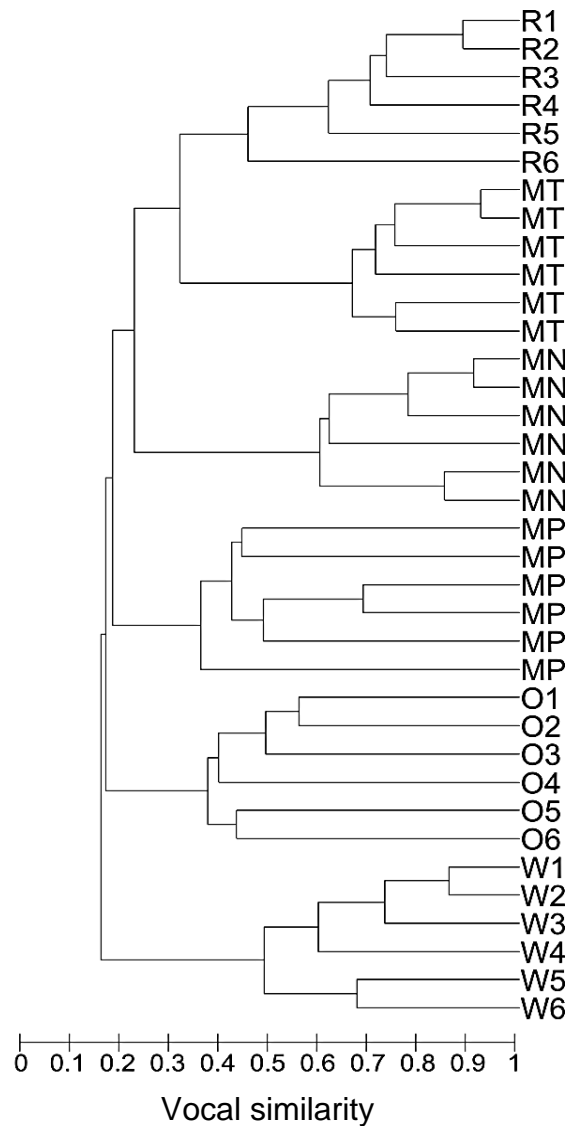
Figure 2.6. UPGMA dendrogram based on modified Jaccard song similarity distance between pairs (designated with numbers) within and between all populations (Mangatutu MN, Mapara MP, Mataraua MT, Otamatuna O, Rotoehu R, and Waipapa W).

2.3.2 Microgeographic effects on song traditions

The hypothesis that decreased connectivity correlates with reduced vocal similarity is further supported by a decreased similarity between portions of the Mapara reserve (a maximum distance of 9.8 km; Fig. 2.7 a, b); we found about 49 ± 3% vocal similarity between pairs within portions in comparison with 30 ± 1 % between portions of this reserve (Mantel test r = 0.61, p < 0.001). The degree of

between-portion similarity varied (F = 13.52, df = 2, $p < 0.0001$), with the larger central and south portions less similar (24 %) in comparison with north and south (29 %) as well as central and north portions (39 %). Within-portion song similarity significantly differed across the three portions (F = 8.36, df = 2, $p = 0.002$; Fig. 2.7 b). The northern and smallest portion showed the highest song similarity among pairs (66 %) followed by the central portion (58 %) and the south portion (41 %).
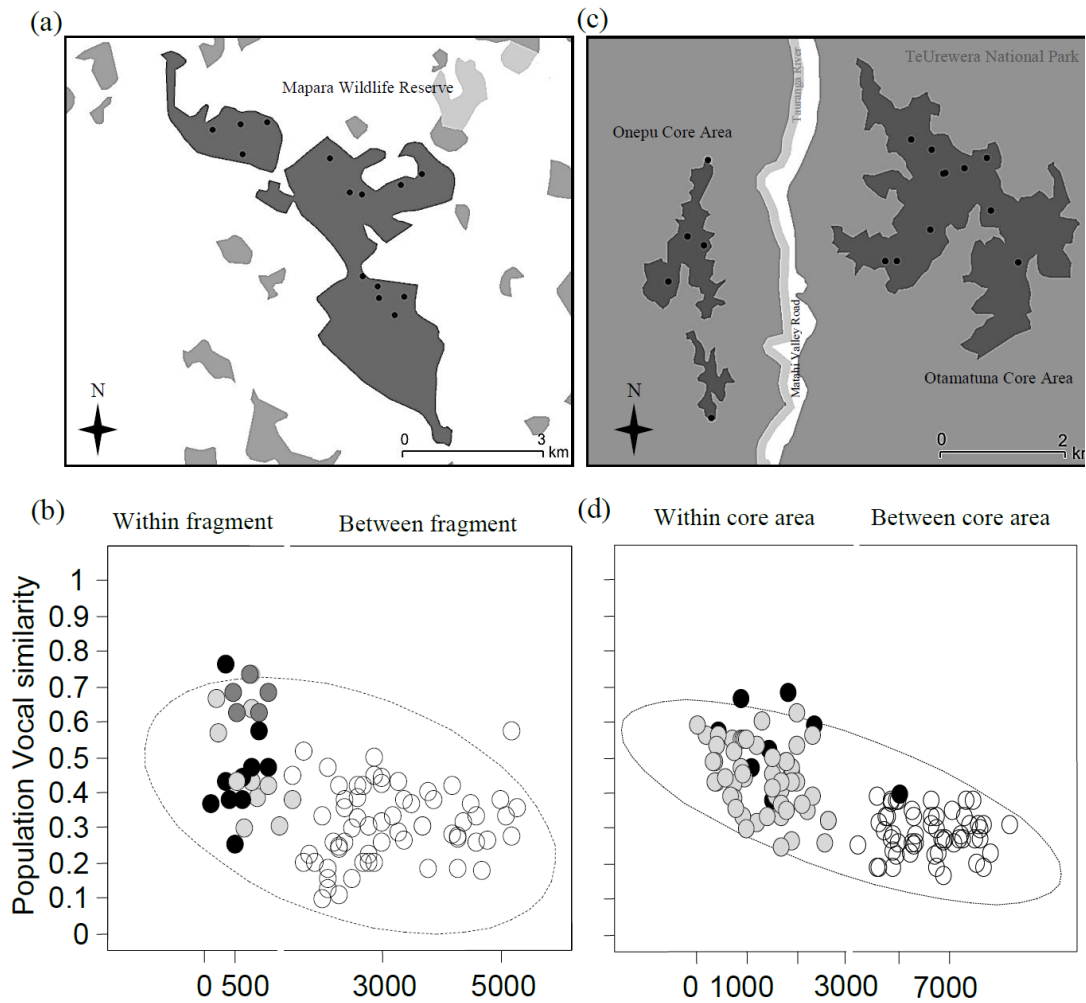
Figure 2.7. Study areas with significant distance effect on within-population vocal similarity (CD #4). (a) Pairs sampled in Mapara Wildlife Reserve (black dots) in three fragments (dark grey) surrounded by pasture (white) and small fragments of unmanaged forest (light grey). (b) Vocal similarity scatterplot of vocal sharing versus geographic distance within north (dark grey), central (black) and south (light grey) fragments of Mapara. (c) Pairs sampled in Otamatuna and Onepu core areas in Te Urewera National Park (dark grey); forested areas with less predator control (light grey) surrounds the core areas. (d) Vocal similarity scatterplot vocal sharing versus geographic distance for Otamatuna.

We found further support in results for the Te Urewera population, where habitat is continuous but pest control is limited to core management areas; in this population, kōkako survival and breeding success rates are very low outside of core areas, leading to areas with extremely low kōkako densities between the

cores. The Mantel test for Te Urewera revealed that vocal similarity is highly related to spatial distances when comparing pair songs from Otamatuna and Onepu core areas (a maximum distance of 10 km; Fig. 2.7 b, d). In this case, we found vocal similarity between pairs of approximately 49 % within Onepu and 44 % in Otamatuna, in comparison with 28 % between pairs from the different core areas (Mantel test: r=0.72, p<0.0001).

2.4   Discussion

Our results show that isolation has resulted in the emergence of distinct large-scale patterns of song variation between and within populations of kōkako, as a result of rapid cultural evolution once connectivity is disrupted. Distinctive dialects in each of the six kōkako populations studied are reflected in greater song sharing and acoustic similarity within populations in contrast with lower similarity between populations. However, we found neither differing similarity in song traditions nor acoustic variation between populations to be related with current isolation distance or fragmentation history. Rapid vocal drift following fragmentation therefore appears to be one likely explanation for the patterns observed. However, at a microgeographic scale, our analyses showed that localized spatial fragmentation and low survival, or 'social fragmentation', may enhance differences in song traditions between portions of habitat or among 'safer' intensively-managed areas within continuous habitat. These differences in song traditions may be also maintained through sexual selection and male competition that may favour biased-copying of local song components. Female preferences for local song (Baker et al. 1981; Baker 1982, 1983; Lampe & Baker 1994) and males' higher success in territorial interactions when sharing local song (Baker et al. 1981; Baker 1982, 1983, Lampe &Baker 1994, Beecher et al. 2000; Wilson et al. 2000) may reinforce song divergence between areas. Low fitness individuals that sing non-local song or, if song developmental plasticity allows, post-dispersal learning may result in song variants between areas.

2.4.1 Geographic distance, past habitat connectivity and vocal similarity

Our results give no clear indication of traceable song patterns for scenarios with song traditions linked to linear geographic distances or the duration of isolation among kōkako populations. For example, a model based solely on time of separation would predict that song from Mataraua would show roughly comparable similarity to Mapara, Mangatutu and Waipapa dialects, but greater similarity to Otamatuna song; this pattern was not borne out in our analyses. However, it should be noted that distance and duration of separation are confounded in many cases. Furthermore, according to available information on forest cover (Fig. 2.1), patterns of separation between populations may be complicated by re-connection one or more times in the last 2000 years. For instance, a major volcanic eruption in 1850 years BP destroyed a large area of forest in central North Island, which may have resulted in the separation of the Ureweras region, and perhaps the Rotoehu Forest, from other populations; however these areas were potentially reconnected after 200 years when forest regeneration occurred (Wilmshurst & McGlone 1996). Subsequent gradual re-isolation would have followed forest clearance by human actions.

In addition, substantial song differences between our populations cannot be attributed to genetic differences. Genetic studies have found significant differentiation between Te Urewera and Mapara populations, but non-significant low differentiation between Te Urewera and Rotoehu as well as between Rotoehu and Mapara (Hudson et al. 2001). Murphy et al. (2006) included individuals from additional populations and found non-random haplotype distribution in two clades. The first clade comprised North Pureora (possibly Waipapa), Te Urewera, and Mataraua, and the second included only Mapara. Allopatric fragmentation, range expansion and colonisation events appeared to explain the first group whereas restricted gene flow with isolation by distance appeared to explain the differentiation of Mapara. Rotoehu did not show clear differentiation. The incongruence of known genetic differences and both acoustic features and sharing of song elements between our surviving populations is consistent with the crucial role of song learning (see juvenile kokako imitation examples in Appendix E) in phenotypic song divergence (Ellers & Slabbekoorn 2003) and the scenario of very

rapid cultural drift after separation, rather than a genetic basis for song differences among populations.

It is possible that founder effects from bottlenecking events or dramatic reductions in population size could have not only led to differing subsets of song elements in newly-isolated populations, but also amplified song divergence and the origin of distinct dialects by generating different cultural trajectories in isolation (e.g., Thielcke and Wüstenberg 1985; Baker & Jenkins 1987; Lynch & Baker 1994; Lynch 1996; Laiolo 2008). All of our six surviving populations of kōkako have undergone severe bottlenecks and the diversity of song elements appears to decrease considerably in small populations (see Chapter 3); therefore, small remaining vocal subsets, isolation and subsequent population increase, due to conservation efforts, may have enhanced rapid vocal drift and independently-evolved cultural song traits.

In contrast to explanations for vocal divergence, song similarity among isolated populations could emerge through convergence from acoustic adaptation to similar habitats, or chance effects in which smaller vocal repertoires can result in similar song elements arising independently in disconnected populations (Tubaro 1991; Lynch & Baker 1994). Interestingly, our results showed consistently high song sharing and acoustic similarity between the smallest populations (i.e., Rotoehu and Mataraua) which have been disconnected for at least the same amount of time as other populations that show lower song similarities. Although acoustic variation is likely to be shaped by local habitat structure that selects vocal signals for local maximum transmission (Morton 1975; Hansen 1979; Richards & Wiley 1980; Slabbekoorn & Smith 2002), we do not directly address this, as kōkako are restricted to habitat patches highly similar in vegetation structure. Thus, acoustic similarity and song sharing in surviving populations of kōkako may have undergone independent rapid cultural changes that may by chance converge mainly between small populations.

2.4.2 Fragmentation effect and rapid cultural drift

Our results from currently discontinuous populations within connected areas (i.e., microgeographic song variation) showed that strong effects of connectivity disruption and subsequent rapid vocal drift can enhance song divergence within

and between populations of kōkako. We found that low connectivity between portions of habitat and additional population disruption, caused by interspersed areas with low survival, have a strikingly strong effect on differentiation of song repertoires. Dispersal patterns and the degree of plasticity involved in the development of song have been recognized as crucial in population song divergence (e.g., Ellers & Slabbekoorn 2003). The observed patterns of song variation in kōkako show that similarity does not necessarily decrease linearly with increasing distance over continuous habitat, despite seemingly high local sharing among neighbours at a small spatial scale (Molles et al. 2006). Moreover, evidence on dispersal within three surviving populations shows that birds disperse not only throughout continuous areas but they also disperse across the tenuously connected areas in Mapara reserve (data derived from Innes et al. 1996, and North 1997; see Fig. 2.8), where we found marked differences in song traditions; dispersing juveniles did not preferentially settle in natal dialect territories ($n=79$, $p = 0.37$, binomial test). This data suggests that song variation in kōkako is consistent with postdispersal learning, and that the emergence of variants is facilitated by habitat gaps between countersinging neighbours rather than young birds' reluctance to leave their natal dialect areas. However, the mechanism for these song differences is unknown and it may help explain the lack of correlation between distance and vocal similarity in undisrupted populations. For instance, one mechanism is selective attrition by which individuals acquire song repertoires from natal territories and only retain songs present in nearby breeding territories (Marler & Peters 1982; Nelson 1992). Another possibility is that they continue to learn from new neighbours (e.g., Payne 1981), which means that song repertoires would depend on the song in natal territories, to some extent, and current neighbours. Studies on kōkako song learning and learning capability are now needed to provide insight into song divergence in fragmented populations.
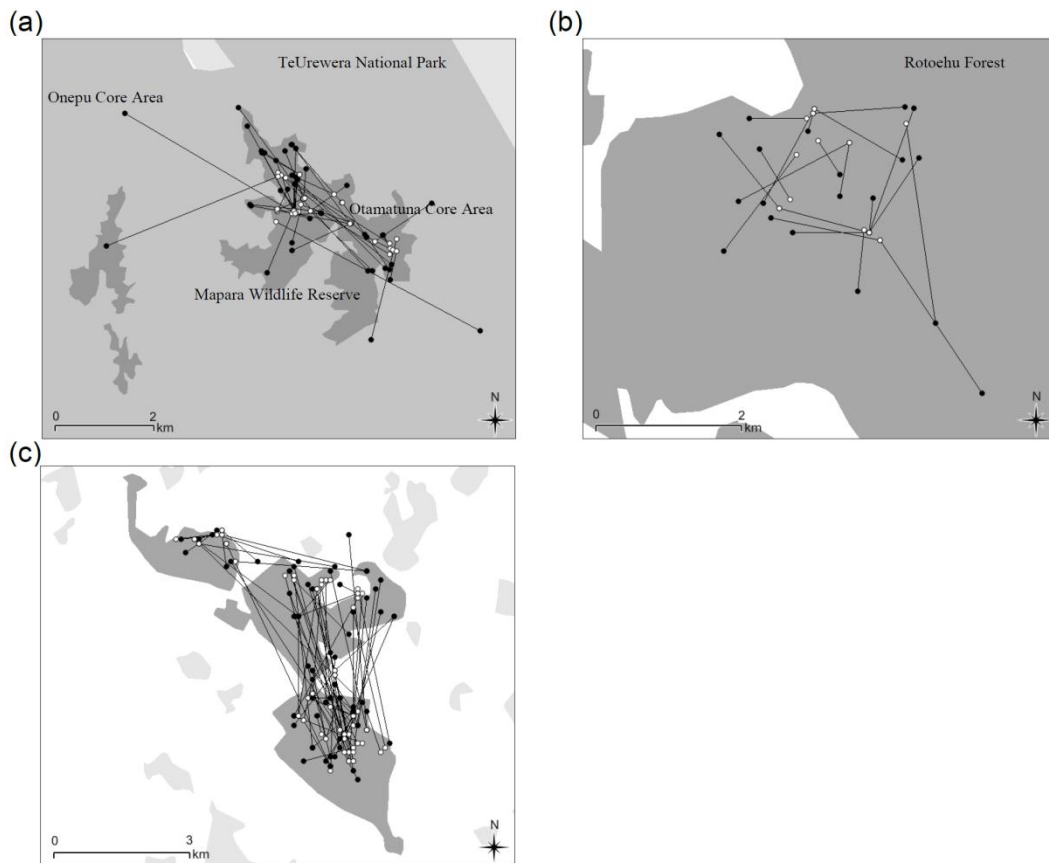
Figure 2.8. Dispersal of kōkako from natal territories (white dots) to established or breeding territories (black dots) in three reserves: (a) Otamatuna, (b) Rotoehu, and (c) Mapara. Forest cover and area under management are indicated (light grey and dark grey respectively).

In addition, rapid cultural drift in disrupted populations may be also influenced by the number of individuals in different portions of habitat. We found higher song similarity within a small portion and lower similarity between adjacent larger portions of an asymmetrically shaped area, which suggests a negative effect of number of individuals on average song similarity. Even if individuals disperse across portions of habitat and carry songs from the natal territory, they may not use them if local song is distinctive and there is rapid accumulation of cultural mutations promoted by intense social interaction or higher numbers of neighbours (Lynch 1996).

In conclusion, after examining similarity in acoustic variation and song traditions in long-separated and tenuously connected populations, we find

evidence for strong and rapid cultural drift due to isolation at a macrogeographic scale and fragmentation of vocal cultures at a microgeographic scale. There are distinct dialects in surviving populations that may reflect differing cultural trajectories, after bottleneck events, and convergence may be due to social selection pressures or chance in small populations. The formation of dialects also occurs independently from genetic flow as dispersal may not be critically restricted while areas are discontinuous and vocal differentiation is locally maintained.

2.4.3 Conservation implications and future avenues

Vocal divergence can affect effective communication among birds, as songs play a critical role in territory defense and mating contests. For example, song sharing with neighbours might offer social benefits, which favour reproductive success, such as song matching possibilities to interact with particular individuals (e.g., Beecher et al. 1997; Nelson et al. 2001; Leader et al. 2008). Therefore, song divergence, due to rapid vocal drift in isolated surviving populations, may prevent effective breeding within and between kōkako fragmented populations. The success of multi-sourced translocated populations may be limited by considerable song divergence. This vulnerability may be particularly important in other species which, like kokako, have specific habitat requirements, low dispersal abilities, and monogamous pair bonds.

Assortative mating after translocating kōkako from multiple sources appears to be prevalent (Rowe & Bell 2007; D. Bradley, Univ. of Waikato, unpublished data). This indicates that pairs from the same population are more likely to communicate effectively and interbreed. Therefore, considering song differences may be decisive in determining compatibility between populations and the viability of translocated and small populations of kōkako. For instance, simulated secondary contact between three recently separated populations (two translocated and a single source after 5-9 years of isolation) showed acoustic divergence and reduced between-population song sharing but no discrimination based on behavioural responses (see Chapter 4). However, in contrast to recently isolated populations, a similar experiment showed that the surviving populations of Rotoehu and Mapara respond significantly stronger to local versus foreign song

when simulating secondary contact (D. Bradley et al., Univ. of Waikato, unpublished data). Further research is needed to establish the effect of vocal divergence on behavioural responses among other surviving isolated populations that can effectively be used as sources for translocating individuals.

Finally, dispersal data support the idea that juveniles can learn songs after dispersal and thus will integrate more easily to a new population. Although alteration of song may also be possible for mature birds, they are likely to be less flexible (e.g., Doupe & Kuhl 1999), and this could pose difficulties for territory establishment and pair formation. This study suggests that active management should incorporate such behavioural considerations, to date largely left aside in management decisions.

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Chapter 3

Reductions in population size compromise song repertoires and complexity of a rare duetting songbird*

By Sandra V. Valderrama

I collected 80 % of the data and carried out 100% of the analysis and write-up. LEM and JRW provided comments and advice.

Abstract

The North Island kōkako (*Callaeas wilsoni*) is an endangered New Zealand forest songbird living in territories year-round. Sedentary habits, poor dispersal abilities and being a predator-naive island species have made the birds especially vulnerable to massive habitat loss and introduced predators. Scattered populations, in isolated conservation areas of various sizes, have been rescued from extinction and are currently recovering. Acoustic communication is crucial for mate choice and territory defense in kōkako but behavioural consequences of isolation are poorly understood despite their potential effect on population viability. We examined demographic effects on key song attributes and tested the prediction that reductions in population size may compromise effective communication. We analysed song repertoires and repertoire sharing, vocal performance, song sharing and syntactical characteristics within surviving and translocated populations. We found that decreases in population size correlate with decreases in population repertoire size, within-bout diversity of phrase types, and certainty in syntactical structure. Our results indicate that song traditions and delivery may crucially depend on high social interaction rates and thus population size. Furthermore, we reveal that song traditions in fragmented populations of rare kōkako resemble song microevolution in island colonization events.

Key words: North Island kōkako, song complexity and repertoires, small populations, fragmentation, behavioural conservation

3.1 Introduction

Conservation of rare species with low population sizes is central to protecting global biodiversity in an era of rapid species decline and extinction (e.g., Saunders et al. 1991). Small populations are known to be susceptible to stochasticity, loss of genetic flexibility, the accumulation of deleterious genes, and Allee effects, all of which result in reduced fitness and can cause extinction. However, less is known about how behavioural changes may influence the viability of small populations and the persistence of rare species in modified habitats (Blumstein & Fernandez-Juricic 2010).

Vocal behaviour and song traditions learned and culturally transmitted among individuals, can be affected by demographic changes within populations (Lynch 1996; Payne 1996). Reductions in population size have historically and naturally occurred when individuals of a species colonize a new area such as an island (i.e., a founding event), but can also occur when there is anthropogenic habitat disturbance (e.g., Pimm et al. 1988; Williamson 1989) which fragments and reduces available habitat. As a result, changes in song patterns may be linked to fragmentation and isolation effects as well as changes in population size and viability (Laiolo & Tella 2007; Laiolo et al. 2008; Briefer et al. 2010). Therefore, insight into divergence of song traditions in disturbed habitats requires knowledge of vocal patterns in local populations, as well as understanding the correspondence between the attributes of vocal signalling systems and demographic factors, and ultimately between microevolutionary changes and conservation.

The North Island kōkako (*Callaeas wilsoni*) is an endangered species endemic to New Zealand. They are large songbirds (length c. 38 cm, weight 218-233g) that only persist in mature hardwood and podocarp forests with abundant tawa (*Beilschmiedia tawa*; e.g., Powlesland 1987; Best & Bellingham 1991) which remain in scattered isolated areas (Lavers 1978; Innes et al. 2006). They are monomorphic and monogamous, and pairs hold territories of up to 14 ha that they defend year-round (Innes et al. 2006). Kōkako are not only sedentary but also, like many remote-island birds, have poor flying abilities that limit their dispersal distance from natal territories to an average of 1.62 km, according to data obtained from four populations (J. Innes et al. unpubl. data in Sinclair et al. 2006).

In this study, we explore relationships between the size of isolated populations of kōkako and song attributes that may be dependent on high rates of social interaction: song sharing, vocal performance (e.g., singing rates), and complexity. Song and element sharing is a consequence of social learning and communicating within and among groups (e.g., Brown & Farabaugh 1997; Molles & Vehrencamp 2001; Todt & Naguib 2000) and allows more effective territorial defense for individual birds of many species (Beecher & Brenowitz 2005). Song performance and complexity have different components, but here we focus on repertoire size, repertoire sharing, and how song is used (i.e., temporal characteristics of performance, versatility and syntactical characteristics). In larger populations, the need to vocally interact with many neighbours and floaters, in order to maintain territories and pair bonds, can result not only in local song similarity but also increased neighbour interaction that in conjunction with vocal drift may promote more complex songs due to improvisation and matching (Mundinger 1975; Bitterbaum & Baptista 1979).

Kōkako males and females sing and combine their songs into loud antiphonal duets, audible over long distances (c. 1.6 km, Maning 1960), with typically greater contributions by the male. However, repertoires of song elements are not sex-specific and the birds sing with immediate variety. Song sharing among neighbouring kōkako and the use of song in response to playback suggest that song has a function in territory defence through countersinging interactions, whilst flexibility in natural duetting song sequences may convey information about pair bonding and motivation (Molles & Waas 2006; Molles et al. 2006). Therefore, the use of song repertoires and song complexity can potentially be directly affected by the amount of social interaction as regulated by population size. Overall territory distribution of kōkako and patterns of juvenile dispersal indicate that they typically cluster by establishing territories near conspecifics (Innes et al. unpublished data in Molles et al. 2008), hence population size where the carrying capacity may not have been reached yet (i.e., current surviving populations) would provide a reasonable proxy for the levels of social interaction birds are likely to experience within populations (c.f. population density).

As opportunities for social interaction vary across kōkako populations that differ in size, we hypothesized three general song responses when populations contract relative to larger populations: (1) smaller populations should exhibit

impoverished song repertoires and increased song sharing as the availability and generation of novel song examples will be reduced relative to larger populations. (2) During song bouts, birds in smaller populations should display lower song rates as well as lower switching rates and diversity of phrase types, as a result of interacting with a more restricted range of conspecifics. (3) Finally, we expected lower sequential entropy values in smaller populations due to the reduced complexity of vocally interacting with fewer conspecifics.

3.2 Methods

3.2.1 Study areas and populations

We studied six natural, recovering populations and two populations created through translocation in mainland reserves under management on the North Island of New Zealand (Fig. 3.1 a). Kōkako populations are regularly surveyed by the New Zealand Department of Conservation following a standardised protocol (Flux & Innes 2001). The six surviving populations include the following areas and corresponding number of territorial individuals: Mataraua Forest Reserve, in the Northland region, covers an area of 650 ha, from 600 m to 670 m a.s.l., and currently supports 82 individuals. Three other study populations located in central North Island are: Mangatutu Ecological Area with 1400 ha, from 462 to 700 m a.s.l., harbouring 139 individuals; Waipapa Ecological Reserve has 2532 ha, from 500 m to 600 m a.s.l, with 230 individuals; and Mapara Wildlife Reserve with 1312 ha, from 250 m to 574 m a.s.l., has 174 territorial kōkako. Rotoehu Forest in the Pongakawa Ecological Area has 440 ha, from 195 m to 285 m a.s.l., and 55 kōkako. The Otamatuna core area is the largest in size (2500 ha) of four core areas under intensive management in Te Urewera National Park and also harbours the largest population of kōkako (about 250 individuals) between 120 and 720 m a.s.l. All six surviving populations have significantly increased since conservation efforts were allocated to predator control (Innes et al. 1999; Fig. 3.1b). The translocated populations included in this study were established by transferring individuals between 2001 and 2007 from the Otamatuna core area in Te Urewera National Park to Boundary Stream Mainland Island and the Ngapukeriki Reserve

(a detailed description of these translocated populations is provided in Chapter 4). Boundary Stream has an area of 800 ha, between 300 m and 1000 m a.s.l., and currently harbours 20 territorial birds that live in a sub-area of 352 ha of mature podocarp forest. Ngapukeriki Reserve has 450 ha, between 200 m and 700 m a,s,l., with 18 kōkako.
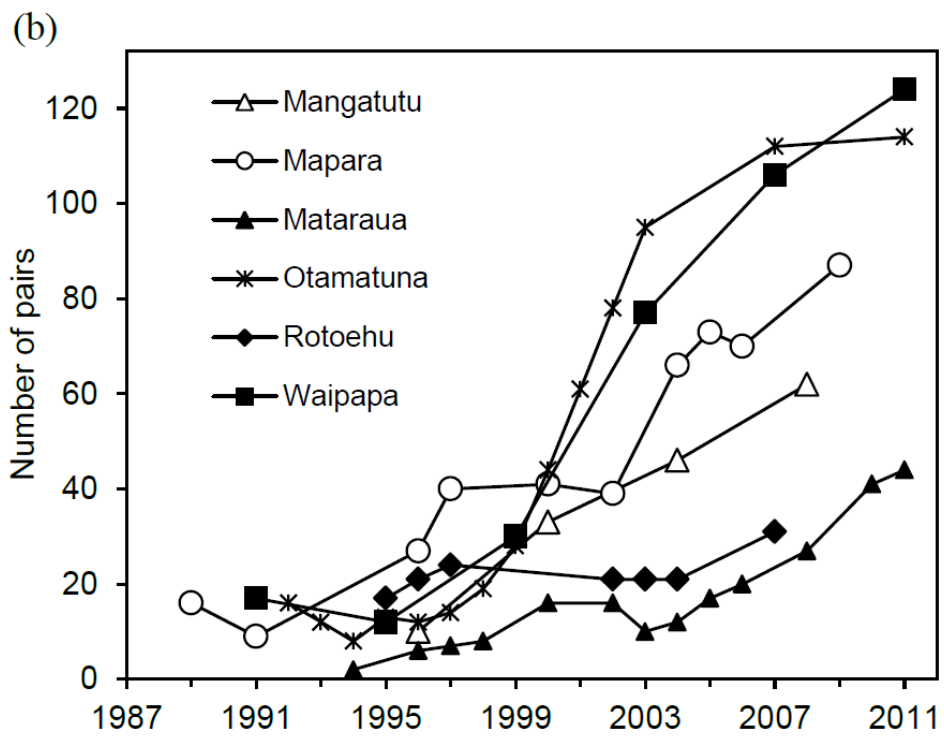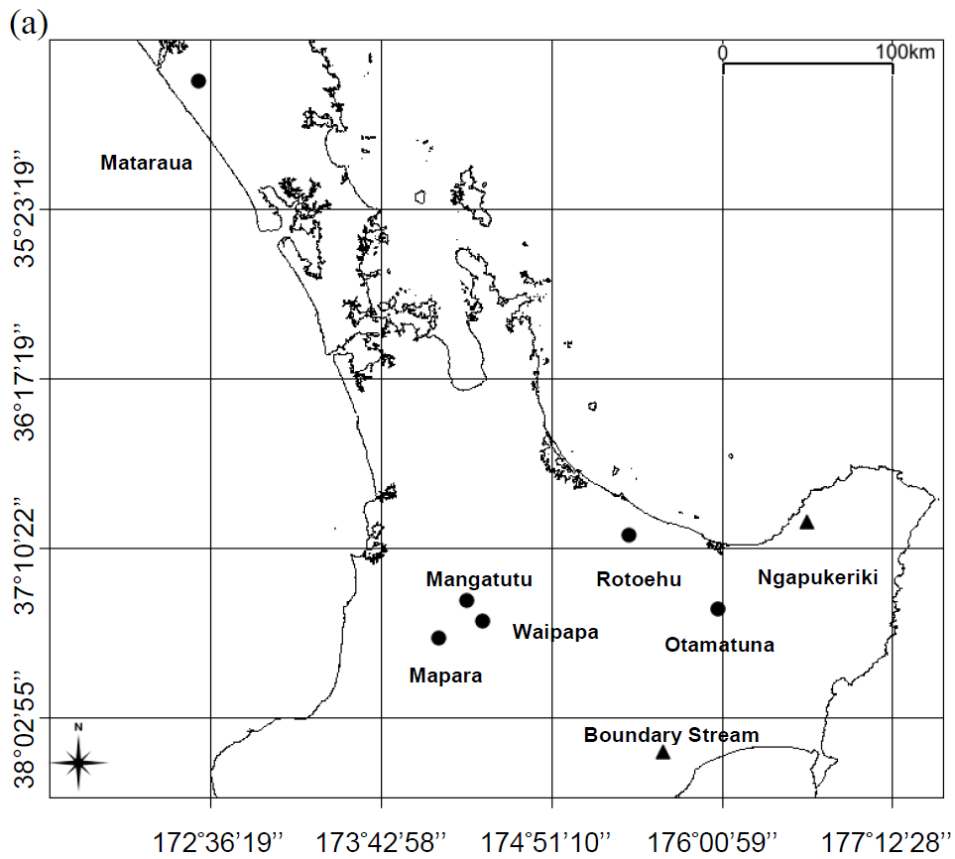
Figure 3.1. (a) Location of six surviving populations (solid circles) and two translocated (solid triangles) kōkako populations, and (b) abundance changes in the six surviving populations of kōkako (1989-2011).

3.2.2 Song recordings and analysis

We recorded songs from a total of 46 pairs in the six surviving and two translocated populations of kōkako in 2008 and 2009. Six focal pairs in each surviving population and five pairs in each translocated population were recorded between 0500 and 1000 hours using Sennheiser directional microphones (ME66, ME67 and MKH416) and Marantz portable PC card recorders (PMD660). All recordings were collected in a Wave file format using a 44.1 kHz sampling rate and 16 bits per sample. Most songs were recorded during spontaneous singing but occasionally it was necessary to stimulate song by using playback of contact calls or local song for up to three minutes.

Kōkako songs can be classified into stereotyped phrases that a pair produces with immediate variety; often these phrases follow sequential patterns described as themes (Molles et al. 2006). Phrases consist of one or more different or repeated syllables (Molles et al. 2006). We used SYRINX (J. Burt, Seattle, Washington) to visually inspect sound recordings of kōkako as sonograms and to classify groups of syllables distinctively produced, in a stereotyped fashion, as phrases. We were able to identify and categorize population repertoires from a total of 15,513 phrases recorded in six surviving populations and 5,316 phrases recorded in the two translocated populations. Because we only had a limited number of recordings with clear separation of male and female contributions we catalogued pair, rather than individual, repertoires. We also catalogued repertoires of phrases for each pair and generated repertoires of phrases for each population. In addition, we identified sequences of phrases produced during continuous natural singing bouts (i.e., without the use of playback).

Song sharing

We calculated pairwise song repertoire similarity scores within populations by performing pairwise comparisons between all pairs. To calculate song similarity scores, we used a modified Jaccard index that includes the difference in repertoire size between pairs (see Chapter 2).

Singing performance

We selected a subsample of two uninterrupted singing bouts of 180 s per pair in order to standardise performance measurements across pairs. The bouts included only natural song (not stimulated by playback). We calculated vocal diversity as the number of distinct phrase types over the total number of phrases per bout, singing rate as the number of phrases per second, and switching rate as the number of times birds switched to a new phrase type (i.e., not repeated) divided by total number of phrases in the bout.

Sequential information

As sequences of phrases are not easily identified in the song of kōkako, we analysed the complexity of phrase-to-phrase transition patterns using measures of entropy. In information theory, entropy values are a measure of uncertainty or improvisation associated with a frequency distribution of occurrence of phrase types in strings of sequences. Briefer and colleagues (2010) suggested using information theory to quantify the amount of information provided by the distribution of song element types among their corresponding transitions. We followed a similar approach by incorporating transcriptions of song bouts with identified phrase types into a Markov chain model. With this model we calculated the conditional probabilities of phrase types being followed by others in first- and subsequent-order transitions. These probabilities represent entropy values or the amount of information contained in sequences. Entropy values were calculated for 0-7 transitions with the Shannon-Weaver formula (Shannon & Weaver 1963; Steinberg 1977). Low entropy values, approaching 0, mean less uncertainty in what phrases are subsequently produced, whereas high values indicate that the

song is less predictable. We included natural and stimulated continuous song bouts, with more than 100 phrases, in further analyses as we did not find substantial differences across bout types.

An additional meaningful measurement derived from entropy estimates is relative entropy and 'redundancy' (which is reciprocal to relative entropy; Legendre & Legendre 1998; Briefer et al. 2010). Relative entropy was calculated as the entropy of a given order relative to the probability assuming equal use of all phrase types which appeared in the bout, and indicates how much 'free choice' of phrases pairs have when naturally singing sequences. Low relative entropy measures reflect greater stereotypy (redundancy) in the organisation of song phrases during a bout.

Lag sequential analysis

We inspected all sequences recorded from each pair in all populations to describe how pairs cycle through the phrase types in their repertoires, and whether particular phrase transitions occur non-randomly. We used the SDIS and GSEQ software packages (Quera & Bakeman 2009) to identify strings of phrase types that occur more often than expected based on their observed frequency. This approach allows us to represent transition patterns of all phrases that each pair uses and, at the same time, we are able to represent entropy and information theory with sequences of phrases that birds sing. We used all phrase types and examined their frequency at the second phrase after the criterion phrase (Lag+1). All phrase types were used as targets and criterions to generate observed and expected probabilities. Sequences and their connection are represented on syntax diagrams that we constructed based on non-random occurrence by transition probability (p-value of < 0.01 and positive z-score; Molles et al. 2006), in which different phrase types designated with numbers are shown in circles and their corresponding transitions in the song are shown as arrows.

Statistical analysis

Differences in repertoire size (pair and population repertoire), within-population song sharing and temporal characteristics of singing performance

across populations were evaluated with Analysis of Variance (ANOVA). Effect of population size on population repertoire size was analysed with a linear regression for all populations. Relationships between within-population vocal similarity, pair repertoire size, song performance variables, and relative entropy with population size were tested using general mixed models (GLMM) and restricted maximum likelihood procedures (REML), where pair was fitted as random variable to account for repeated sampling within populations. Fixed effects included population size, entropy and entropy drops; repertoire size as well as sequence length were also fitted as fixed-effect covariates. Normality and homogeneity of variance were verified for all dependent variables using the Shapiro-Wilk statistic, and the Levene's test respectively. We represent the effect of population size on song performance in the fitted GLMM using leverage plots in which effects included in the models are shown. We used SPSS for variance, correlation, and mixed model REML procedures. For Markov chain analysis we used the 'infotheo' package (Meyer 2009) in the R software environment (R Development Core Team 2011).

3.3   Results

We identified between 39 and 62 phrase types per surviving population, within which pair repertoires ranged from 14 to 33 phrase types. In the translocated populations, we found pair repertoires of between 17 and 24 phrase types from population repertoires of 30 to 39 phrase types. Overall, repertoire size varied across all populations (F = 5.38; df = 5; p = 0.001). However, we did not find an effect of population size on pair repertoire size (GLMM: R^2 = 0.0001, $F_{1,7}$ = 0.005, p = 0.95) possibly due to an exceptionally large repertoire size for pairs at Mataraua, one of the smallest and most northerly surviving populations (Fig. 3.1a). When Mataraua is excluded, there is a significant positive relationship between population size and pair repertoire size (GLMM: R^2 = 0.15, $F_{1,7}$ = 11.10, p = 0.02) that may be important despite the low correlation due to within-population variation in repertoire size. Population repertoire size, however, showed a significant positive correlation with population size (R^2 = 0.59; F = 48.47; p < 0.0001; Fig. 3.2).
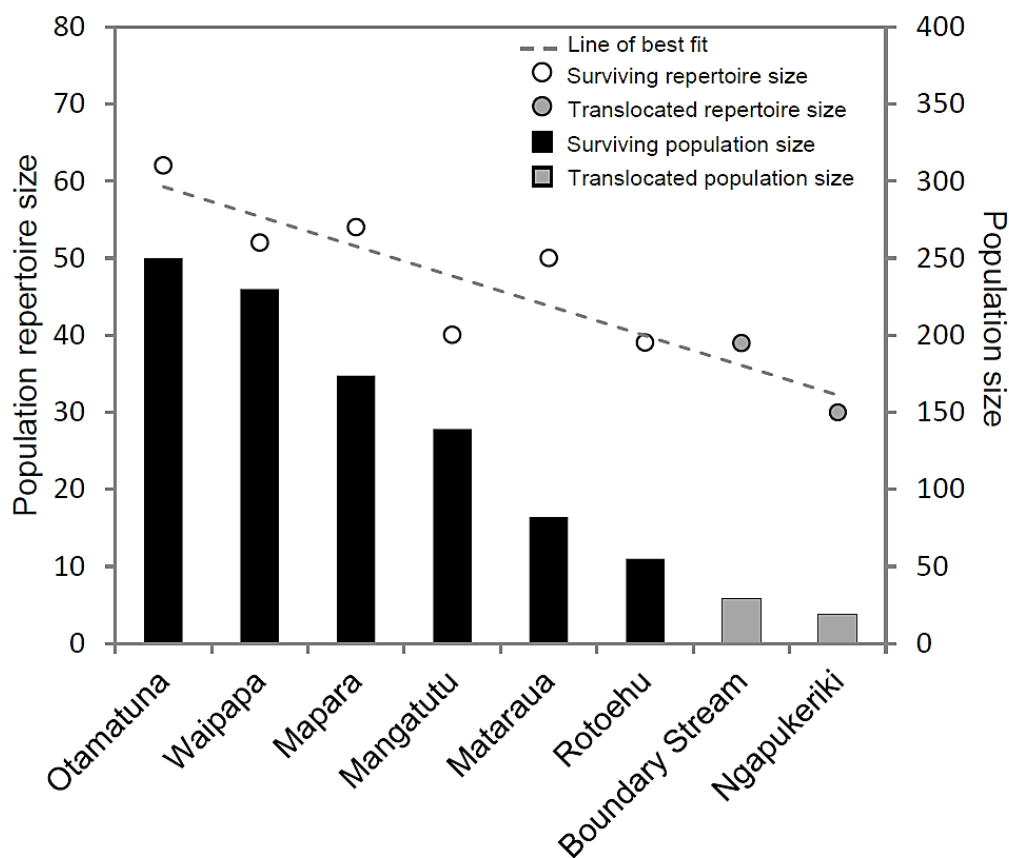
Figure 3.2. The linear relationship between population repertoire size (bars) and population size (regression line).

Song sharing varied among populations from 35-48% (Otamatuna) to 65-78% (Mataraua) repertoire similarity between pairs. We found significant differences in local song similarity among populations ($F_{1,7} = 16.49$, df = 5, $p < 0.0001$; Fig. 3.3). However, we did not find a correlation between pair-wise vocal similarity within populations and population size (GLMM: $R^2 = 0.50$, $F_{1,7} = 4.60$, $p = 0.08$); one of the larger populations, Mapara, had very low vocal similarity among pairs (43%; Fig. 3.3) relative to the population size.
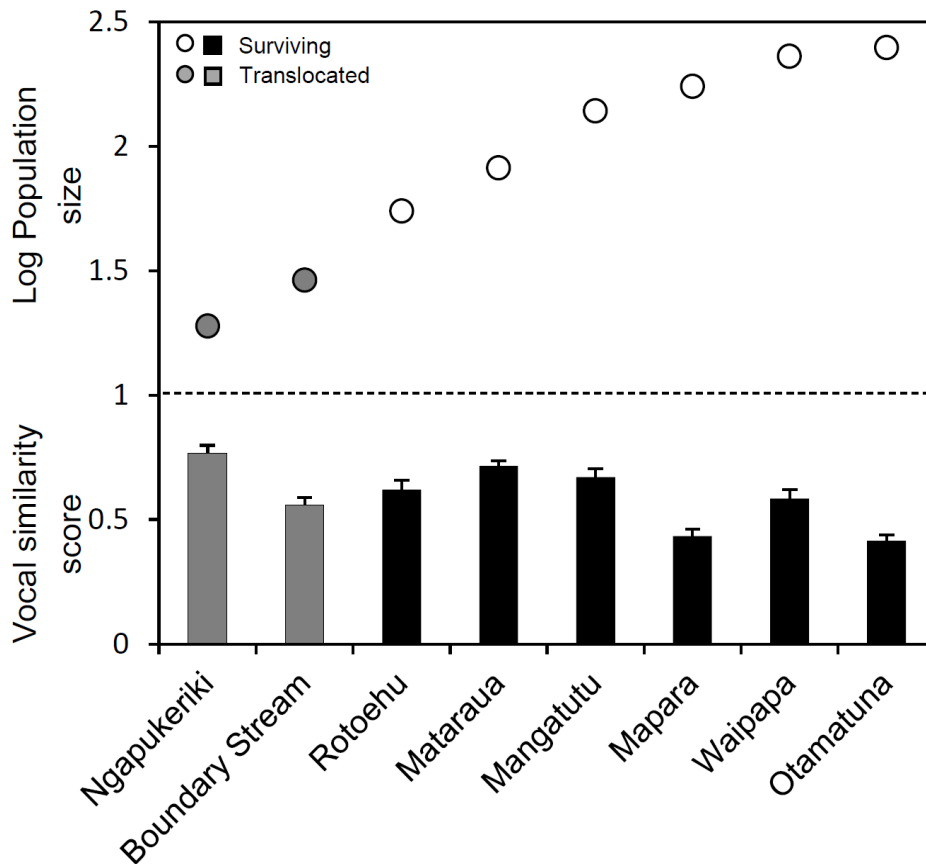
Figure 3.3. Mean (SE) pair-wise Jaccard index and population size in six natural and two translocated kōkako populations.

The three performance variables (diversity, singing rate and switching rate) not only significantly differed between populations (Table 3.1), but also song diversity and switching rate were affected by population size; the diversity (GLMM: $F_{1,5} = 9.59$, p = 0.004) and switching of phrase types (GLMM: $F_{1,5} = 7.25$, p = 0.01) increase with population size (Fig. 3.4) whereas singing rate does not show a population size effect (GLMM: $F_{1,5} = 0.31$, p = 0.58).

Table 3.1. Differences in song performance variables of the six populations of kōkako ordered from largest to smallest. Values for each population are given as means ± SE.

Variable	Otamatuna	Waipapa	Mapara	Mangatutu	Mataraua	Rotoehu	Boundary Stream	Ngapukeriki	F	p
Diversity	0.48±0.02	0.46±0.04	0.5±0.02	0.47±0.03	0.41±0.03	0.36±0.03	0.35±0.03	0.44±0.03	10.47	0.005
Singing rate	0.24±0.02	0.26±0.02	0.17±0.02	0.21±0.02	0.32±0.02	0.22±0.02	0.27±0.03	0.21±0.02	4.38	0.004
Switching rate	0.50±0.03	0.47±0.03	0.54±0.03	0.48±0.03	0.42±0.03	0.38±0.03	0.36±0.04	0.45±0.03	8.15	0.01
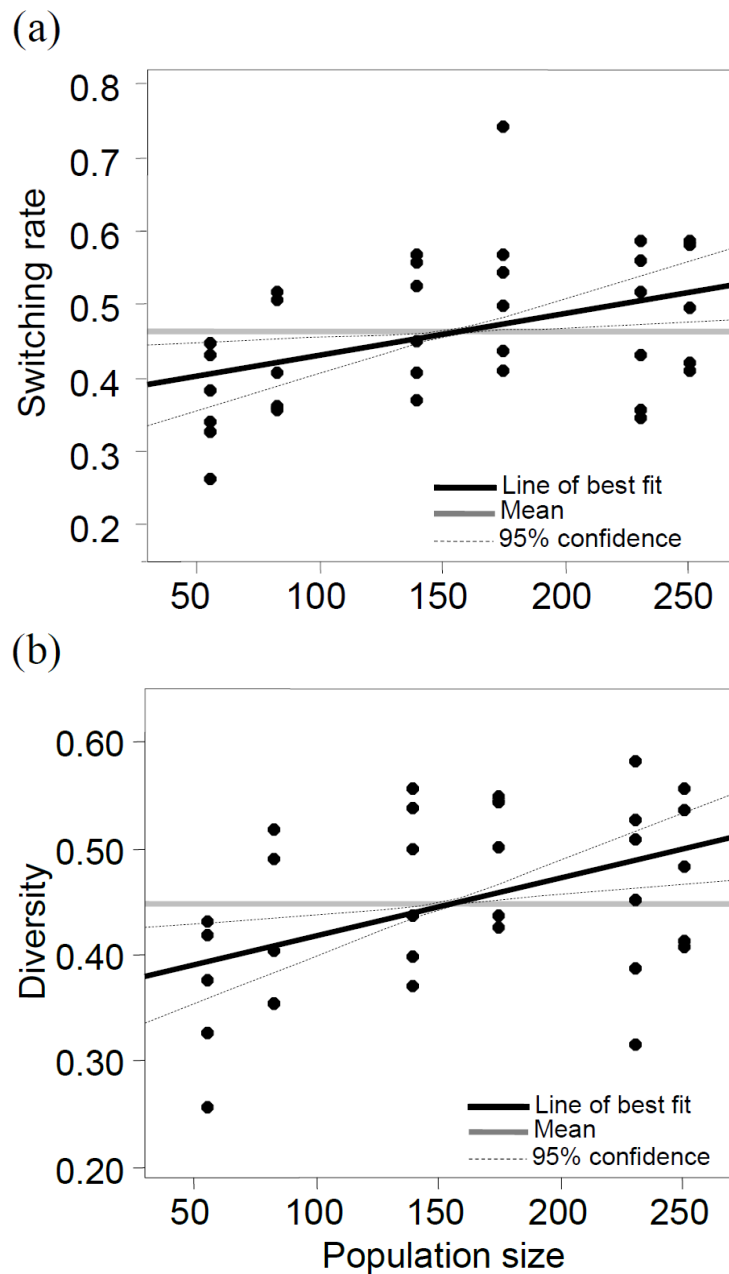
Figure 3.4. Leverage plot of the significant relationship between population size and within-population song performance (regression line and 95% confidence intervals calculated with respect to each performance variable while holding population size constant at their sample value): (a) Switching rate as a function of population size, and (b) Diversity of phrase types as a function of population size.

The Markov chain analysis showed that in kōkako song sequences, the phrase types produced depend mainly on the immediately preceding phrase as an abrupt drop in entropy occurs from the first to the second order Markov chain; from the second to fifth order there is a more gradual reduction in uncertainty (Fig. 3.5).

We found entropy, relative entropy and entropy drop values that significantly differ between surviving populations (Table 3.2). However, all populations showed a similar pattern of entropy reduction among all transitions or Markov-chain orders as shown by the information graph (Fig. 3.5). Mataraua has the highest uncertainty or "loose syntax," due in part to higher repertoire sizes, whereas Rotoehu and Ngapukeriki have the lowest uncertainties at the start of a sequence (Table 3.2, Fig. 3.5). Diagrams generated based on non-random sequences produced by each pair also reflect more linearity of overall sequences used in populations with lower relative entropy values, in contrast with less linear overall sequences in populations with higher relative entropy values or more 'free choice'. Figure 3.6 provides representative examples of song sequences from a pair in a population with a high (Fig. 3.6 a) versus low relative entropy (Fig. 3.6 b).
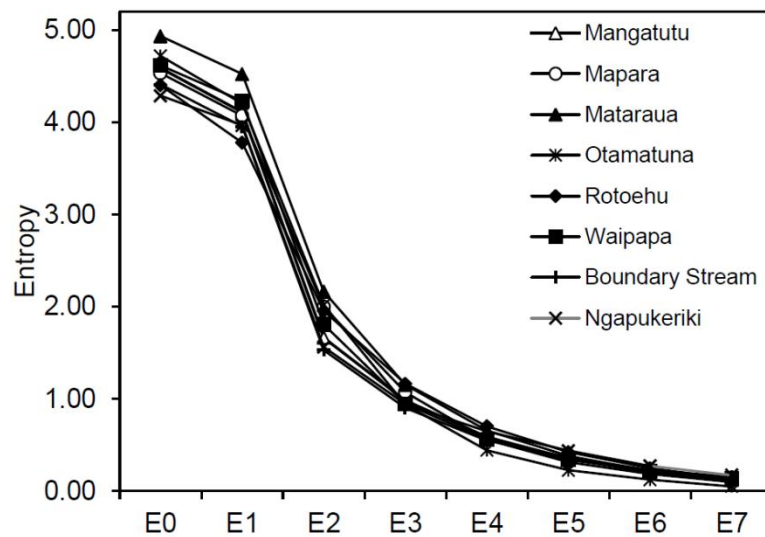
Figure 3.5. Mean ± SE entropy values for 0-7 transitions in song sequences from six populations (see section 3.2.2 on sequential information for details).

Table 3.2. Variation in syntactical information of song sequences and repertoires in six populations (ordered from largest to smallest).

Information value†	Otamatuna	Waipapa	Mapara	Mangatutu	Mataraua	Rotoehu	Boundary Stream	Ngapukeriki	F	p
E0	4.72±0.06	4.62±0.18	4.53±0.09	4.59±0.10	4.93±0.08	4.40±2.27	4.41±0.10	4.29±0.05	2.23	0.08
E1	4.20±0.08	4.23±0.18	4.07±0.08	4.11±0.08	4.52±0.08	3.78±0.17	3.95±0.12	3.97±0.18	4.09	0.01
E2	2.02±0.12	1.81±0.07	2.00±0.15	1.66±0.09	2.16±0.11	1.95±0.11	1.53±0.12	1.56±0.12	2.28	0.07
E3	0.94±0.12	0.94±0.04	1.07±0.07	0.98±0.05	1.15±0.10	1.16±0.05	0.90±0.12	0.94±0.06	1.72	0.16
E4	0.44±0.08	0.56±0.04	0.55±0.05	0.58±0.06	0.66±0.03	0.70±0.04	0.55±0.09	0.64±0.04	2.91	0.03
E5	0.22±0.05	0.34±0.04	0.31±0.04	0.35±0.05	0.38±0.02	0.42±0.02	0.37±0.08	0.44±0.04	2.61	0.04
E6	0.12±0.04	0.22±0.04	0.18±0.04	0.20±0.04	0.21±0.02	0.25±0.02	0.22±0.06	0.27±0.03	1.50	0.22
E7	0.05±0.01	0.13±0.03	0.09±0.04	0.12±0.03	0.12±0.02	0.13±0.01	0.15±0.05	0.17±0.03	1.50	0.22
RE1	0.89±0.02	0.92±0.01	0.90±0.01	0.90±0.01	0.92±0.01	0.86±0.01	0.90±0.02	0.92±0.01	3.29	0.02
RE2	0.43±0.03	0.39±0.01	0.44±0.03	0.36±0.02	0.44±0.02	0.44±0.01	0.35±0.03	0.36±0.04	2.38	0.06
RE3	0.20±0.03	0.20±0.01	0.24±0.01	0.21±0.01	0.23±0.02	0.26±0.01	0.20±0.03	0.22±0.03	2.57	0.05
RE4	0.09±0.02	0.12±0.01	0.12±0.01	0.13±0.01	0.13±0.01	0.16±0.01	0.13±0.03	0.15±0.02	3.32	0.02
RE5	0.05±0.01	0.07±0.01	0.07±0.01	0.08±0.01	0.08±0.01	0.10±0.01	0.08±0.02	0.10±0.01	2.76	0.03
RE6	0.02±0.01	0.05±0.01	0.04±0.01	0.04±0.01	0.04±0.01	0.06±0.01	0.05±0.02	0.06±0.01	1.67	0.17
RE7	0.01±0.01	0.03±0.01	0.02±0.01	0.03±0.01	0.02±0.01	0.03±0.01	0.04±0.01	0.04±0.01	1.44	0.24
Drop E0-E1	0.52±0.08	0.39±0.03	0.46±0.05	0.48±0.06	0.41±0.05	0.62±0.06	2.43±0.19	2.41±0.20	2.09	0.09
Drop E1-E2	2.19±0.17	2.42±0.12	2.07±0.15	2.44±0.11	2.36±0.07	1.83±0.08	0.63±0.08	0.62±0.06	3.65	0.01
Repertoire size	26.5±1.06	25.5±2.83	23.43±1.49	24.33±1.48	30.83±1.70	21.83±2.27	21.5±1.34	19.67±0.95	2.71	0.04

†Key: E, entropy; RE, relative entropy
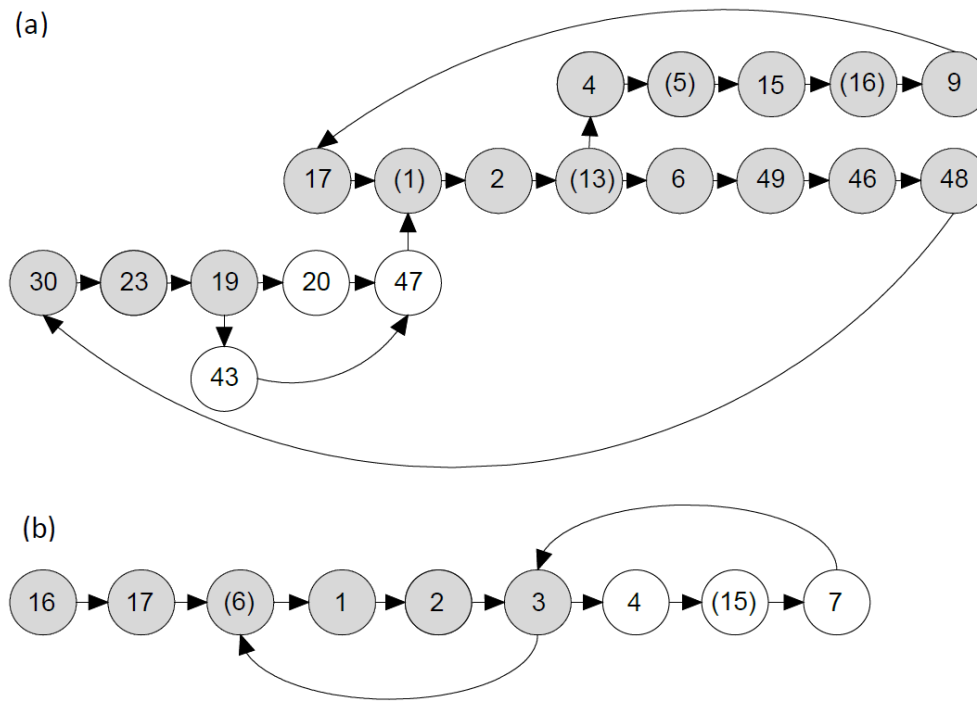
Figure 3.6. Example diagrams of the sequences used by a pair in Mataraua (a), a population with high relative entropy, and a pair in Rotoehu (b), a population with low relative entropy. Most frequently used sections are highlighted (grey) and frequently omitted phrases are indicated (brackets).

We also found evidence to suggest that complexity in song syntax varies with population size. Mixed model analyses of variance show that there were significant decreases in higher levels of relative entropy in sequences of three to five phrases (RE3, RE4, and RE5) in larger populations (Fig. 3.7; Table 3.3). The pairs from the six surviving populations analysed have 20-27% 'free choice' or uncertainty of what phrases they sing in the third position, 9-16% in the fourth position, and 5-10% in the fifth position in a song sequence, and this free choice decreases with increasing population size. Similarly, smaller translocated populations followed the same trend with 13-31%, 5-22% and 3-17% 'free choice' at the level of three, four and five phrases respectively.
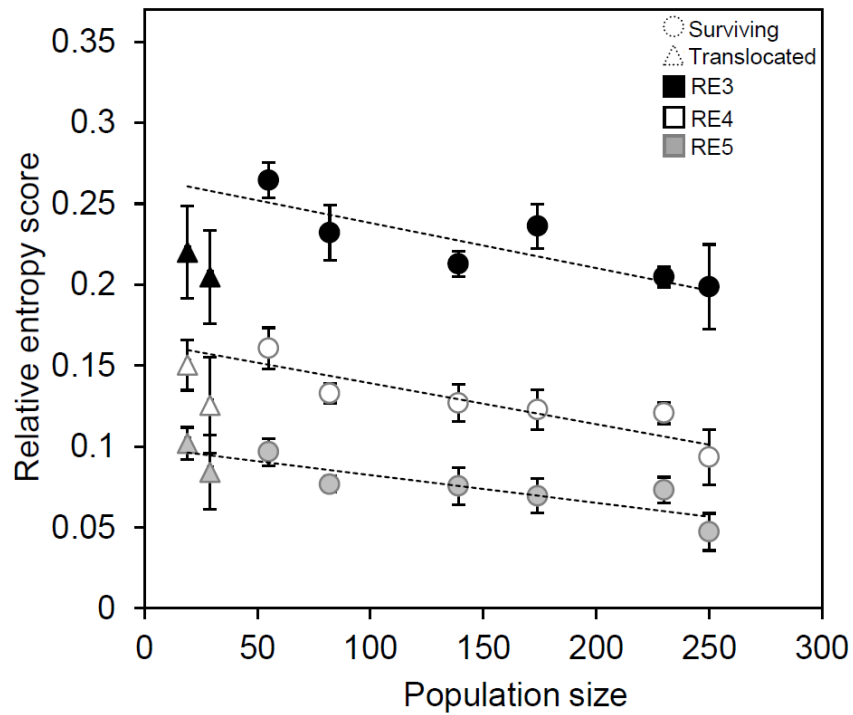
Figure 3.7. The relationship between population size and syntax uncertainty of strings including three (RE3), four (RE4) and five phrases (RE5).

Table 3.3. General mixed model of syntax entropy values and their relationship with population size.

Information value†	Population size effect			
	R^2	F	df	*p*
RE1	0.32	0.74	1	0.44
RE2	0.24	0.36	1	0.58
RE3	0.20	9.26	1	0.03*
RE4	0.24	15.73	1	0.02*
RE5	0.22	9.68	1	0.04*
RE6	0.11	4.19	1	0.11
RE7	0.10	2.12	1	0.22

†Key: RE, relative entropy

3.4   Discussion

In evaluating the effect of population size on singing behaviour in remnant and newly-established populations of kōkako, our results showed that: (1) population repertoire size, but not necessarily pair repertoire size, decreases in smaller populations but there was no clear evidence of a relationship between population size and song sharing within populations; (2) within-bout diversity of phrase types and switching rate decrease with population size, but not the singing rate; and (3) song sequences in kōkako populations exhibit a consistent pattern of an initial sharp decrease in uncertainty at the level of second-order entropy, followed by a smaller decline in uncertainty at higher levels of organization. We also found significant differences between populations associated with population size at the level of three, four and five phrases in a sequence; sequence uncertainty decreases in larger populations, in opposition to our prediction.

Our finding that song repertoires of kōkako populations are influenced by population size is consistent with a neutral model in which variation in song repertoires depends on population size if mutation rate is similar among populations (Lynch 1996). This has been found to be the case for populations of common chaffinches on Atlantic islands where a population with high density has more syllables (Lynch & Baker 1993). Also, small populations of the rare Dupont's larks (*Chersophilus duponti*), distributed in patches of habitat similar to kōkako, have individual repertoires that decline with population size (Laiolo & Tella 2005; Laiolo & Tella 2007).

Although population repertoire size was positively associated with population size, the same was not true for pair repertoire sizes within populations. We found, however, that this result was driven by one population: pairs in Mataraua have a much greater repertoire size than expected for the population size (when Mataraua is excluded from the analysis, a significant positive association occurs between population size and pair repertoire size). Turnover in territory ownership and a recent population increase from only a few individuals at Mataraua could have led to unusually large repertoires for pairs through several mechanisms. Relaxation in selection for population-specific songs may lead to retention of novel song types and mutations. In high-turnover populations, individuals may retain songs from natal territories as well as acquire songs after dispersal; both old and new song

types may be frequently recombined between pair members and neighbours when these relationships are unstable. In consequence, a number of new variants may diffuse across pairs (Lynch 1996). The Mataraua population increased from 2 to sixteen pairs in 14 years, contracted again to 10 pairs, then rapidly expanded to 44 pairs in 9 years. Thus, this population has recently and rapidly increased and may be undergoing more dynamic interactions between young neighbouring kōkako than is typical of relatively stable populations.

Pairwise similarity scores showed that population size does not have a clear effect on song sharing within populations. Although there is a trend for sharing to increase with population size (at p=0.08), the Mapara population in particular showed incongruously low vocal similarity relative to population size. This suggests that other factors may also strongly influence song similarity within populations. Habitat connectivity within populations, for instance, could affect dispersal and cultural transmission of song elements (Thielcke 1973; Ellers & Slabbekoorn 2003; Riviera-Gutierrez et al. 2010; Laiolo & Tella 2007). In great tits (*Parus major*) and Dupont's larks, more song types are shared among males in small fragments than in large fragments of habitat, and sharing is negatively affected by habitat discontinuities (Riviera-Gutierrez 2010; Laiolo & Tella 2005). It is likely that habitat connectivity is lower in Mapara, in contrast to the other five areas which comprise more continuous habitat. The Mapara Reserve is an elongated and asymmetric fragment of habitat surrounded by farmland; therefore overall song sharing in kōkako may be negatively affected in populations distributed over tenuously connected sections of habitat with reduced transmission of song traits between those sections (see Chapter 2), similar to great tits and Dupont's larks in fragments where dispersal is disrupted.

Disruption of connectivity between populations on a larger scale could help explain the overall trend of increased sharing in smaller populations that we found. Isolation, in conjunction with historical population bottlenecks, may have limited the number of song models for vocal learning (Baker & Jenkins 1987; Lynch 1996), increasing sharing levels with decreasing population repertoire size. We suggest this process is more likely to drive patterns of repertoire size and sharing in kōkako than enhanced singing interactions in larger populations due to competition for resources (e.g., Lachlan & Slater 2003; Laiolo and Tella 2005). Similarly, Briefer et al. (2010), studying populations of European sky larks

(*Alauda arvensis*) on fragmented habitat, found a relationship between low population density and increased song sharing. Kōkako populations went through bottlenecks and are still recovering; therefore, although they tend to establish territories near other pairs, the availability of unoccupied suitable habitat within reserves suggests that competition for resources may not be critical yet. Thus, population depletion has mostly affected song sharing patterns in kōkako, similarly to sky larks on fragments, and induced cultural impoverishment.

While differences in repertoire size and sharing may be better explained by isolation and bottlenecks than current competition levels, our results suggest that increasing population size influences song performance by increasing diversity and rates of switching between phrase types. Previous studies have suggested that the frequency of territorial interactions between individuals (often represented by population density) can result in variation of singing activity and divergence between populations in willow warblers (*Phylloscopus trochilus*; Goretskaia 2004), European blackbirds (*Turdus merula*; Ripmeester et al. 2010), and two mimicking lark species (*Galerida cristata and G. theklae*; Laiolo et al. 2011). Higher density has been found to promote temporal shifts in song, such as longer singing periods and phrases as well as more variable songs with more notes (Goretskaia 2004; Laiolo et al. 2011) and shorter pauses (Ripmeester et al. 2010). We found that within-bout singing activity in kōkako is more dynamic in larger populations, with more song variety and alternating phrase types despite similar song rates. This shows that population song characteristics of a territorial duetting songbird species are also susceptible to demographic changes, corroborating previous results in species where only territorial males sing. Furthermore, we also show that social interaction may enhance vocal complexity (i.e., diversity and switching) but that vocal output may be enhanced by stronger competition for space which is currently low or absent in most recovering populations of kōkako.

The results of our analyses of syntactical complexity also showed that variation in 'free choice' of phrase types in song sequences varies among populations. Furthermore, we found that these differences are associated with population size. However, in contrast to our prediction of more uncertainty in sequences sung in larger populations, where social interactions which disrupt organised duet sequences are presumably more frequent, syntactical patterns exhibited the opposite relationship. In smaller populations, kōkako pairs produce

songs with less structured syntax, while songs in larger populations showed less uncertainty. These results may reveal that despite increasing social interaction and population-wide song variety, distinct song sequences may be strongly favoured in larger populations as an indicator of pair experience, or as a means of 'directing' song to a particular receiver among many neighbouring pairs. Alternatively, higher uncertainty in small but growing populations may reflect age structure. Younger birds produce more plastic songs and tend to recombine song elements (i.e., during song learning) that they develop into more stereotyped songs modeled on those of older tutors (e.g., Marler & Peters 1982; Podos et al. 1999; Hulsch & Todt 2004). Thus, the 'withdrawal of learning hypothesis' has been proposed to explain song variation in founding populations on islands. This hypothesis suggests that improvisation of new song elements and loose syntax is a consequence of song development in absence of adequate song models (Thielcke 1973). On the other hand, in small colonizing populations, a relaxation of selective pressures for song distinctiveness may occur (Lynch & Baker 1993, Lynch 1996). In kōkako, smaller populations may consist of more recently established territorial pairs; therefore, the higher 'free choice' of phrase types that we found supports the 'withdrawal of learning hypothesis' and the possibility that there is less selective pressure for syntactical distinctiveness and stereotypy in smaller populations.

Finally, from both evolutionary and conservation perspectives, the observed variation in singing behaviour by social modulation raises questions about reproductive success and adaptation to differing social conditions. It is possible that differing song profiles within populations are efficiently adjusted to the social environment such that in small populations, birds simply do not need more complex songs of greater diversity due to reduced social interaction. However, an unusually reduced 'social mileu' in small populations could result in more lasting effects on reproductive behaviour that may have important consequences on fitness. For example, in other avian species song stimulates reproductive activities, and processes leading to ovulation, that affect the latency to egg laying and reproductive synchrony (e.g., Waas 1995; Waas et al. 2000, 2005). In kōkako, larger population repertoires and individual song diversity might better stimulate reproductive 'readiness' in females. Also, kōkako may be less likely to form bonds with partners that have 'impoverished' social attributes. As a result, in

multiple-source translocated populations, individuals from smaller socially impoverished populations may be less likely to find a mate in comparison with birds from larger and culturally diverse populations. Furthermore, maintaining large populations and increasing small populations by implementing management regimes, like intensive pest control, may contribute greatly to conserving natural social environments for kōkako. Investigating the role of song in social stimulation is suggested as a future avenue of paramount importance in understanding the behavioural ecology of kōkako. Song may be critical to increasing the viability of fragmented surviving populations as well as translocated populations of kōkako, maintaining an important reservoir of behavioural biodiversity, and therefore helping to optimize conservation efforts.

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Chapter 4

Divergence in song and variable playback response in translocated populations of the endangered North Island kōkako in New Zealand*

By Sandra V. Valderrama

I collected 100 % of the data and carried out 100% of the analysis and write-up. HS, LEM and JRW helped with the experimental design, provided comments and advice.

Abstract

Translocating individuals from healthy source populations to (re-)colonize suitable habitat is an extreme tool for the conservation of a species. Several demographic and genetic factors will affect translocation success, but especially for birds, in which acoustic signals play a crucial role in conspecific recognition, cultural factors may also be important. We investigated the divergence in song and response to song of the endangered North Island kōkako (*Callaeas wilsoni*) in New Zealand in two translocated populations and their source population. We found significant song divergence in the translocated populations which had reduced repertoire sizes and increased repertoire sharing, as well as structurally different song elements of higher frequency and shorter duration compared to the source population. Despite the song divergence and clear variability in the nature and level of response among populations, reciprocal playback did not reveal any reduced non-local recognition. The reduced vocal variability can be regarded as cultural erosion, which is also typical of small populations in fragmented habitat, and may undermine the viability of the translocated populations. Persistence of response levels suggests that the emergence of behavioural restrictions on gene flow require at least a few decades of separation after translocation. However, more studies are needed for a proper evaluation of the potential impact of culture on translocation success for species conservation.

Key-words: behavioural conservation, North Island kōkako, translocated populations, vocal divergence

4.1   Introduction

Translocation of individuals from threatened to safe habitat patches within the former distribution range can be a last-option conservation strategy to fight extinction in declining animal species (Griffith et al. 1989). Previous research on translocated populations has addressed management issues (e.g., Scott & Carpenter 1987; Lovegrove 1996; Wolf et al. 1996), ecological aspects (e.g., Cunningham 1996, Armstrong et al. 1999, Armstrong & Ewen 2001; Jamieson & Wilson 2003) and also genetic consequences (Stockwell et al. 1996, Storfer 1999; Cardoso et al. 2009; Bronwyn et al. 2010). As on islands (Frankham 1996) and in fragmented habitats (Segelbacher et al. 2008), translocated populations may face reduced genetic diversity and excessive genetic divergence due to founder effects and genetic bottlenecks, which may threaten their survival (Newton 2003; Cardoso et al. 2009). Negative effects may also arise through reduced behavioural diversity and excessive cultural divergence (Håkansson & Jensen 2005; Laiolo & Jovani 2006), although little is known about the effects of translocation and isolation on behavioural differentiation among populations and the potential consequences for successful exchange of individuals (Clemmons & Buchholz 1997).

New Zealand represents a well-known extreme scenario in conservation biology. Because of its high endemism, New Zealand is one of the 25 biodiversity hotspots in the world (Myers et al. 2000). It is also one of the places most dramatically affected by habitat destruction and, more recently, by the introduction of non-native species that have become widespread (i.e., Allen & Lee 2006; Saunders & Norton 2001, Kelly & Sullivan 2010). Invasive herbivores and predators have had a severe impact on bird habitat and population size, which has led in many cases to local or global extinction (Allen & Lee 2006). Intensive pest control on mainland reserves over the last 20 years has allowed numerous translocations of threatened species back to remnants of habitat where they used to occur (Armstrong & McLean 1995; Clout 2001; Saunders & Norton 2001). Translocation has been a successful conservation tool in New Zealand and it has served as a model implemented worldwide since the 1970's (Jamieson et al. 2006; Taylor et al. 2005).

Cultural variation and local song diversity have recently been put forward as potentially critical factors in conservation biology (Gaunt & McCallum 2004; Laiolo 2010) and may also be important to consider in translocation projects. Geographic variation in birdsong concerns a well-studied paradigm in studies on function and evolution of animal behaviour and may also affect the viability of small populations associated with habitat fragmentation or translocation efforts. Song learning occurs by copying from conspecifics during which pupils often incorporate parental or local song elements into their own song. However, inaccuracies can accumulate and result in cultural drift and rapid vocal diversification among populations (Payne 1996; Ellers & Slabbekoorn 2003; Podos et al. 2004). The critical role of song variation in species recognition and mate choice means that such vocal diversification can affect individual success in territory establishment and reproductive activity and thereby reduce gene flow between divergent populations (Grant & Grant 1996; Slabbekoorn & Smith 2002). Vocal diversification of learned songs has also been linked to habitat fragmentation (Laiolo & Tella 2005; Laiolo & Jovani 2006; Laiolo & Tella 2006), and shown to predict population viability (Laiolo et al. 2008). Hence, we believe it is important to collect data on song variation and its behavioural consequences in the context of conservation through translocation efforts.

The North Island kōkako (*Callaeas wilsoni*) is an endangered songbird endemic to New Zealand (BirdLife International 2009). Kōkako were once widespread in the North Island but there are currently only a few scattered populations marooned in isolated areas with suitable habitat (e.g., Lavers 1978; Innes et al. 1999), and bird numbers are still declining in unmanaged areas (Innes et al. 1999; Basse et al 2003). Typically, kōkako prefer habitat that includes tall mature hardwood and podocarp forest with abundant tawa (*Beilschmiedia tawa*; e.g., Powlesland 1987; Best & Bellingham 1991). The historical decline was due to massive habitat loss and fragmentation, while more recent threats involve several introduced predators, such as rats (*Rattus rattus*, *R. norvegicus* and *R. exulans*), possums (*Trichosurus vulpecula*), and stoats (*Mustela erminea*; Innes & Flux 1999). However, the Department of Conservation has implemented predator control programs since the 1980's and it has also launched translocations of kōkako to areas with suitable habitat and pest control since the 1990's (Innes et al. 2006; Sinclair et al. 2006; Molles et al. 2008). Many kōkako have been

translocated from the largest remaining populations in the central and eastern North Island, with 71 individuals being transferred to various islands between 1981 and 2005, and 117 individuals being transferred to other mainland areas between 1996 and 2010 (listed in Molles et al. 2008).

In the current study, we describe vocal divergence among three North Island kōkako populations: two populations established by translocation efforts and their source population. Previous studies on kōkako vocalizations have addressed duetting behaviour (McLeod 1998; Molles & Waas 2006), acoustic variation within a single natural population (Molles et al. 2006), and dialectal variation among populations (McLeod 1998; Hudson 2001; Innes at al. 2006). Here we hypothesized that vocal divergence would be evident in song sharing, spectral and temporal structure and that divergence from the source population would be greater for the first-established translocated population. Furthermore, we hypothesized that vocal divergence among translocated populations and the source population would yield reduced response levels to song from non-local birds. The latter hypothesis was tested using a reciprocal playback experiment with source- and derived-population songs in the three populations. Our results provide insights into population aspects of cultural divergence and the potential emergence of behavioural barriers to reproduction. Such insights could be critical for directing future conservation efforts and may stress the importance of attending to vocal diversification and behavioural diversity when planning translocations.

4.2   Materials and methods

4.2.1   Study sites

We conducted our study in three isolated mainland reserves (Fig. 4.1). Te Urewera National Park, the source population, is located in the central east of the North Island, and it sustains the largest surviving population of North Island kōkako in New Zealand. Although the total area of the park is 2126.7 km^2, kōkako survive mainly in five core areas with intensive pest control. In total, Te Urewera has been estimated to harbour 366 birds in the core areas currently under management, 21.5% of all extant kōkako (Moorcroft et al. 2010). We conducted

our experiment in Otamatuna (38°20'3.1''S, 177°83'8.1''E), the largest core area (25.3 km^2), where an estimated 224 individual kōkako reside. Between 2001 and 2007 kōkako were transferred from Otamatuna to two areas. In 2001, five pairs were transferred to Boundary Stream Mainland Island (T1), held in a captive breeding program for three years, and then released along with their offspring in 2004. In 2007, another 10 birds from the same parent population were released to increase the translocated population. Boundary Stream Mainland Island covers an area of 8.0 km^2, between 300 m and 1000 m above sea level, over the Maungaharuru range in the south east of the North Island (39°6'24.2''S, 176°49'5.2''E). Only 3.6 km^2 in T1 are covered with mature podocarp broadleaf forest, and the 10 pairs and 9 single kōkako at this site may have faced greater spatial restriction and competition over resources than suggested by the overall reserve size. At the time of this study, T1 comprised seven founders from the first introduction plus five of the founders' offspring and three females from the second translocation. Ngapukeriki Reserve (T2) is located in the eastern Raukumara ranges (37°50'33.1''S, 177°42'9.7''E) and comprises an area of 4.5 km^2, between 200 m and 700 m above sea level. In 2005, 19 birds from Otamatuna were translocated to the reserve; the estimated population in 2010 was 18 kōkako. T1 is separated from the source population by around 90 km and T2 is about 65 km from the source.

Yearly monitoring surveys have been carried out by the Department of Conservation in both translocated populations. We thoroughly surveyed three areas in Otamatuna in 2009, where we collected recordings and conducted our playback experiment. Here we determined population density as the number of neighbours within minimum convex polygons (Calsbeek 2009). Euclidean distances to the nearest neighbour in each population were also calculated. The mapped locations of the pairs correspond to approximately the centres of their territories. We used Quantum GIS (Quantum GIS Development Team, 2010) for spatial analyses. The density in the source population is considerably greater (0.62 individuals per hectare) compared with T1 and T2 (0.14 individuals per hectare for both T1 and T2). Furthermore, the nearest neighbour distances are significantly greater in the translocated populations than in the source population ($\chi^2 = 27.31$, df = 2, p < 0.01). The mean distance between neighbouring pairs in

T1 is 279.59 (26.77) m whereas in T2 is 324.86 (48.72) m, and in the source is 125.43 (12.70) m.

4.2.2   Song differentiation

We collected recordings of natural song in all three populations between 2009 and 2011. Focal pairs were recorded between 0500 and 1000 hours using Sennheiser directional microphones (ME66, ME67 and MKH416; Sennheiser, Berlin, Germany) and Marantz portable PC card recorders (PMD660; D&M Professional, Kanagawa, Japan). All recordings were collected in a Wave file format at a 44.1 kHz sampling rate and 16 bits per sample. We visualized and classified all songs collected into phrase types to document phrase type repertoires for 11 pairs from the source population and eight pairs from each derived population. A phrase is identified as a stereotyped short sequence of one or more syllables; syllables are not generally produced individually and can also be incorporated into more than one phrase type. All recordings were inspected using SYRINX-PC (J. Burt, Seattle, Washington). We calculated 351 pair-wise comparisons using Jaccard's similarity coefficient to calculate phrase repertoire sharing among individuals within and among all three populations. We adjusted the Jaccard's coefficient to control for different sample sizes (e.g., length of recording per pair) by incorporating the difference in phrase repertoire size between each of the two pairs compared; this adjustment has been shown to improve the robustness of song similarity estimates (Tracy & Baker 1999; Stewart and MacDougall-Shackleton 2008; MacDougall-Shackleton et al. 2009). Jaccard's coefficients can range from a minimum of 0 when there is no similarity, up to 1 when all song elements are shared between two pairs.

We characterized the spectral and temporal structure of the songs from each population by measuring one example of each phrase type recorded from every pair. We measured peak frequency, fundamental frequency, peak frequency of the loudest harmonic, minimum frequency and maximum frequency, as well as duration and number of syllables. All measurements were made using Avisoft SASLab Pro, version 5.1.14 (Avisoft Bioacoustics, Berlin, Germany). Spectrograms were produced with a fast Fourier transformation of 1024 points,

25% frame size, 224 Hz bandwidth (43 Hz resolution) and 93.75% overlap on a Hamming Window.

4.2.3   Playback experiment

Stimulus preparation

We selected and processed songs with the highest signal-to-noise ratio (recorded < 20 m from the songsters). We used a band-pass filter procedure in Adobe AUDITION version 3.0 to remove noise below 0.3 kHz. We also selected other bird sounds that did not overlap kōkako song and faded the amplitude to background noise level. Finally, we normalized all the songs to optimally exploit the available dynamic range. Male and female kōkako sing duets comprising stereotyped sequences, or 'themes', of up to eight phrases produced with immediate variety (Molles et al. 2006). We selected one long theme and one short theme from each pair in each population for use as playback stimuli (Fig. 4.1). For each stimulus, the long theme was followed by a natural pause length of silence and the subsequent short theme; this pattern was then repeated once yielding a total of 4 themes per stimulus. We used themes from different and distant pairs for each trial to reduce problems of pseudoreplication (Kroodsma 1989; Slabbekoorn & Bouton 2008). In addition, subjects and stimulus pairs were selected from at least two territories apart to avoid an impact of familiarity with direct neighbours.
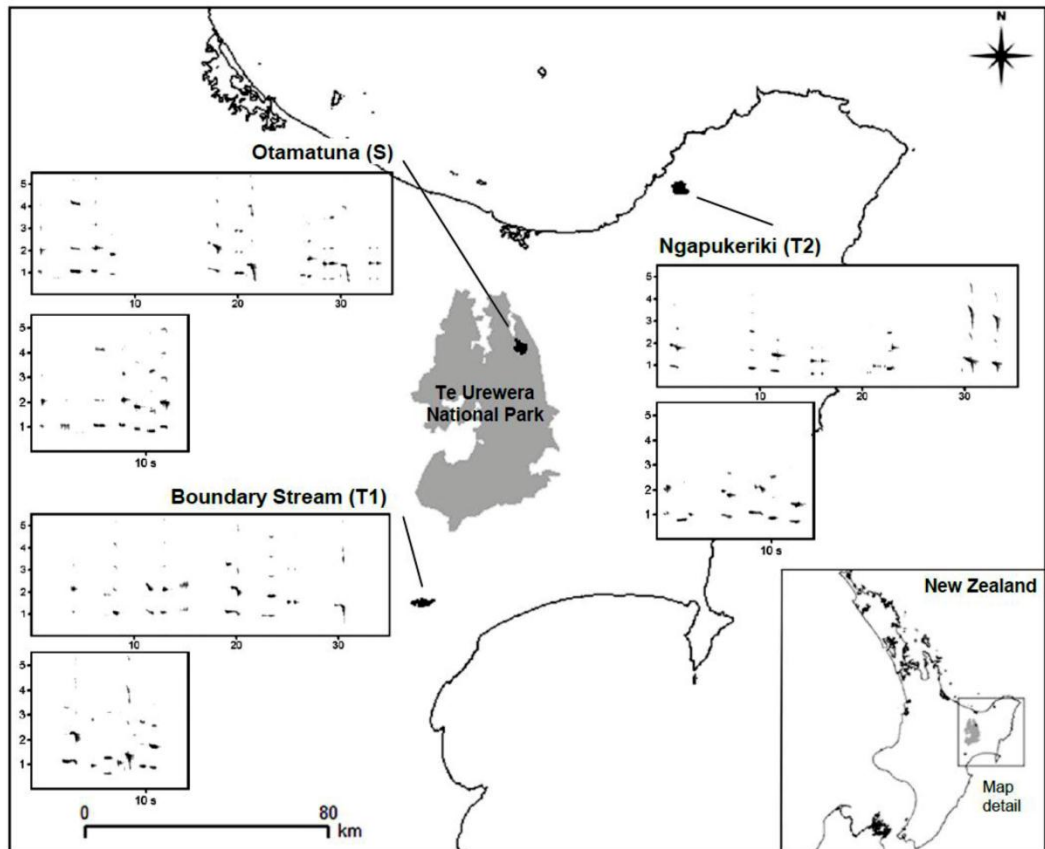
Figure 4.1. Map of the three study areas and corresponding example sonograms of long (top) and short (bottom) themes from the source and the two translocated populations (CD #5).

Experimental design

We tested a total of 23 pairs in the two derived populations and the source population from the 16th of August until the 16th of November 2010. Six pairs were tested in T1: one female in this group was released in 2007 (tested three years post-translocation); all other birds tested were founders or their offspring (nine years post-translocation). Eight pairs were tested in T2 (five years since translocation; focal birds included founders and their offspring). We presented each focal pair with two playback treatments: 1) songs from the original source and 2) songs from their own translocated population. A reciprocal experiment was performed by similarly testing nine pairs in the source population. In the source population, we presented four pairs with T1 songs (nine years since translocation) and five pairs with T2 songs (five years since translocation). Comparisons

between vocal responses and proximity measures yielded no differences based on the origin of translocated population stimuli. Therefore, we pooled data from T1 and T2 stimuli for the analysis of responses in the source population. Similarly, responses of founder pairs and offspring in translocated populations were concurrently analysed as they did not differ in any of the stimuli. We balanced the order of the treatments in all populations by starting every subsequent test with another song stimulus with respect to origin. Pairs from contiguous territories were tested at least two days apart to avoid an impact of previous playback-induced activity levels of neighbours on current response strength to playback in their own territory. We recorded natural singing behaviour before presenting subjects with stimuli to allow comparisons of vocal behaviour before and after playback. Vocal adjustments in response to the stimuli were used to assess singing flexibility and matching ability, as well as to quantify the effects of playback on song output and song diversity.

Trial procedure and acoustic variables

We conducted our trials between 0600 and 0900 hours. Each trial included a 10 min period before any playback was broadcast, during which we recorded natural vocalizations. Immediately after the pre-playback period we set up a single wireless speaker and playback system (Foxpro FX5), positioned 3m above the ground and facing up, 5-10 m from the song post used by the focal birds during the pre-playback period. We subsequently initiated the trial using the speaker remote control (TX200, www.gofoxpro.com) to broadcast the stimuli. Speaker volume was standardized at 70 dB(A) for the peak amplitude at 1 m from the speaker. Each trial began with one of the two stimuli (local or non-local; duration 130 s), followed by a 10 min silence. This post-playback period was followed immediately by the second stimulus (duration 130 s) and a second 10 min silent period. Consequently, pairs were recorded and monitored before, during and after playback for almost 35 minutes. Two observers, blind to the order of stimulus categories, recorded approach and vocal responses by using respectively an M-Audio Micro Track 24/96 digital recorder with a portable clip microphone and a Marantz portable PC card recorder (PMD660) with a Sennheiser directional microphone (ME67). Observers were previously trained to estimate distances,

from one object and between two objects, to enhance accuracy. Approach variables included: 1) proportion of time spent ≤15 from the playback speaker; 2) time pair members spent ≤5 m apart; and 3) proportion of time pair members spent ≥10 m apart when they were between 0-15m from the speaker. We used SYRINX-PC software (J. Burt, Seattle, Washington) to visualize our sound recordings and obtain the data to calculate the following vocal response variables during post-playback periods: 1) singing rate; 2) phrase type rate (i.e. number of different phrases per second); 3) Shannon-Wiener diversity; 4) innovation versatility (i.e. number of switches to a new phrase type relative to the total number of switches, taking into account the available number of different phrase types relative to the total number of phrases produced); 5) number of new phrase types relative to the phrase types sung during the pre-playback period; 6) phrase type similarity score for post-playback songs with the correspondent stimulus previously played; 7) phrase type sharing index of post-playback songs with the pre-playback period; 8) Frequency of occurrence of theme and non-theme phrases.

4.2.4 Statistical analysis

Song similarity within and between populations was evaluated using a Kruskal-Wallis test. We performed a principal component analysis (PCA) to obtain composite variables that describe spectral characteristics of the songs from the three populations. Correlations were previously checked to avoid redundant variables included in composite variables. Analysis for sampling adequacy and sphericity were performed using Kaiser-Meyer-Olkin and Barlett's test to verify the suitability of the variables to run a PCA. Subsequently, we used the composite variable that explained most of the variance in the spectral measurements to compare spectral characteristics of song among our focal populations through analysis of variance (ANOVA).

Comparisons of vocal and approach responses for the same period (playback or post-playback) between treatments were carried out using paired Student's t-tests for the parametric data or Wilcoxon signed-rank tests for the non-parametric data. We also used t-tests for pre- and post-playback comparisons. To compare all response variables across populations, we used Kruskal-Wallis tests. Vocal responses were measured as the mean percentage that vocal variables changed

during the post-playback period relative to the pre-playback period. Differences for all statistical tests were considered significant for p ≤ 0.05. SPSS version 15.0 (SPSS, Chicago, Illinois) was used for statistical analyses.

4.3 Results

4.3.1 Song diversification

Our song similarity measure showed that there is high similarity within source and within translocated populations, but low similarity among the three populations (Fig. 4.2). Furthermore, population T2 showed significantly higher within-population song similarity, in comparison with population T1 (earlier translocated) and the source population ($\chi^2 = 13.02$, df = 2, p < 0.01). We also found that songs from the source population are more similar to the songs from population T2 than to the songs from population T1 (t = 7.89, df = 62.85, p < 0.01). T1 songs are as similar to the source as they are to T2 songs (t = -1.00, df = 9.8, p = 0.34). Spectral characteristics of the songs significantly differ between populations (F = 35.23, df = 2, p < 0.001; Fig. 4.3). The primary differences are that phrases sung by birds from the source population are typically longer and have lower frequencies than those sung by birds in both translocated populations (Table 4.1).
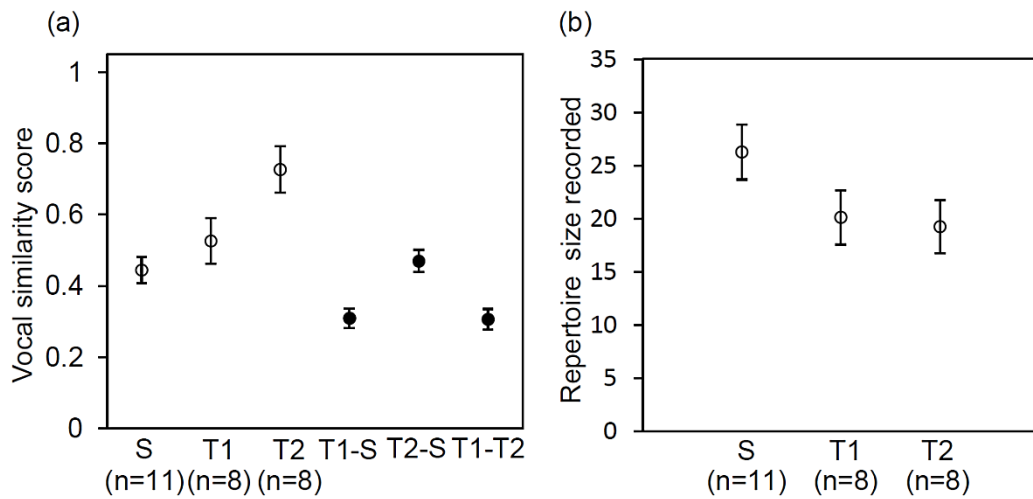
Figure 4.2. The vocal divergence of song elements between the parent population and two translocated populations. (a) Mean Jaccard (3SE,) indices comparing songs shared within and between the source, T1 and T2. Blank circles indicate within-population song similarity; bold circles indicate song similarity between populations. (b) The mean repertoire size (SE) shows the differences between populations.
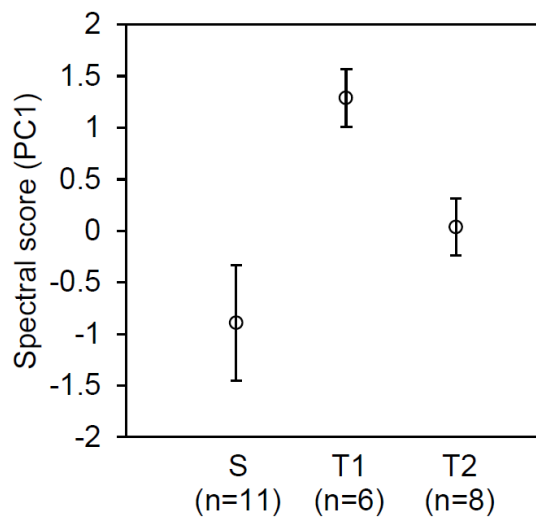
Figure 4.3. Comparative mean values (2SE) of the PCA composite variable representing differential spectral characteristics between source and translocated populations.

Table 4.1. Differences in temporal and spectral song structure between source and translocated populations.

Variable	S		T1		T2		F	p
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**F**	***p***
Number of syllables	2.37	0.09	2.24	0.13	2.07	0.15	1.53	0.241
Duration of phrases (s)	0.63	0.01	0.53	0.02	0.62	0.02	7.35	0.004*
Peak frequency (Hz)	1302.41	31.53	1408.63	23.18	1385.05	25.57	3.94	0.036*
Fundamental frequency (Hz)	869.78	9.83	967.72	11.41	913.81	10.93	19.75	< 0.001*
Peak frequency of the loudest harmonic (Hz)	2145.77	38.47	2440.79	68.94	2287.59	38.01	9.58	0.001*
Minimum frequency (Hz)	582.17	8.41	685.01	13.96	635.34	11.52	21.13	< 0.001*
Maximum frequency (Hz)	1483.20	29.45	1768.81	95.23	1593.78	56.58	5.72	0.011*

Significant differences between group

4.3.2　Response to playback

We found significant between-population differences in responses to local song versus non-local song, with no evident discrimination between treatments within populations (Fig. 4.4 & 4.5; Tables 4.2 & 4.3). T1 presented the highest singing rate and number of phrase types, followed by the source population, which is in contrast to the low singing rate and reduced number of phrase types of T2. T2 pairs also sang at a significantly lower rate and used fewer phrase types than T1 and S in response to both playback stimuli.
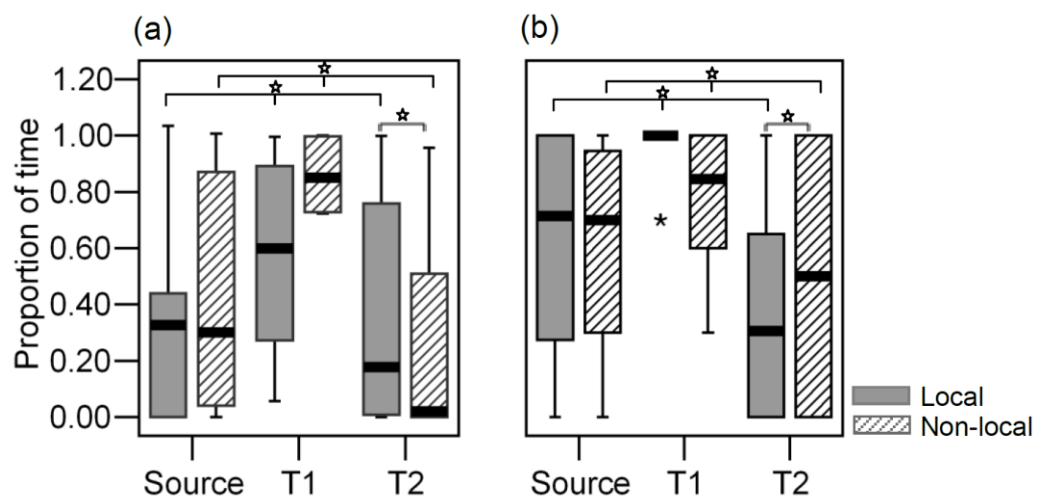
Figure 4.4. (a) Proportion of time spent within 15m of the speaker, and (b) proportion of time individuals of a pair spent less than 10m apart in each population. Adjacent bars represent subjects during the post-playback period for each treatment. Stars over horizontal bars indicate significant response differences between playback periods and across populations.

Although the versatility of vocal responses did not differ between populations, we found a major difference between populations regarding the number of new phrase types that birds added in response to local and non-local song relative to the repertoire recorded before playback (Table 4.2). T1 birds incorporated more new phrase types than other populations in response to both playback types, with the difference being greater for non-local song playback (Fig. 4.5). T2 pair responses incorporated relatively few new phrase types to both

playback treatments. The responses by pairs in the source population to local and non-local song were somewhat intermediate between T1 and T2 (Fig. 4.5 & 4.6). During the Source treatment, pairs from T2 spent considerably less time close ($\leq$ 15m) to the speaker and closer to each other, than did pairs in T1 (Fig. 4.4; Table 4.2). There were no other differences in proximity measures between treatments or populations.
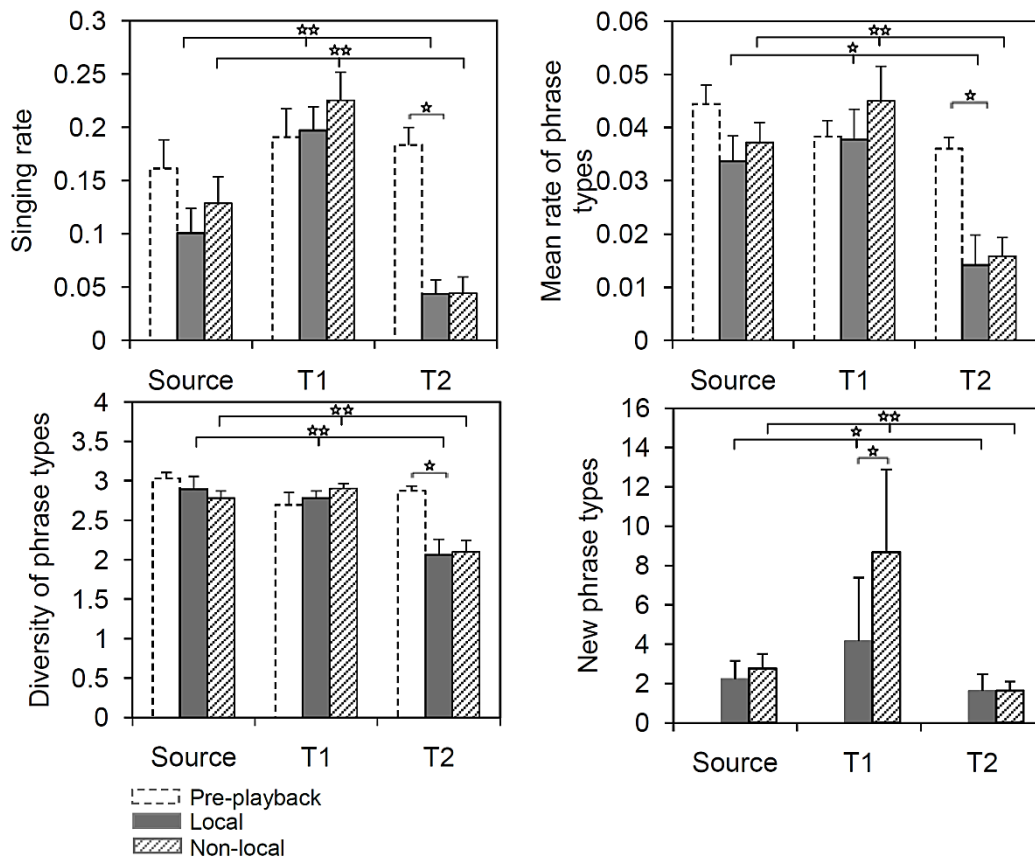
Figure 4.5. Mean vocal output (SE) recorded in each population (Source: n = 9; T1: n = 6; T2: n = 8) during pre-playback, after local stimulus, and non-local stimulus. Stars over horizontal bars indicate significant response differences between playback periods and across populations.
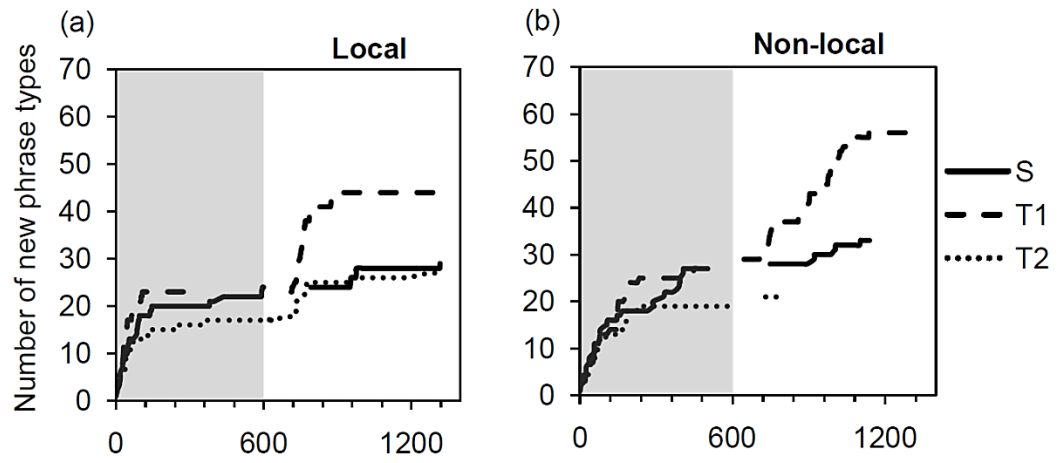
Figure 4.6. Examples of cumulative number of new phrase types incorporated by two pairs from each population during the pre-playback period (grey interval) through (a) local, and (b) non-local phases.

Table 4.2. Comparative significance of response variables to stimuli between populations.

| Variable | Local | | | | | | | | Non-local | | | | | | | |
| | S | | T1 | | T2 | | Kruskal-Wallis | | S | | T1 | | T2 | | Kruskal-Wallis | |
	Mean	SE	Mean	SE	Mean	SE	χ^2	p	Mean	SE	Mean	SE	Mean	SE	χ^2	p
Speaker distance < 15m	0.38	0.13	0.59	0.11	0.38	0.13	1.99	0.03	0.44	0.12	0.85	0.06	0.27	0.14	7.01	0.03
Pair distance < 10m	0.57	0.14	0.94	0.05	0.39	0.15	6.00	0.34	0.50	0.14	0.80	0.10	0.50	0.20	2.16	0.34
New phrase types	3.00	1.07	6.00	3.27	1.75	0.84	1.63	<0.01	2.89	0.68	11.67	3.74	2.00	0.71	12.88	<0.01
Relative singing rate	28.97	14.76	12.42	18.08	-74.83	15.66	8.51	<0.01	-14.96	15.31	34.27	18.75	-75.00	16.24	12.32	<0.01
Relative phrase type rate	-18.42	14.81	1.13	18.14	-60.64	15.71	6.34	0.01*	-12.39	10.47	17.31	12.82	-55.64	11.10	10.21	0.01
Relative phrase type diversity	-14.42	11.83	6.09	14.49	-55.88	12.55	6.94	<0.01	-7.78	7.52	9.79	9.22	-36.44	7.98	10.48	<0.01
Relative versatility	26.08	34.89	-0.55	42.73	3.58	37.01	0.74	0.56	6.69	24.45	15.38	29.94	54.69	25.93	1.17	0.56

Table 4.3. Significance of the influence of playback on vocal output with relative change associated.

Variable	Population	df	t	p	Mean difference[a]	SE	% Change
Singing rate	S	8	-2.34	0.02*	-0.05	0.020	-28.83
	T1	5	0.62	0.56	0.02	0.033	10.84
	T2	7	7.31	<0.01*	-0.14	0.019	-76.01
Phrase type rate	S	8	-2.04	0.07	-0.01	0.004	-20.25
	T1	5	0.65	0.54	0.003	0.005	7.98
	T2	7	-5.83	<0.01*	-0.02	0.004	-58.27
Diversity of phrase types	S	8	-1.62	0.14	-0.19	0.120	-6.40
	T1	5	0.68	0.52	0.14	0.210	5.34
	T2	7	-5.08	<0.01*	-0.83	0.163	-28.86
Versatility	S	8	0.74	0.48	0.08	0.111	8.68
	T1	5	0.00	1.00	0.00	0.092	0.03
	T2	7	0.50	0.63	0.10	0.201	15.64

*Significant differences between groups
[a]Negative values mean decrease and positive values increase in response variable

4.3.3 Playback effect on vocal behaviour

Vocal output was altered after playback in the source population and in T2 but not in T1 (Fig. 4.5). The singing rate decreased in the source, and T2 birds considerably decreased their overall vocal output after playback with reduced singing rates (t = -7.31, df = 7; p < 0.01), phrase type rates (t = -5.83, df = 7, p < 0.01) and diversity of phrase types (t = -5.08, df = 7, p < 0.01). We did not find any significant changes in the overall performance of the same phrase types after playback. Similarly, the overall spectral frequency (e.g. frequency, duration,

number of syllables) of the total composition of phrases sung before playback did not change significantly after playback.

4.4   Discussion

We have shown divergence in song and playback response in two translocated populations of the endangered North Island kōkako. Singing behaviour from birds in two translocated populations differed significantly from their source population in having smaller individual repertoire sizes and more repertoire sharing among pairs. Furthermore, song elements were of higher frequency and of shorter duration in songs from translocated populations compared to those from the source population. Our reciprocal playback results revealed no general population discrimination tendencies as kōkako pairs tended to respond with equal strength to local and non-local songs. However, responsiveness in the translocated populations differed in two ways from the responsiveness in the source population. In the oldest and acoustically most divergent population T1, pairs spent more time close to simulated intruders and exhibited stronger vocal response (singing rate and phrase type rate). In the more recent and less divergent population T2, pairs exhibited overall low levels of response and approach to the stimuli.

4.4.1   Acoustic divergence in translocated populations

Our data revealed significant variation in vocal repertoire size and repertoire sharing which indicates that the sub-sets of vocalizations retained from the large source population have been different from the start of separation (founder effects, c.f. Baker 1996; Parker et al. 2010) and/or that vocal repertoire use has diverged over the 5–8 years of separation. The latter effect may be due to random changes that occur independently of population size or may be attributable to the small cluster of individuals (see e.g., Lynch & Baker 1994; Lachlan and Slater 2003). Studies on Dupont's larks (*Chersophilus duponti*) in Spain (Laiolo & Tella 2005; 2007) also showed that with a reduction in male numbers, associated with a reduction in habitat fragment size, repertoire sharing among neighbours increased while individual and population repertoire sizes became smaller, as in our two

translocated kōkako populations. The patterns in the Dupont's larks were explained by the likely severe competition for limited resources among neighbours in remnants of suitable habitat. Laiolo & Tella (2005; 2007) argued that the increased value of vocal interactions for mediating conflicts over resources could have resulted in more repertoire sharing within population fragments. We believe that the kōkako may be comparable to the larks in that a lack of vocal interactions and lack of connectivity may explain divergence among population fragments in vocal repertoire use, while limited resources may play a particularly strong role in one of the translocated populations (T1). The reduced repertoire size in birds from both translocated populations relative to birds in the source population may therefore be related to increased levels of territorial interactions or just a reduced number of long-term neighbours. The latter could be rather a general phenomenon of small clusters of birds separated from larger clusters by unsuitable habitat (Koetz et al. 2007; Rivera-Gutierrez et al. 2010).

Not only what kōkako sing in translocated populations, but also how they sing differs from kōkako in the source population. Geographic variation in acoustic structure may concern ecologically neutral features related to random changes yielding patterns of isolation-by-distance (reviewed in Podos & Warren 2007), to variation in the impact of sexual selection (Prumm 1998; Price & Lanyon 2002) or to variation in environmental selection pressures (Wiley & Richards 1980; Slabbekoorn & Smith 2002). In general, relatively open woodland may select for relatively high, frequency-modulated songs with rapid repetitions of simple song elements while more dense vegetation may select for lower frequency notes of longer duration (reviewed by Slabbekoorn et al. 2002; Barker 2008). In addition, the combined vocalizations of animal communities in different habitats may yield variable noise profiles which can impose severe and divergent selection regimes (e.g. Ryan & Brenowitz 1985; Slabbekoorn 2004; Dingle et al. 2008). The habitat in which the translocated populations survive was selected to be similar to the original habitat and former distribution of kōkako (Lavers 1978; Leathwick et al. 2004) and is currently still highly similar to the habitat for the source population (Leathwick et al. 2003; Walker et al. 2006). We therefore believe that the higher and shorter notes in the translocated populations are most likely due to founder effects, random changes over time, or a reduced role for sexual selection, but not due to differences in environmental selection pressures.

4.4.2 Response variation in reciprocal playbacks

Despite significant variation in the nature of the playback response between one of the translocated populations and the source population and relatively low response levels in the other translocated population, there was no evidence for discrimination against foreign population songs in any of the populations. There are many studies showing reduced response levels to foreign population songs associated with geographic distance (Searcy et al. 1997; Nelson & Soha 2004) or ecological divergence (Dingle et al. 2010; Ripmeester et al. 2010). The kōkako from our recorded populations all originated from the same geographic area and reside currently in highly similar habitat, which may explain the lack of similar patterns of non-local discrimination. However, changes in songs over time within the same population may also yield reduced response level as reported for white-crowned sparrows (*Zonotrichia leucophrys*) tested with playback of historical recordings (Derryberry 2007). Although the sparrow recordings were more than twenty years old and the kōkako birds have been separated by translocation for less than ten years, recognition among kōkako could be affected by the relatively small number of translocated birds and the dramatic social changes inherent to translocation (capture and forced divorce, differing periods of captivity, and resettling in a new territory). Nevertheless, although we only have two samples of translocated populations which do show significant changes in vocal behaviour, there is no indication yet of a reduction in mutual response levels.

A study on the North Island saddleback (*Philesturnus carunculatus*) from New Zealand, closely related to kōkako, did reveal discrimination between local and non-local songs via playbacks, albeit after longer periods of separation (Parker et al. 2010). The saddlebacks are confined to off-shore island populations, and birds in a single translocated population were tested using playback recordings from several different source populations. The separation in time since translocation varied from 21-40 years and included multi-level translocation events in which birds were not only translocated from an original source population but also from successfully translocated populations. The saddleback study suggests that one or more bottlenecks or a few decades of separation can be enough to yield divergence in both song and response for a system which is highly similar to the translocated populations of kōkako. Therefore, we believe

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that given the current divergence in song features and vocal response behaviour among the two translocated populations and the source population, it is a matter of time for the kōkako to also develop population-dependent song discrimination.

4.4.3   Implications for conservation

Geographic variation in songs that are used for territorial defence and mate attraction can be important for conservation in several ways (Håkansson & Jensen 2005; Laiolo & Jovani 2006; Laiolo 2010). Independent of the causes, reduced repertoire sizes and increased repertoire sharing rates may have consequences for individual reproductive success, possibly leading to lower efficiency in deterring competitors or in attracting and stimulating mates. Lower vocal activity levels may also lead to reduced immigration rates of dispersing birds in already small clusters of active breeders (Laiolo et al. 2008). This would restrict natural dispersal towards translocated populations from natural or other translocated populations. Furthermore, song variation among populations is also perceived by the birds themselves and results in lower response levels to non-local songs; hence the potential for successfully immigrating birds may further deteriorate and reduce gene flow as well as connectivity among populations. Reports of translocated kōkako populations with a mixture of individuals from multiple source populations in which birds paired up assortatively based on source population origin (Rowe & Bell 2007; D. Bradley, Univ. of Waikato, unpublished data), confirms that despite currently persisting acoustic recognition, the present numbers of birds may not reflect actual numbers of active breeders.

Consequently, we believe that kōkako translocations are most likely to be successful if source populations are sufficiently large or close together to provide a culturally homogenous reservoir of translocatable birds. Persistent establishment of translocated populations are most likely when habitats are similar to those of the source population and frequent influx of individuals occurs by subsequent translocations or, if possible, natural dispersal between areas. The current playback results indicate that periods of up to a decade of separation are unlikely to impose restrictions. However, longer periods of isolation at a small population size may reduce the chances of translocated populations becoming independent of artificial immigration. Obviously, we still only have very limited insight into this

question from the studies on kōkako and saddlebacks (Parker et al. 2010), and divergence in song and perception may depend on many factors such as species-specific life history parameters, vocal heritability and learning capacity as well as the impact of ecological selection pressures (Slabbekoorn & Smith 2002). More studies are required to investigate rates of acoustic divergence, emergence of discrimination tendencies, and their impact on individual reproductive success and population viability (Clemmons & Buchholz 1997; Newton 2003; Laiolo et al. 2008; Cardoso et al. 2009).

4.5   Conclusions

Our study shows the potential importance for bioacoustic analyses during translocation efforts. The reduced variability in vocal behaviour, reported here for two translocated kōkako populations after less than a decade of separation, has the potential to undermine population viability but also to signal critical stages of establishment to conservationists. The divergence of recognition in translocated saddlebacks after more than two decades of separation (Parker et al. 2010) and the lack of discrimination in our translocated kōkako provides us some insight into the pace at which song-dependent behavioural barriers may arise which may also play a critical role in population viability through the impact on connectivity among different translocated and natural populations. More studies are required in terms of both the number of translocated populations within species and the number of different species to form a better picture of the optimal conservation approach. We now need more quantitative insight into the impact of vocal variation on for example the minimum number of individuals required and the maximum geographical or ecological distance acceptable for successful colonization or recolonisation of suitable habitat. Besides the relevance for investigating cultural variation in conjunction with genetic variation due to its potential impact on population viability, bioacoustic analyses may provide an important and relatively non-invasive tool for monitoring and predicting success of extreme conservation efforts such as translocation.

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Chapter 5

Summary and conclusions

By Sandra V. Valderrama

Te Urewera National Park 2009

In this thesis, I explored the topics of cultural diversity and dialect formation in fragmented populations of the North Island kōkako. More specifically, I investigated three fundamental questions: (i) Are there distinctive population-specific dialects that reflect patterns of historical association or proximity? (ii) Are fragmentation and population size significant ecological factors influencing song variation? (iii) What are the potential early effects of isolation on song divergence and the response of kōkako to divergence?

Chapter 2 explored the extent of cultural diversity in kōkako song and relationships among surviving kōkako populations, taking into account geographic distance. I performed dialect comparisons based on repertoires of song traditions and specific acoustic characteristics. In doing so, I observed and quantified discrete dialects across kōkako populations. However, when comparing song cultures between populations, I did not detect a relationship with linear geographical distance or historical patterns of isolation by habitat loss and fragmentation. Although historical pattern of isolation did not appear to explain patterns of song similarity, fragmentation effects may be more apparent at a local level. Vocal drift may have blurred relationships after a long period of separation. Therefore, I evaluated microgeographic variation of song repertoires to elucidate the role of population connectivity in song traditions. I studied specific continuous and discontinuous populations, along with individual dispersal data. From these analyses, I illustrated how fragmentation can lead to cultural variation in patchy populations, and how it may influence the formation of dialects. However, I found that tenuous connectivity is not a barrier to juvenile dispersal and hence genetic flow. Isolation and patch size influence interactions between organisms and behaviours, such as dispersal, that may determine distribution, abundance, and structure of populations.

Studies of habitat fragmentation effects have been mainly based on direct evidence from ecological processes, such as changes in population density and reproductive success (e.g., Stouffer 1995, Stephens 2003, Martinez-Morales 2005, Arriaga-Weiss et al. 2008). Only recently has indirect evidence been investigated, employing molecular techniques to determine patterns of genetic change. However, as genetic change occurs gradually, long-term studies are necessary to detect the effects of habitat fragmentation on populations. In contrast, cultural variation can occur rapidly, due to multiple transmission opportunities (i.e.,

vertical, horizontal and oblique; Cavalli-Sforza & Feldman 1981). Cultural variation can therefore represent more immediate evidence of the overall impact of natural and human-induced fragmentation upon populations (Brainard & Doupe 2002; Laiolo & Tella 2005, 2006). Thus, cultural variation in kōkako song (described in chapter 2 and 3) suggests, for the first time in this species, effects of fragmentation that are yet to be reflected in genetic differences among populations.

An important ecological factor that can affect cultural transmission and influence the emergence of song variation is population size. Changes in abundance are especially pertinent for kōkako populations as they have undergone not only isolation but also contraction (i.e., associated with predation) followed by recovery due to management actions. Similar to effects on genetic diversity, bottlenecking events can lead to the degradation and/or emergence of cultural diversity. In Chapter 3, I demonstrated that cultural erosion occurs in small populations, evidenced by reduced song complexity and singing versatility; erosion was especially prominent in translocated populations. Thus, in addition to finding less predictable syntax in smaller populations, the data indicated that divergence in song traditions is probably best understood as a result of founder effects, 'withdrawal of learning' (Thielcke 1973), and a neutral model of cultural divergence due to drift and differing cultural trajectories (Lynch & Baker 1993; Lynch 1996; Grant & Grant 1996, 1997).

In addition to discussing evolutionary causes and consequences of behavioural variation, cultural variation over a short timescale is an important process in biodiversity conservation. For instance, greater behavioral diversity might represent greater flexibility of a population or an individual to cope with fluctuating environments (Blumstein &Fernádez-Juricic; Kappeler & Kraus 2010). Individuals from culturally eroded small populations of kōkako (Chapter 3) may have more difficulty adjusting to new social environments as represented by translocation scenarios. Implications of reduced song diversity in small isolated populations needs investigation.

An important question that emerges from discovering clearly distinctive dialects in isolated populations (Chapter 2), along with remarkable rapid divergence in small translocated populations, regards the significance of this variation for individual birds. Territory defense and mate attraction depend on

effective communication, ultimately affecting survival and reproductive success. However, we know very little about how individual kōkako respond to non-local song, which may be crucial for compatibility (e.g., pair formation) when individuals from different populations are brought together for conservation purposes (e.g., in translocations). Chapter 4 reveals that divergence in vocal behaviour has occurred between two recently isolated translocated populations and their source. Moreover, response intensity to simulated secondary contact varied across populations. However, although differential response levels have already emerged, current levels of acoustic and song repertoire divergence has yet to result in discrimination in the context of territorial interactions.

Variable behavioural responses between translocated and source populations (Chapter 4) shed light onto the potential effect of cultural erosion – prevalent in small populations – and impaired social environment on response flexibility to social changes. Low song diversity and weak vocal response in small populations of kōkako could be further associated with stronger stress responses, reduced fitness and low survival (Reid et al. 2005; MacDougall-Shackleton et al. 2009). Perhaps, the impoverished social environment in depleted populations of kōkako determines both song development and adult stress responsiveness. In small populations delimited by small patches of habitat, social behaviour can be also affected by intense competition (Chapter 4). As a result, intense aggression and increased stress levels with associated low thresholds for agonistic behaviours may occur in crowded isolates where competition is intense (Håkansson & Jensen 2005). Overall, in small habitat fragments, initial cultural erosion as well as highly frequent singing contests for territories and mates (as populations reach carrying capacity) may drive song divergence and changes in behavioural flexibility or thresholds among populations under differential selection – relaxed selection with low competition and low aggression, versus strong selection with high competition and high aggression.

In summary, the combination of observational and empirical data presented here revealed that independent cultural evolution of song traits rapidly occurs. Isolated populations of kōkako are subject to founder effects and disruption of 'cultural connectivity' by a range of ecological events (e.g., bottlenecks, habitat fragmentation, and low survival due to predation). This detailed study of kōkako song cultures, over a large scale, is an example of the enormous relevance of

behavioural ecology at a landscape level, in the face of population fragmentation (Lima & Zollner 1996).Whether the observed vocal variation in isolated populations directly affects fitness and viability of small populations, and whether this variation may represent a premating isolation barrier between the most distinct populations described in this thesis, will need further detailed examination and experimental approaches. Future research on the impact of song variation is imperative, as secondary contact between populations occurs when conservation management involves translocations from different populations either to new areas or existing populations.

5.1   Future directions

This thesis suggests interesting future avenues of research to understanding vocal divergence and its consequences. In light of the three interacting mechanisms involved in the communication system of vocal learners (Fig. 1.1), some research questions on the behavioural ecology of kōkako are suggested:

5.1.1   Adaptation, mechanical constraints and song cultures

The song variation found between surviving (Chapter 2) and translocated kōkako populations (Chapter 4) requires further investigation. Acoustic adaptation to habitat, morphological variation, and sexual selection could be also involved in song cultural divergence between populations (e.g. Grant & Grant 2002; Slabbekoorn & Smith 2002; ten Cate et al. 2002; Podos et al. 2004; Badyaev et al. 2008; Derryberry 2009). Although I did not include measures of habitat – which is qualitatively similar among the study areas – or body size in Chapters 2 and 4, there is a possibility that the spectral song attributes observed are related to differences in habitat and/or morphology. Sound properties, such as long-distance transmission, omnidirectionality and penetration, have important implications for the transmission of acoustic signals in different habitats and environmental conditions (e.g., wind, temperature; Morton 1975; Wiley 1991; Slabbekoorn & Smith 2002). Therefore, selection for effective communication between sender and receiver may result in divergent evolution of signal design to reduce acoustic degradation in different environments (Wiley & Richards 1982; Endler 1992;

Slabbekoorn et al. 2002). Although forest structure may be similar among kōkako populations, acoustic transmission studies in different environmental conditions (e.g., wind, rain, humidity and temperature) and terrain, would provide insight into song variation due to acoustic adaptation.

Differences in body size can also result in acoustic differences. It is also possible that the spectral frequency shifts observed in translocated populations (Chapter 4) are related to changes in morphology, which can occur in small populations susceptible to genetic drift (Crow & Kimura 1970; Whitlock & Barton 1998). For example, low frequency song elements may be particularly associated with larger body size or better condition (Appleby & Redpath 1997; Galleoti et al 1997; ten Cate et al. 2002; Geberzahn et al. 2009). Higher frequency song elements in translocated populations might reflect smaller body sizes. Although body-size data for these populations was limited, future research including morphological data would contribute to understanding the effect of genetic traits on song divergence. In addition, sex differences in morphology within and between populations are also unclear as song types are not sex-specific. However, kōkako males are known to be typically larger than females (Innes et al. 2006). Although I attempted to pinpoint distinctive spectral acoustic patterns between males and females (Appendix D, CD #7), data from the limited number of banded known-sex individuals from different populations indicated little sex differentiation overall. Establishing an association between morphology and song variation would assist in the use of bioacoustics as a non-invasive technique to monitor additional population changes (e.g., demographic).

5.1.2 Learning mechanisms and individual plasticity

I indicated in Chapter 2 that kōkako appear to learn songs after dispersal. However, further research on the learning process would help to better understand song variation and the influence of social experience (see juvenile imitation in Appendix E). For example, exactly when kōkako learn songs, and whether learning is based on experience or age and varies with sex, may have important implications for individual flexibility and adaptation to short-term environmental changes. Although I did not observe substantial song changes in translocated individuals after a period of isolation, I could only compare these songs with

current source population repertoires; original individual repertoires before translocation were not recorded (Appendix C). Detailed song studies should include banded individuals in source populations, as well as translocated individuals, to investigate juvenile and adult learning plasticity over a longer period. In the absence of tutors, for instance, the juvenile sensitive phase of song learning could be extended to adulthood (Eales 1985; Slater et al. 1988; Livingston et al 2000). In addition, steroid hormones may also determine sex-specific song development and plasticity (Konishi 1985; Holloway & Clayton 2001). Low testosterone levels are characteristic during the song-learning sensitive phase, while a testosterone increase promotes song crystallisation (e.g., Marler et al. 1988; Brenowitz 2008). The influence of hormonal levels in learning plasticity means that altered hormonal (e.g., testosterone) levels by social modulation (e.g., number of tutors) could potentially stimulate or inhibit song learning in both adults and juveniles. For example, induced high testosterone levels in juveniles can generate crystallisation of abnormally simple songs (Korsia & Bottjer 1991; Whaling et al. 1995). In depleted populations of kōkako, with reduced social stimulation (e.g., low number of tutors with unbalanced sex-ratio), not only stress but also sex-hormone levels are perhaps substantially altered. It is possible that restrained territorial and sexual contests stimulate only low levels of steroid hormones, which could explain low aggressive responses (Chapter 4). Loose syntax in small populations is perhaps an indication of reduced social interaction and low levels of testosterone (Plamondon et al. 2010). Expansion of quantitative song analysis, in this thesis, into the learning process and plasticity by social modulation at multiple time scales can illuminate changes (e.g., physiological and ethological) under varying ecological conditions and cultural evolution (Lipkind & Tchernichovski 2011).

5.1.3 Cultural transmission

At a population level, the rate and pattern of song change over time (e.g., through copy-error and innovation rates) remain to be fully investigated. I observed historical changes in song repertoires from a limited sample within two populations (Appendix C). However, continued research, from the large sample collected for this thesis, would help identify rates of cultural evolution under various ecological conditions (e.g., in populations that differ in size or dispersal opportunities). On the basis of this thesis, I suggest that a better understanding of the divergence of kōkako cultures requires detailed information on multigenerational changes in vocal parameters to yield a cultural model of song transmission, including: (i) rates of innovation, (ii) song selection mechanisms (e.g., Mesoudi & Lycett 2009) and convergence that lead to song sharing (Bjorn 2009), (iii) biases in learning preferences and transmission (e.g., Jablonka et al. 1998; Cavalli-Sforza & Feldman 1981; Richerson & Boyd 2005; Byers et al. 2010), and (iv) individual variation in innovation and social-learning abilities (e.g., personality). As culture can alter evolution by generating rapid cultural adaptation to local environments, knowledge on social learning and transmission may provide intriguing clues concerning the interplay between genes and culture (Richerson & Boyd 2005).

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Appendix A

Details of song structural analyses between six surviving kōkako populations (Chapter 2)

Table A. 1. Correlations between each song structure parameter measured and the functions that distinguish among all six populations in the DFA. The DFA distinguished significant differences in acoustic characteristics between population samples.

Variable	Function 1	Function2
Phrase duration (s)	0.178	0.331
Minimum frequency (kHz)	-0.079	-0.099
Mean pitch goodness	0.044	-0.005
Peak frequency of the loudest harmonic	-0.003	0.170
Mean amplitude modulation	0.206	-0.006
Mean entropy	0.148	-0.225
Mean frequency	-0.087	-0.117
Mean frequency modulation	0.107	-0.051
Peak frequency	-0.199	-0.048
Number of syllables	0.205	0.095
Maximum frequency	0.109	0.181
Eigen value	6.845	4.065
% variance	52.3	31.0

Table A. 2. Differences in song structure measurements between six surviving kōkako populations.

Variable	Mangatutu	Mapara	Mataraua	Otamatuna	Rotoehu	Waipapa	Kruskal-Wallis H	*p*
Number of syllables per phrase	1.75 ± 0.1	2.24 ± 0.20	2.10 ± 0.06	2.33 ± 0.18	2.01 ± 0.17	1.92 ± 0.09	9.96	0.08
Phrase duration (s)	530.96 ± 14.36	684.67 ± 33.90	550.53 ± 15.37	679.32 ± 31.43	692.62 ± 47.85	651.77 ± 40.78	16.82	0.004
Peak frequency (Hz)	1465.70 ± 71.24	1424.73 ± 29.85	1438.97 ± 46.06	1283.82 ± 25.21	1396.11 ± 49.40	1442.36 ± 32.05	9.54	0.09
Peak frequency of loudest harmonic (Hz)	2040.10 ± 69.17	2130.59 ± 117.89	1899.10 ± 62.40	2135.00 ± 81.18	1749.20 ± 115.58	2047.44 ± 96.27	10.31	0.07
Minimum frequency (Hz)	682.32 ± 27.63	670.14 ± 27.02	656.81 ± 21.16	625.60 ± 15.20	570.39 ± 18.87	595.02 ± 12.60	15.23	0.01
Maximum frequency (Hz)	1182.40 ± 34.13	1519.98 ± 81.54	1348.44 ± 89.28	1509.96 ± 87.18	1389.81 ± 116.87	1348.43 ± 34.23	12.09	0.03
Mean frequency (Hz)	1506.59 ± 45.06	1437.90 ± 27.00	1488.03 ± 34.79	1407.74 ± 39.33	1546.99 ± 46.43	1474.34 ± 44.21	7.67	0.18
Frequency modulation (absolute estimate)	6.62 ± 0.66	6.83 ± 1.34	7.99 ± 0.86	8.56 ± 0.99	7.11 ± 1.11	6.79 ± 0.64	2.9	0.71
Amplitude modulation (1/ms)	0.003 ± 3.03E-05	0.003 ± 9.81E-05	0.003 ± 4.70E-0.5	0.003 ± 0.32E-0.5	0.003 ± 7.30E-05	0.003 ± 1.08E-04	10.02	0.07
Entropy	-4.62 ± 0.22	-5.23 ± 0.36	-4.23 ± 0.16	-4.03 ± 0.32	-4.32 ± 0.12	-4.69 ± 0.10	11.73	0.04
Pitch goodness	123.25 ± 2.96	119.23 ± 7.00	124.01 ± 4.05	131.26 ± 13.03	133.00 ± 5.07	129.00 ± 6.19	6.71	0.24

Appendix B

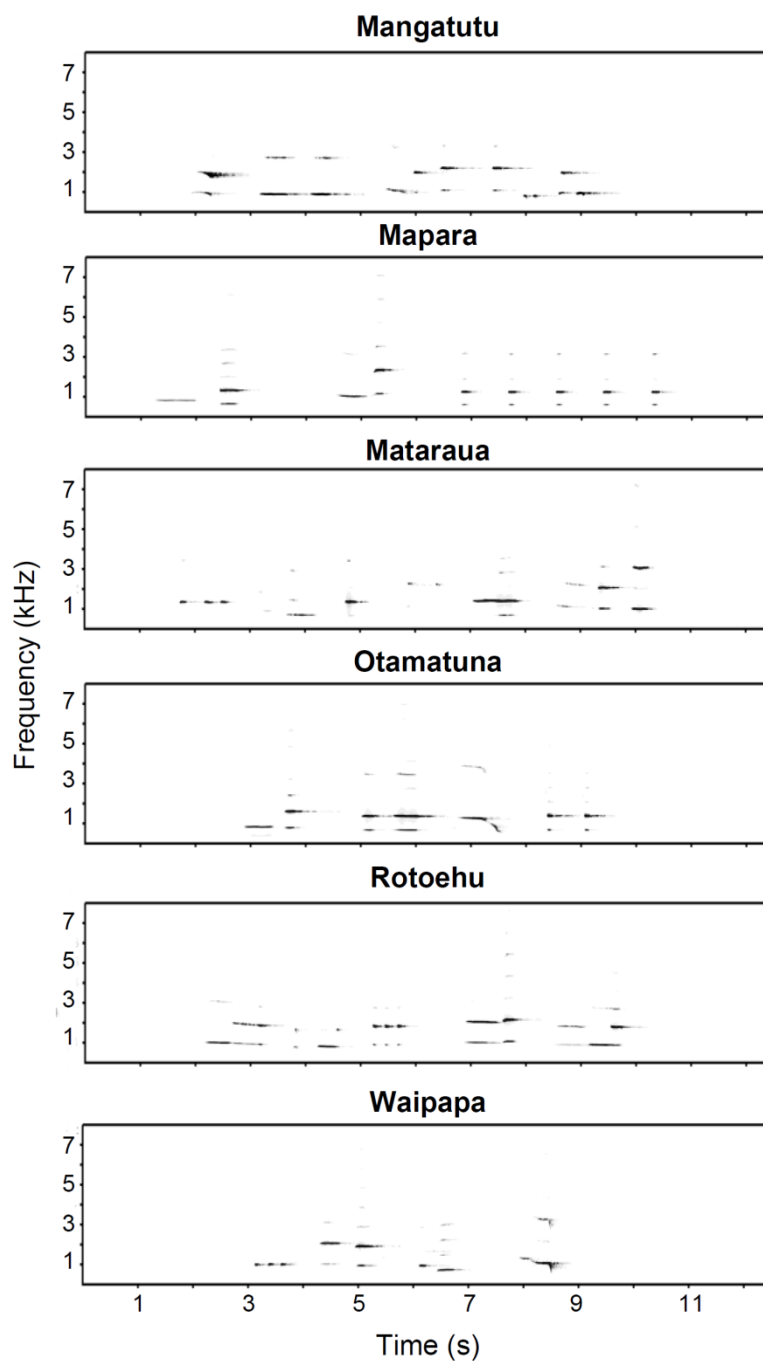# Typical song traditions in six kōkako populations (Chapter 2)

Figure B. 1. Sonograms of songs from six populations (CD #6).

Appendix C

Vocal drift over time in two kōkako populations

C. 1. Historical within-population song differences

Surviving populations were vanishing when intensive management started. However, they have been increasing since the implementation of management to date (Chapter 3; Fig. 3.1). I analysed a limited sample of sound recordings from Mapara and Otamatuna populations collected in 1997 and 1998 respectively. I compared historical with current song to investigate vocal drift after 11-12 years, a period when remarkable demographic changes occurred because of intensive management of predators.

Otamatuna appeared to have undergone highly significant vocal drift shown by a strong association between vocal similarity (as measured by Jaccard index, see details in Chapter 2) and time of recording (1998 versus 2009; Mantel-test $r = -0.74$, $p < 0.001$; Fig. C.1). The association between vocal similarity and time of recording was still significant, but less clear, in Mapara (Mantel-test $r = -0.12$, $p = 0.05$; Fig. C.1). In Mapara, pairwise repertoire similarity between years (0.31 ± 0.01) was similar to within-population similarity in 2009 (0.36 ± 0.02, from Chapter 2). A more dramatic difference, between within-period sharing levels for 1997 versus 2009, might reflect population growth within each of the three habitat portions; hence increasing song diversity and lowering song sharing levels across all portions of Mapara Reserve. Although I included repertoire size in pairwise similarity, greater diversity within the 2009 period could also explain higher between-periods similarity. In Otamatuna, lower between-period repertoire similarity (0.24 ± 0.01) may be explained by a more rapid population increase, in comparison with Mapara. Greater repertoire diversity within Otamatuna in 2009 (0.44 ± 0.01, from Chapter 2), and still low similarity with 1998's repertoires, suggests that vocal drift has occurred rapidly. The between-period similarity index is interestingly similar to that of the average between six surviving populations (0.19 ± 0.03, from Chapter 2). These results suggest that population trends over time may influence how quickly vocal drift occurs.
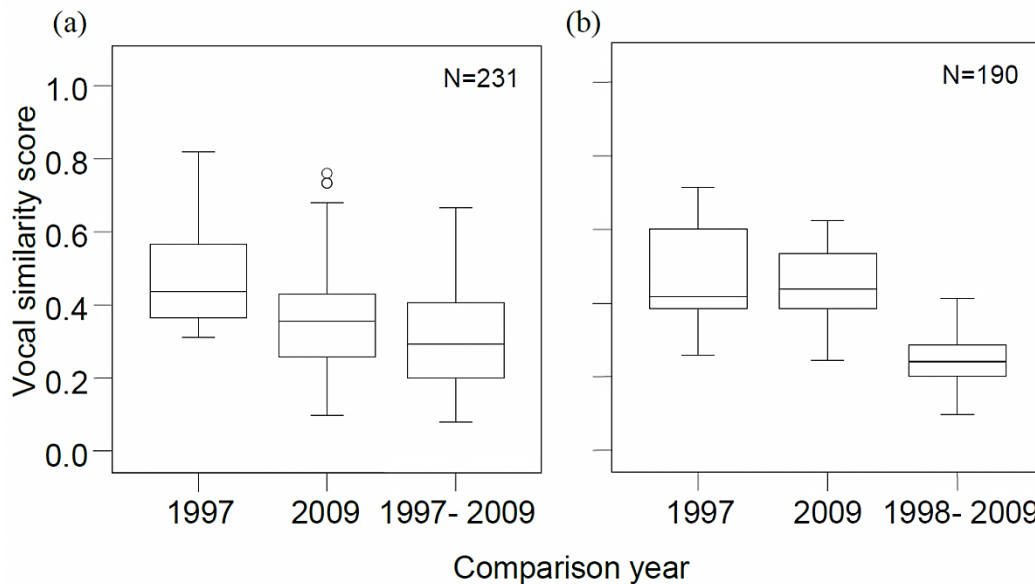
Figure C.1. Box plots of pair-wise vocal similarity of old and current song in two populations: (a) Mapara (Kruskal-Wallis test = 26.39, p < 0.001), and (b) Otamatuna (Kruskal-Wallis test = 113.95, p < 0.001).

C. 2. Repertoire changes in translocated individuals

I compared 6 pairs formed from translocated birds transferred in 2007 to the Hunua Ranges with 10 pairs from the source population (Mapara; Chapter 1; Fig. 1.2). I did not find significant differences in vocal similarity (Mantel test: r = -0.09, p = 0.15). I found 0.40 ± 0.04 song sharing between translocated pairs and 0.30 ± 0.01 repertoire sharing between translocated and source pairs. Similarly, pairs within the source population shared 0.31 ± 0.02 of phrases. I did not find evidence of substantial changes in the song repertoires of translocated birds that could suggest incorporation of new song elements by these adult birds.

Appendix D

Male and female kōkako song

D. 1. Methods

I used a logistic discriminant analysis model to test the accuracy of sex determinations based on 12 selected acoustic variables (see Chapter 2 for details) measured from a sample of 392 phrases. Logistic regression suits data in which dependent variables have two values (in this case male and female) and generates predicted values of group membership, while it does not assume a linear relationship between dependent and independent variables, or equal variances. My sample included phrases from 30 known-sex individuals (220 phrases from 15 males and 172 phrases from 15 females). Gender was reliably determined by observing singing behaviour and colour-banded individuals whose sex had been previously determined by breeding behaviour or DNA procedures. Highly correlated variables were excluded to avoid redundancy.

I ran my logistic regression model with a balanced subset of six randomly selected phrases: six female phrases and six male phrases per population (see examples in Fig. D.1 & D.2). I subsequently cross-validated this analysis with the remaining phrases to verify the accuracy of sex classification by the logistic model. In addition, I used a Cochran-Mantel-Haenszel test to inspect if sex classification accuracy by the logistic model was also dependent on population identity.

D. 2. Results

The logistic regression model correctly assigned 78.57 % of female phrases and 60.64 % of male phrases (Fig. D.3), with a corresponding sex bias of 18%. The proportion of phrases assigned to the correct sex differed among populations (Cochran-Mantel-Haenszel test: $\chi^2 = 52.08$, df = 1, p < 0.0001). The likelihood ratio test indicated that number of syllables ($\chi^2 = 4.47$, df = 1, p = 0.03), number of

notes ($\chi^2 = 10.2$, df = 1, p = 0.001), and main minimum frequency ($\chi^2 = 73.11$, df=1, $p < 0.0001$) contribute importantly to sex classification.
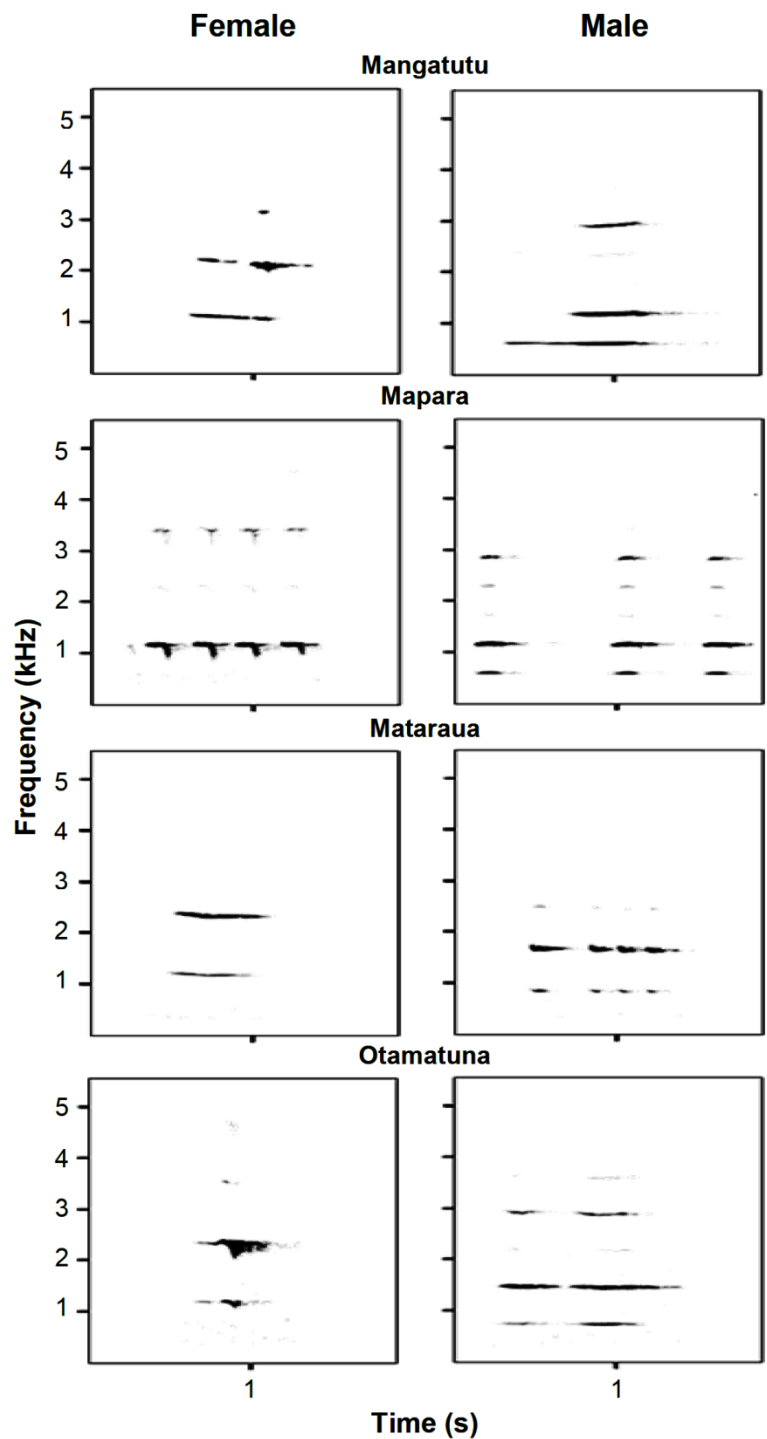

Figure D.1. Examples of female and male phrase types from four populations (CD #7).
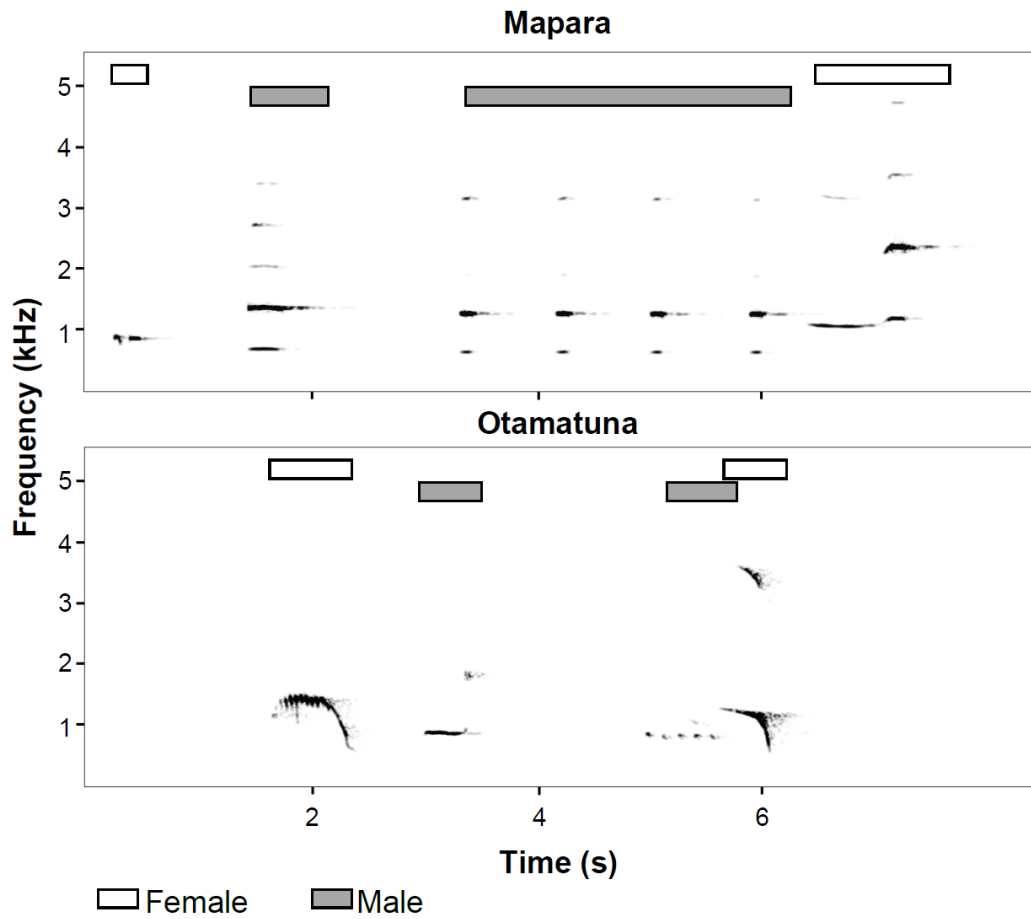
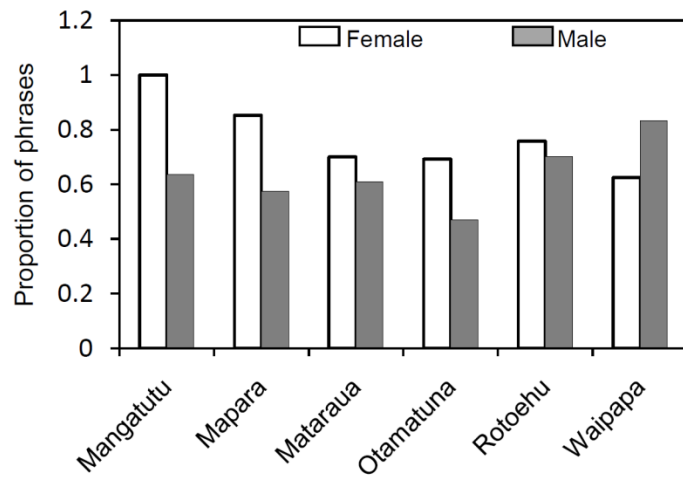Figure D. 2. Female and male contributions in duet examples from two surviving populations (CD #8).

Figure D. 3. The proportion of phrases in each population correctly assigned to the corresponding sex by cross-validation with the logistic regression model.

Appendix E

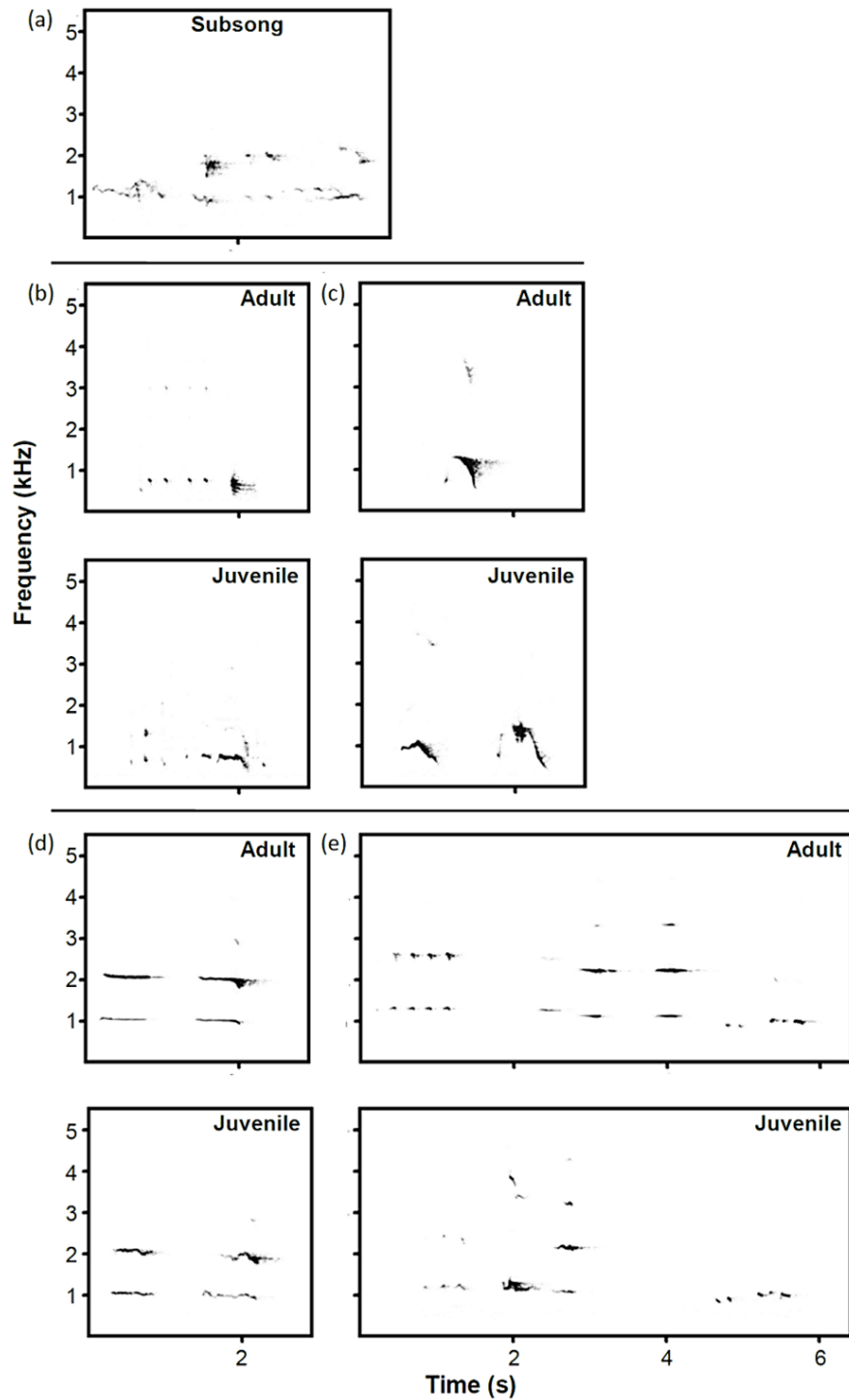# Kōkako adult and juvenile song imitation

Figure E.1. Sonogram samples of adult and juvenile song (CD #9): (a) subsong, (b) soft call, (c) loud phrase/syllable type, (d) loud phrase type, (e) theme.