Evolutionary Significance and Conservation Implications of Vocal Dialects in North Island Kōkako (*Callaeas wilsoni*)

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The kōkako stole its voice from the bag-moth. Our story is that the goddess of flute-music embodied her secret in the bag-moth. So in order to get the heavenly sound of the flute to beautify its own voice, the kōkako ate the bag-moth. And now, to keep that sound in its voice it must keep on eating bag-moths – the little flutes hanging from the branches. In this way, the kōkako has kept the secret and become the guardian of flute-music for life.

– Account of Maori oral tradition by Syd Morrison *in* Morris R, Smith H, 1988. Wild south: saving New Zealand's endangered birds. New Zealand: TVNZ in Association with Century Hutchinson.

Abstract

Kōkako (*Callaeas wilsoni*) are endangered, duetting songbirds endemic to New Zealand and are confined to a small number of managed mainland reserves and offshore islands. Each fragmented population exhibits distinctive vocal traditions. Conservation of the species is centred on intensive site management of introduced mammalian predators – the current leading cause of kōkako population decline – followed by re-establishment of populations through translocation. Translocated populations are often sourced from multiple areas, leading to an artificially created scenario of secondary contact between behaviourally diverged populations.

I studied the consequences of kōkako song traditions, and the effect of population-specific behaviours on conservation of the species. During a transfer of 20 birds from two distinct "song neighbourhoods" (c. 25% between-neighbourhood phrase sharing), I explored the utility of neighbourhood specific acoustic playback as a conservation tool in preventing excessive post-release dispersal. I found that birds dispersed less far than predicted by a random walk model, yet were no more attracted to same- than different-neighbourhood song playback. These results suggested that while playback appeared to reduce dispersal, this effect was not driven by neighbourhood-specific song. Following release, kōkako also used the available habitat disproportionately, preferring to remain in the short term, and to establish breeding territories within a forest type similar to that where they were caught. The vocal differences I detected between the neighbourhoods at the source sites were also insufficient to promote assortative mating following release. The findings of this experiment confirmed that neighbourhood-scale song variation does not act as a barrier to gene flow, or inhibit post-translocation population establishment.

To assess whether more distinct vocal differences between populations (c. 5% between-population phrase sharing) represent more salient signals to kōkako, I performed reciprocal stereo playback experiments in two populations frequently used as translocation source sites. In one experiment I tested for discrimination between local and foreign dialect duets and found that pairs responded vocally to local duets with less delay, and produced more song phrases, with a lower diversity, compared to playback of foreign duets. This suggested that local song represented more of a threat to pairs than unfamiliar song. In a second experiment I presented pairs with two types of synthesised local-foreign mixed-dialect duets; each stimulus differed depending on the sex of the local duet stimulus component. I found that pairs responded with equal overall strength to both stimuli, and did so in a qualitatively similar way to pure local duets. As pairs did not discriminate between these stimuli, this indicates that if mixed-dialect pairs form, they should be able to effectively communicate with, and defend against territorial intruders. From an evolutionary perspective this further suggests that dialectal differences might not prevent gene flow in kōkako if pair formation between dialects can occur. Importantly, these findings also suggest that animals translocated for conservation purposes need not necessarily exhibit homogeneous cultures to acquire and defend resources.

Sexual selection leading to positive assortative mating based on song dialect may act as an isolating barrier to gene flow, thus promoting speciation. From a conservation perspective this process could be problematic by hindering population establishment following translocation of a small number of individuals from multiple sources. To assess this tendency in kōkako, I harnessed an existing 18-year data set from reports prepared by the New Zealand Department of Conservation documenting multi-source translocations to six sites from 11 source populations. Based on these reports, in each breeding season at each site I compiled a list of the possible same- and mixed-dialect pairs that could have formed, which I then compared to the actual pairs in each season. In doing so, I statistically confirmed that, following release, kōkako pairs form assortatively based on dialect more often than expected by chance. However, mixed-dialect pairs did form in low numbers at two sites, either when an existing "core" population was present at the time of translocation, or following the release of a captive-reared sub-adult bird with potentially plastic song. These results suggest that sufficiently large differences in a sexually selected behavioural trait, such as song, can inhibit gene flow between populations.

Taken together, my findings suggest that vocal variation among fragmented, allopatric populations may influence a species' cultural and genetic history, and could affect the success of conservation strategies. However, as kōkako pairs can form across dialects, and postnatal dispersal sometimes occurs between areas with different song traditions, complete genetic isolation of populations is unlikely to occur. Further research on the timing of song-learning in kōkako, dispersal patterns, and vocal plasticity in territorial adults will greatly advance our knowledge base and shed light on the function and conservation implications of song dialects in kōkako.

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Chapter 1: General Introduction

1.1 Communication in birds

Communication plays a central role in the ecology and evolution of animal societies. All animals must survive and reproduce, and communication facilitates these basic life processes by allowing individuals to locate conspecifics, attract breeding partners, and mediate social interactions such as resource defence and mate choice. Communication can be defined as the intentional production and transmission of sensory information from a sender to a receiver, which is conveyed in the form of signal (Smith, 1965; reviewed in Bradbury and Vehrencamp, 2008 and 2011). When we think of communication in birds, bright colours and melodious songs first come to mind. In fact, visual communication (Hill, 2006; Hill and McGraw, 2006) and auditory communication (reviewed in Catchpole and Slater, 2008) are the most highly developed ways of transferring information between birds. Examining the ways in which animals communicate, and the specific functions of different animal signals, enhances our appreciation of both the ecological and evolutionary processes that govern behaviour.

The tremendous diversity of vocal signals produced by birds reflects the diversity of the approximately ten thousand avian species on earth (Clements, 2009). Owing to this diversity, avian bioacoustics has received considerable attention from the scientific community (e.g. Kroodsma et al., 1996; Marler and Slabbekoorn, 2004; Catchpole and Slater, 2008). Bird song varies in both form and function between taxa. Given that songbirds (and several other avian groups, see section 1.2) learn their songs, it follows that variation exists due to different social and physical environments that young birds experience in the formative song learning period (Hultsch and Todt, 2004). The learning process can involve mistakes, innovations, and improvisations that can lead to changes in song structure between individuals. The function of song also varies. Research in temperate environments demonstrates that male birds use song in two main ways: in order to attract females, and to defend territories (Catchpole, 1989).

Experimental support for these two functions of bird song can be found in many published studies. For example, in a groundbreaking study of pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*Ficedula albicollis*) in Sweden, Eriksson and Wallin (1986) showed that female flycatchers choose nest boxes that contain a loudspeaker broadcasting male song over silent nest boxes (for a similar study on European starlings, *Sturnus vulgaris*, see Mountjoy and Lemon,1991). These and many other studies highlight the importance of song in mate attraction. The territory defence role of bird song was first explicitly tested by Goransson and others (1974), who showed that thrush nightingales (*Luscinia luscinia*) frequently invaded neighbours' territories after the neighbour had been experimentally removed, but rarely invaded territories where the neighbour was replaced with speakers broadcasting male song. Krebs (1977) used a more sophisticated approach to show the same effect of song on territory invasions in the great tit (*Parus major*). Taken together, these field studies clearly demonstrated the two major functions of bird song, eloquently illustrating two components of sexual selection in birds: mate attraction in the context of mate choice, and territory defence in the context of male-male competition (reviewed in Andersson, 1994). Given its importance in the fundamental life history processes of reproduction and resource acquisition, bird song is an excellent system to investigate the ecology and evolution of animal communication.

1.2 Song learning in birds

Songbirds are one of only six groups of animals known to acquire their vocalizations through a learning process (reviewed in Catchpole and Slater, 2008), along with bats (e.g. Boughman, 1997), cetaceans (e.g. Reiss and McCowan, 1993), parrots (e.g. Pepperberg, 1994), hummingbirds (e.g. Baptista and Schuchmann, 1990), and humans. Song learning in birds is thought to occur across a series of phases, building on an innate, yet crude, template of a species-specific song (Figure 1.1).

During the Memorization Phase (Figure 1.1), a young bird matches its innate song template to external stimuli provided by conspecifics, often those living close

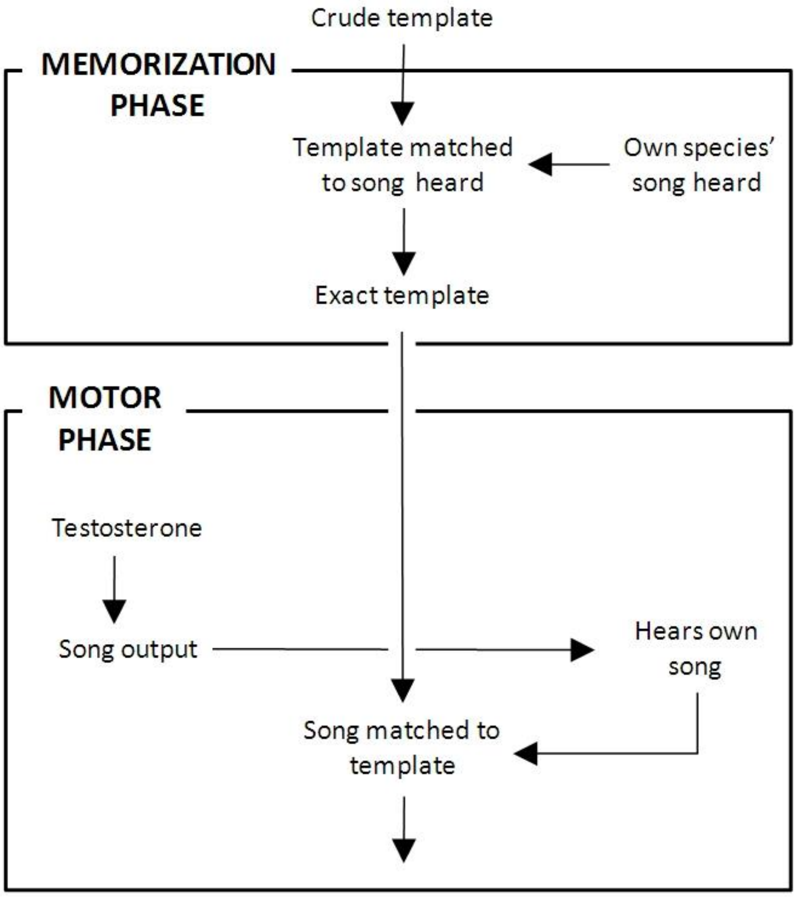

Figure 1.1 The 'auditory template model' of song learning in birds (adapted from Catchpole and Slater, 2008).

to the bird's natal site, and forms an exact template upon which to model its own vocalizations. Following this phase, the bird may reach sexual maturity and enter the Motor Phase of song learning (Figure 1.1). Increases in testosterone circulation lead to increases in song output by the bird, although this early song is often in an unrefined form, akin to babbling in human infants, known as "sub-song". Upon hearing its own song, the bird then compares this stimulus to the exact template formed during the Memorization Phase, and modifies it to match that template. This final stage in song learning is known as crystallization, in which the song is cemented in form (Marler 1964).

The above model of song learning is known as the 'auditory template model', and is based on the idea that songbirds possess an innate standard on which to model their vocalizations. Although this model may have been first used by Marler (1964), this idea was further assessed and developed by others (Konishi, 1964; Marler and Tamura, 1964; Konishi, 1965; Konishi and Nottebohm, 1969; Marler, 1970), often by either rearing young birds in acoustic isolation or by deafening birds at an early age and then observing the accuracy with which the birds produced songs as adults.

1.3 Geographic variation and dialects in birdsong

Learned animal behaviours are transmitted culturally from one individual to another, leading to the aggregation of specific forms of behaviour in geographically localized groups. Bird song is an example of such a learned behaviour; localized forms of bird song are known as dialects.

It has long been recognised that birds learn their songs from other individuals in the population through a form of intra-specific mimicry (Payne, 1982). Variations in the phonology and syntax of bird vocalizations may arise randomly in a population through errors in the song learning process, much as genetic mutations may arise in a bird’s genome, or as the result of innovation. If these novel vocal forms confer a fitness advantage to birds that produce them, or if they are merely not selected against, then these forms can "fix" in a population and spread locally. As song learning in most birds either encompasses both the nestling and post-fledgling period and is followed by limited post-natal dispersal, or occurs after dispersal when a territory is established, this may lead to the geographic clustering of song variants. The vocalizations of a particular species may then begin to display marked geographic variation exhibiting a range of potential spatial patterns, such as random variation (Figure 1.2a), gradual and shallow clines (Figure 1.2b), and steep clines with stepped variation (Figure 1.2c).

The initial process by which dialects form and are transmitted was investigated in New Zealand in a landmark study by Jenkins (1977), who examined dialect development in a population of North Island saddleback (*Philesturnus rufuscater*) translocated to predator-free Cuvier Island in 1968. At the time of study in 1970,

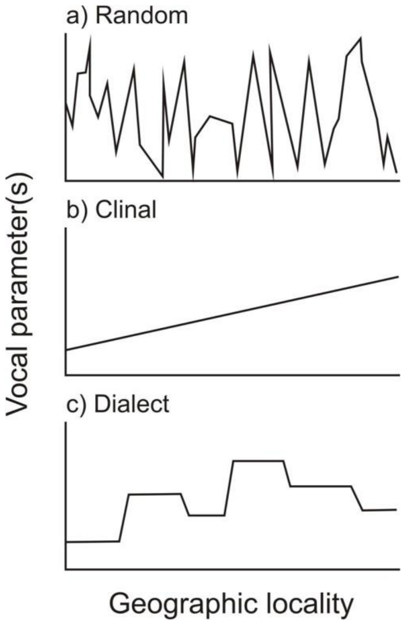

Figure 1.2 Schematic representations of three potential patterns of geographic variation in bird song. Geographic variation in vocal parameters between localities can be manifested at varying scales, including: a) randomly, b) gradually, and c) featuring sharp changes, with relative consistency within localities (modified from Podos and Warren, 2007).

the saddleback population had increased to 28 pairs from the original 29 individuals that were released. Jenkins determined that male birds produced a temporally stable rhythmical song pattern that was shared with a restricted group of between two and eight neighbouring males. He examined these dialect groups over a four year period to determine the level of dialect transmission between fathers, sons, and neighbours. He found that birds occupying territories abutting two dialect zones produced the songs of both dialects. Juveniles hatched on Cuvier copied songs of the original translocated birds, but in some cases did so imperfectly, leading to the formation of novel patterns. This example highlights one of the hypothesis for dialect formation – imperfect copying. That Jenkins (1977) found dual-dialect individuals supported his suggestion that song was culturally transmitted in saddlebacks.

It is well known that vocal dialects exist in the many avian species that learn their vocalizations. However, dialects have rarely been demonstrated in species that produce songs as duets, a behaviour in which two birds combine their songs in a temporally coordinated manner (Farabaugh, 1982). Some of the few duetting species known to exhibit regional dialects are the slate-coloured boubou, *Laniarius funebris* (Wickler, 1972; Sonnenschein and Reyer, 1984; Wickler and Sonnenschein, 1989), and the North Island kōkako, *Callaeas wilsoni* (Hudson, 2001; Molles et al., 2006), the focal study species in this thesis (I review duetting behaviour in kōkako in detail in Chapter 3).

Geographic variation in song can occur over different spatial scales and can be described for a number of different vocal parameters. For example, variation in song structure has been shown to occur over microgeographic scales of hundreds of metres (Leader et al., 2000) as well as over macrogeographic scales of hundreds of kilometres (Warren, 2002). An early definition of a song "dialect" came from the study of the white-crowned sparrow (*Zonotrichia leucophrys*) by Marler and Tamura (1962), who considered a dialect "a consistent difference in the predominant song type between one population and another of the same species". Essentially this refers to a greater degree of variation between songs of two populations than within those populations, with a sharp boundary between those populations. Nottebohm (1969) noted that where contiguous populations of the rufous-collared sparrow (*Zonotrichia capensis*) meet, the integrity of the respective dialects is maintained with a boundary between them. Mundinger (1982) also considered a song dialect to be "a variant song tradition shared by other members of a local population of birds, with a dialect boundary delineating it from other variant song traditions". Similarly, Rothstein and Fleischer (1987) considered dialects to occur in "separate, adjacent aggregations of birds, with well-defined boundaries and with different vocalizations". All of the above definitions stress the importance of a boundary delineating adjacent dialect groups. The presence of abrupt behavioural boundaries between dialect groups (as in Figure 1.2c) suggests selection as a maintaining force (Podos and Warren, 2007). If females prefer males who sing local songs, or males cannot successfully defend territories with non-local song, then geographic variation in bird song may act as a pre-mating isolating mechanism and play an important role during speciation (Slabbekoorn and Smith, 2002; Remsen, 2005).

The presence of vocal dialects in solo-singing bird species may influence the ability of pairs to form, and ultimately to produce offspring. Duetting has also been shown to function in joint territorial defence (Seibt and Wickler, 1977), and thus the presence of dialects in duetting species may impact on a pair's ability to communicate with neighbours and defend resources. It is these fitness costs and benefits to vocal dialects that have led to a large number of dialect function studies, largely involving solo-singing species (reviewed in Baker and Cunningham, 1985; Podos and Warren, 2007).

1.4 Dialect function

The adaptive function of vocal dialects is an area of research that has generated much discussion in the scientific literature. There are several main hypotheses for the evolutionary function of song dialects, which may not be mutually exclusive:

(1) The *Local* or *Genetic Adaptation Hypothesis* posits that females gain fitness benefits from mating with males of the same dialect region in preference to males from a foreign dialect region (Marler and Tamura, 1962; Nottebohm, 1969; Baker et al., 1981; Baker et al., 1982; Baker, 1983). This fitness advantage is expressed in the adaptations that the offspring of same-dialect pairs will have to local ecological conditions, also termed "co-adapted gene complexes" (Baker, 1982; Baker et al., 1982). This hypothesis has been tested in numerous studies, yet the results have been equivocal. Although ultimately testing for the same effect (i.e. a preference for same-dialect mating), those studies can be divided in two types based on methodology. One technique used has been to directly assess patterns of assortative mating or mate preference between dialect groups (summarized in Table 1.1). Several studies of this kind have found evidence of positive assortative mating, or mating preference based on dialect origin. For example, studies of the yellowhammer (*Emberiza citronella,* Baker et al. 1987) and the white-crowned sparrow (Baker and Mewaldt, 1981; Baker, 1982, 1983; Lampe and Baker, 1994),

Table 1.1 Summary of published assortative mating studies examining the *Genetic Adaptation Hypothesis* for avian vocal dialect function.

Species	**Study**	**Year**	**Support hypothesis?**	**Methods used**
Brown-headed cowbird	O'Loghlen and Rothstein	1995	yes	Copulation-solicitation display assay with playback of local and foreign dialects.
North Island kōkako	Rowe and Bell	2007	yes	Assessment of pair formation in translocated birds of multiple dialects.
Rufous-collared sparrow	Petrinovich and Baptista	1984	no	Testosterone implants in ♀♀ to determine if song matched breeding partner.
White-crowned sparrow	Baker and Mewaldt	1978	yes	Band-recapture study showed cross-dialect migration less than theoretical model.
	Baker	1982	yes	Copulation-solicitation display assay with playback of local and foreign dialects following tutoring with local songs.
	Baptista and Morton	1982	no	Testosterone implants in ♀♀ showed that female natal song did not match mate's song.
	Baker	1983	yes	Copulation-solicitation display assay.
	Tomback and Baker	1984	yes	Testosterone implants in ♀♀ captured near dialect boundaries, tested if song matched mate's song.
	Chilton et al.	1990	no	Examined natural mate choice in a dual-dialect population.
	Lampe and Baker	1994	yes	Playback experiments to captured ♀♀ of 2 subspecies in the field and to ♂♂ of two subspecies in the laboratory to determine their response to the two subspecies' songs.
	Chilton and Lein	1996	no	Copulation-solicitation display assay with playback of local and foreign dialects and testosterone implants to induce song in ♀♀.
	MacDougall-Shackleton et al.	2001	yes	Captured ♀♀ prior to dispersal, exposed them to natal and foreign dialect song in captivity at 1 year old, then tested with copulation-solicitation assay at 2 years old.
Yellowhammer	Baker et al.	1987	yes	Copulation-solicitation display assay with playback of local and foreign dialects.

have assessed differences in the number of copulation-solicitation displays produced by captive-held females in response to playback of local and foreign dialects. The assay technique used in such studies is controversial however, as it involves elevating hormones beyond normal levels, and may therefore not reflect natural situations.

Assessment of assortative mating between dialect groups has also been made in the North Island kōkako. Rowe and Bell (2007) found that translocated female kōkako preferentially chose males whose repertoire was typical of the acoustic environment they experienced before translocation. The length of time taken to form pairs was also higher for those mixed dialect pairs that did form, compared to same dialect pairings, though sample sizes were very low in this study. Despite these observations, analysis of pair formation of kōkako hatched on Kapiti Island indicates that the observed assortative mating was a temporary phenomenon in the years after translocation, which did not continue following juvenile recruitment (Rowe and Bell, 2007). Therefore, it seems that in the kōkako, juvenile song acquisition may negate any assortative mating influence of dialect membership in generations following translocation.

An alternative method of testing the *Genetic Adaptation Hypothesis* has been to perform genetic analyses using mitochondrial DNA (mtDNA), or microsatellite allele frequencies of birds from different dialect regions (summarized in Table 1.2). As discussed above, humans and songbirds are two of only a small number of animal groups known to learn their vocalizations from conspecifics. In humans, there is a strong relationship between variation in the genetic structure of a population and variation in a culturally learned trait, such as language (Sokal et al., 1990). If mating preference in birds is determined by dialect group membership, then we can expect there to be a similarly tight relationship between population genetic structure and dialect group. However, in reviewing the published literature, I have found that there is only weak correlative support for this pattern (Table 1.2).

These studies include examples of both species that are "open-ended" learners (i.e. they can learn new sounds throughout their lives), such as the yellow-naped

Table 1.2 Summary of published genetic differentiation studies examining the *Genetic Adaptation Hypothesis* for avian vocal dialect function.

Species	Study	Year	Support hypothesis?	Methods used
Indigo bunting	Payne and Westneat	1988	no	Comparison of genetic structuring using polymorphic enzymes between distinct song neighbourhoods.
Orange-tufted sunbird	Leader et al.	2008	no	mtDNA sequence variation and allele frequencies at 5 microsatellite loci from two distinct song dialects of sunbirds.
	Yoktan et al.	2011	no	mtDNA sequence variation at 5 microsatellite loci from 13 sunbird populations.
Rufous-collared sparrow	Handford and Nottebohm	1976	no	Allelic frequencies compared between 200 birds from 5 sample sites which show distinct and abrupt dialectual differences.
	Lougheed and Handford	1992	no	Allozyme and non-enzymatic protein-coding loci compared between individuals from different vocal dialect regions.
	Lougheed et al.	1993	no	mtDNA sequence variation examined along 50 km, spanning 3 dialect boundaries.
Satin bowerbird	Nicholls et al.	2006	no	Compared genetic divergence derived from 11 microsatellite markers with a metric of phenotypic divergence derived from male bower advertisement calls.
Swamp sparrow	Balaban	1988	yes/no[1]	Genetic variation at 9 polymorphic enzyme loci for birds from 7 locations each with distinctive song structure differences (dialects).
White-crowned sparrow	Baker	1975	yes/no[2]	Allozyme frequency variation within and between dialects.
	Baker et al.	1982b	yes	Enzyme polymorphisms variation in relation to dialects.
	Zink and Barrowclough	1984	no	Re-analysis of work by Baker et al. (1982b). Enzyme polymorphisms/allozyme variation in relation to dialects.
	Hafner and Petersen	1985	no	Genetic distances determined from allelic frequency data for 8 polymorphic loci and compared between dialects.
	MacDougall-Shackleton and MacDougall-Shackleton	2001	yes/no[3]	Microsatellite allele frequencies from 18 sample sites representing eight dialect regions.
	Soha et al.	2004	no	Comparison of allele frequencies at four microsatellite loci in males from 11 sites spanning 6 dialects.
Yellow-naped amazon	Wright and Wilkinson	2001	no	mtDNA sequence variation in 41 samples from 2 neighbouring dialects in relation to vocal dialect variation using haplotype analysis, genetic distance analysis, a maximum-likelihood estimator of migration rates, and phylogenetic reconstructions.
	Wright et al.	2005	no	Microsatellite allele frequencies in relation to dialects.

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[1] Song and genetic variation were correlated between two population subdivisions, but not a third.

[2] The two populations studied (Colorado and California) showed conflicting patterns of support for a relationship between song and genetic variation.

[3] The authors found no significant relationship between dialects and geographic distance, nor did dialect groups form distinct genetic groups. However, beyond within-dialect region allelic differences, most variation was significantly attributable to differences among regions.

amazon, *Amazona auropalliata* (Wright and Wilkinson, 2001; Wright et al., 2005), and "closed-ended" learners (i.e. they have a limited period of sensitivity when young to learn new songs), such as the white-crowned sparrow (Hafner and Petersen, 1985; Soha et al., 2004). On the one hand, we might expect that open-ended learners would simply incorporate new song elements either horizontally (e.g. Slater, 1986) or obliquely (Lachlan and Feldman, 2003) following dispersal, and thus dissociate their dialects from their natal population genetic structure. Close-ended learners, on the other hand, should acquire their songs vertically from their parents or obliquely from their natal-territory neighbours during a short sensitive learning period, and much like humans (e.g. Cavalli-Sforza et al. 1988), exhibit dialect specific genetic signatures.

Although numerous studies have examined the relationship between genetic structure and dialects in birds, few have provided clear evidence in support (Table 1.2). One such study was performed by Baker and Mewald (1978) who found that across-dialect movement was less than expected by random-dispersal, suggesting that dialects may restrict gene flow. MacDougall-Shackleton and MacDougall-Shackleton (2001) found a weak positive correlation between genetic structure and dialect grouping, which suggests that gene flow is inhibited by dialects. However, other studies have found no correlation between genetic structure and dialect grouping (Chilton et al., 1990; Chilton and Lein, 1996). In the indigo bunting (*Passerina cyanea*), song neighbourhoods did not show any significant genetic differences, though these neighbourhoods were possibly too small to exhibit genetic differentiation (Payne and Westneat, 1988). Some authors have suggested that dialect boundaries in the white-crowned sparrow act as barriers to dispersal, supported by evidence that dialects correspond to demes with reduced allele migration between dialects (Baker, 1975).

Continuing the debate on dialect function in the white-crowned sparrow, Soha et al. (2004) compared allele frequencies at four microsatellite loci from six different dialects in the western U.S.A., and found that individuals from different dialect regions are no more genetically diverged than within dialect regions. Dialects in this species are known to be maintained for up to fifty years in the face of ongoing gene flow between dialect regions. The authors suggest that birds acquire multiple dialects when in their sensitive song learning phase, and then only retain the dialect that matches their neighbours' songs when they disperse and settle on a breeding territory (see also Nelson, 2000). More recently, Yoktan and others (2011) assessed genetic differentiation of 13 populations of the orange-tufted sunbird (*Nectarinia osea*) and found no relationship between genetic structure and dialect grouping, potentially because cultural evolution can proceed at a much faster rate than neutral genetic divergence (e.g. Noad et al., 2000). The authors instead found that genetic structure was strongly predicted by geography, suggesting a pattern of isolation-by-distance (see *Epiphenomenon Hypothesis* below).

The dissociation between genetic structure and dialect groupings in the majority of studies (Table 1.2) could be explained in at least two ways: (1) by a departure from vertical song transmission whereby sub-adults learn new song elements from territorial neighbours following dispersal, or (2) by selective use of learned song elements that most closely match those of territorial neighbours following dispersal (i.e. "selective attrition"; Marler and Peters, 1982; Nelson, 1992; Nelson, 2000; Nordby et al., 2007).

(2) The *Social Adaptation Hypothesis* for the function of dialects posits that individuals gain fitness advantages by singing songs similar to those of other birds in their region, whereas those birds that sing nonlocal songs are subject to social penalties such as territorial exclusion (Verner, 1975; Payne, 1981; Baptista, 1985). Conformity to learning local song dialects is therefore enforced by discrimination of non-local vocal variants (Ellers and Slabbekoorn, 2003; Lachlan et al., 2004; Wright et al., 2008). This hypothesis has been tested by several authors. For example, Wright and Dorin (2001) performed playback experiments on the yellow-naped amazon to test responses to dialect variation. They found that birds responded more aggressively to local dialect duets than to foreign dialect duets (Wright and Dorin, 2001). Similarly, Nelson (1998) tested the responses of free-living male white-crowned sparrows to local and foreign dialects, finding a stronger response to playback of local and geographically distant variations of the

same dialect than to a foreign dialect (Nelson, 1998). Jenkins (1977) suggested that young male saddlebacks learn the songs of locally dominant males to facilitate social interactions. This idea was supported by observations that young male indigo buntings that learned and matched the songs of older neighbouring males had a higher mating and breeding success than those that did not (Payne, 1982). In this way, dialects can be viewed as "interactive social units" (Payne, 1981). Rothstein and Fleischer (1987) divided the *Social Adaptation Hypothesis* to highlight the different mechanisms by which it can occur. Under the *Honest Convergence Hypothesis* of dialect function (Rothstein and Fleischer, 1987), dialects are maintained as a reliably honest signal of high social status and quality as a potential mate. Newcomers and foreign dialect birds that cannot produce the local dialect are therefore discriminated against by local birds. Alternatively, under the *Deceptive Convergence Hypothesis*, variably called *competitive mimicry* (Payne, 1982) or *deceptive mimicry* (McGregor and Krebs, 1984; Baker and Cunningham, 1985), dialects arise because males imitate the vocalizations of dominant males to facilitate interactions. The main difference between the two forms of the *Social Adaptation Hypothesis* is that deceptive convergence predicts the temporal stability of dialects to be low, as dominant birds would gradually develop new vocal variants to counteract the mimicry by subordinate birds, whereas mimicry through honest convergence is temporally stable due to its honesty in conveying male quality.

(3) The *Acoustic Adaptation Hypothesis* states that songs undergo selection for optimal transmission through the acoustic environment (Morton, 1975; Wiley and Richards, 1978; Bowman, 1979; Gish and Morton, 1981; Nottebohm, 1985). While this hypothesis is clearly functional in that songs optimally adapted for transmission in a particular environment will be accurately copied and learned by other local birds, it is not necessarily functional in an adaptive sense in that the locus of acoustic adaptation is site specific and thus does not necessarily favour geographic diversification (Podos and Warren, 2007). Evidence supporting this hypothesis has been provided by Nicholls et al. (2006). Although not investigating dialects in a strict sense, the authors found that geographic variation in male satin bowerbird calls did not correlate with genetic markers, thus refuting the *Genetic*

Adaptation Hypothesis. Instead, they found that the genetic structure of the population followed a vicariant model of evolution, with the differentiation of isolated populations and isolation-by-distance among continuous populations. They suggest instead that call structure is strongly influenced by the acoustic environment of different habitats of the sample sites, and stress the importance of habitat-related selection in shaping the vocal structure of the population. Additional support for the role of habitat in shaping vocal variation and population differentiation came from Lougheed and Handford (1992), who investigated the relationship between allozymic characteristics of dialect groups in the rufous-collared sparrow. The authors found that although genetic structure did vary in the population, this was not correlated with variation in dialects.

(4) The *Epiphenomenon (Historical Processes) Hypothesis* posits that dialects are created by occasional inaccuracies in song copying and are functionless by-products of the patterns of song learning and juvenile dispersal, maintained merely by geographic isolation (Andrew, 1962; King, 1972; Baptista, 1975; Payne, 1981; Petrinovich et al., 1981). The timing of song acquisition and the pattern of juvenile dispersal evolve under selection pressures unrelated to dialect formation, yet their interaction may impact on the significance of dialects. If birds acquire their songs for a period beyond dispersal and territory acquisition then this may lead to preferential learning of local dialects and consequently a geographically mosaic pattern of song variants (Slater, 1986). In a recent study, Leader et al. (2008) investigated the relationship between dialects and population genetic structure in the orange-tufted sunbird at a microgeographic scale, using mitochondrial DNA (mtDNA) sequence variation together with allele frequencies at five microsatellite loci. They found no relationship and conclude that their results can best be explained by juvenile dispersal across dialect boundaries and subsequent acquisition of local song variants upon territory establishment.

The debate on the functional significance of song dialects remains unresolved. The *Epiphenomenon Hypothesis*, while perhaps the simplest to explain, is troublesome to test directly as it is the null hypothesis against which alternate hypotheses must be compared. Recent reviews have found that none of the four hypotheses alone could account for all or even a majority of dialect examples (e.g. Slabbekoorn and Smith, 2002; Podos and Warren, 2007), even when only a single species, such as the white-crowned sparrow, is considered. Nevertheless, assessing dialect function may be not only pertinent, but critical for the management of endangered species that exhibit behavioural variation relevant to conservation.

1.5 Conservation and translocations in New Zealand

New Zealand is an isolated oceanic island, 1,600 km from the nearest major land mass, Australia. It was first settled by humans c. 700 years ago (Wilmshurst et al., 2008), who brought with them rats (*Rattus rattus*, *R. norvegicus*, and *R. exculans*), cats (*Felis catus*), possums (*Trichosurus vulpecula*), and mustelids (*Mustela erminea*, *M. furo*, and *M. nivalis*). As a result of human settlement, New Zealand has faced, and continues to face many of the same conservation problems witnessed by other islands; namely that the fauna evolved in the absence of those mammalian predators and herbivores brought by humans. Due to their naiveté (Milberg and Tyrberg, 1993; Grant, 1998), or even their reluctance to fly (Diamond, 1981), the birds were, and still are particularly prone to predation (Blackburn et al., 2004; Duncan and Blackburn, 2004). At least 62 species of bird, representing 47% of those present at the time of human arrival, have succumbed to extinction (Duncan and Blackburn, 2004). In New Zealand, two approaches used either in concert, or sequentially, to conserve remaining species are predator management with the use of traps and/or poisons, and translocations to protected areas or islands.

A translocation is defined by the International Union for Conservation of Nature (IUCN) as the "deliberate and mediated movement of wild individuals or populations from one part of their range to another" (IUCN, 1998). Translocations may have several goals, which often include, but are not limited to: saving species from extinction, salvaging populations threatened by human activities, restoring species to their former range and restoring whole ecological communities. In New Zealand, translocations have been a valuable conservation tool to protect dwindling populations from extinction. The translocation of species to islands or intensively managed mainland areas with fewer or no mammalian predators is an important conservation tool in New Zealand and has been used successfully to save several species, including kakapo (*Strigops habroptilus*), black robin (*Petroica traversi*), and South Island saddleback (*Philesturnus carunculatus*) from likely extinction (Horne and Garton, 2006). A potential risk with translocation to a mainland site located within contiguous habitat is that released individuals will disperse widely, potentially compromising the success of the translocation. A technique employed to mitigate this loss, known as "acoustic anchoring" (Molles et al., 2008), whereby conspecific vocalizations are played during the release process, can potentially aid in the conservation of translocated species.

When deciding which populations to source for translocation, low genetic diversity at the release site is often a leading concern for conservation managers (reviewed in Mock et al., 2004). Less emphasis, however, is placed on the protection of cultural diversity of those source populations used for translocations (but see Laland and Janik, 2006; Laiolo and Jovani, 2007). This is especially pertinent when translocations involve multiple geographically and culturally distinct populations. Additionally, post-release behavioural interactions, such as pair formation and territoriality between members of different source populations may have significant implications for the efficacy of conservation. For example, it has been suggested that pair formation between birds translocated from culturally distinct populations may be inhibited and/or delayed (Rowe and Bell, 2007), which could reduce short-term reproductive output of the founder individuals, and thus reduce the effectiveness of the translocation.

1.6 Study species: The North Island kōkako

To investigate the functional basis and conservation implications of song dialects, I examine the North Island kōkako (kōkako hereafter), a threatened songbird endemic to New Zealand. Kōkako are members of New Zealand's unique wattlebird family (Callaeidae), an ancient group thought to have been present in New Zealand since it separated from Australia with the breakup of Gondwana c. 50 million years ago (Fleming, 1962). Although the exact taxonomic placement of the family has been debated (Ewen et al., 2006; Murphy et al., 2006; Shepherd and Lambert, 2007; Irestedt and Ohlson, 2008), it is widely accepted to fall within the oscine songbirds (sensu Barker et al., 2004). Additional members of the Callaeidae family include the extant North Island saddleback and South Island saddleback, and the extinct huia (*Heterolocha acutirostri*), which was last seen in 1907 (Heather and Robertson, 1997). The congeneric South Island kōkako (*C. cinereus*) was last sighted in 1967 (McBride, 1981), and is now considered extinct (Gill et al., 2010).

Kōkako are large (c. 38 cm; male, 233 g; female, 218 g), blue-grey coloured songbirds sexually monomorphic in plumage. They have a black facial mask extending from the base of the beak, across the forehead to behind the eyes (Figure 1.3). The colourful facial wattles of the kōkako, for which the Callaeidae family is named (Innes et al., 2006), and which grow from the gape and fold under the beak, are bright blue in adults (Figure 1.3), pink in nestlings, and lilac at fledging (Hay, 1981). Although poor fliers, kōkako have long legs (tarsus length = 62.1-67.1 mm, Innes et al., 2006) and are capable of moving through vegetation with speed and agility as they bound along branches and jump between trees (Innes et al., 2006). Kōkako typically form stable, monogamous pairs lasting for several years, with low rates of divorce (Innes et al., 2006). Pairs jointly defend year-round territories 7-14 ha in size, and may produce multiple clutches across a breeding season (Innes et al., 2006). As an iconic forest bird, kōkako are well known to produce beautifully haunting songs, which exhibit discrete dialects between remnant populations (Hudson, 2001; Molles et al., 2006; Tracks 1-4, Appendix 1). Both male and female kōkako produce song as a sequence of phrases, sometimes lasting up to 30 seconds, and which are often combined into non-repetitive duets (Molles et al., 2006). Song-phrase repertoires in kōkako are moderately sized (mean repertoire size = 18; Molles et al., 2006), and phrase type sharing is high among neighbouring kōkako (c. 86%; Molles et al., 2006). While phrase types are usually sex-specific within pairs, they are not necessarily sex-exclusive between pairs (Molles et al., 2006; Molles and Waas, 2006). Although repertoire sharing between the sexes of non- duetting species has been widely

Figure 1.3 Adult kōkako showing blue-grey plumage, long powerful legs, black facial mask, and blue facial wattles.

documented, sex-specificity of song is far more common in those species that duet (e.g. Sonnenschein and Reyer, 1983; Levin, 1996; Wright and Dorin, 2001; Seddon et al., 2002; Slater et al., 2002; Mann et al., 2003; Rogers, 2004; Mennill and Vehrencamp, 2005). There are, however, several examples of partial sharing of song types between the sexes in some species. For example, slate-coloured boubou (*Laniarius funebris*) have been shown to at times learn songs from the other sex (Wickler and Sonnenschein, 1989), and individual eastern whipbirds (*Psophodes olivaceus*) have been observed to produce both duet parts (Watson, 1969). However, both of these are exceptional cases in these species, and sex-specificity of duet contributions is more common (Sonnenschein and Reyer, 1983; Mennill and Vehrencamp, 2005). It has been suggested that the observed variation in pair contributions to kōkako duets, and the resulting flexibility in duet production, could be used by other conspecifics to assess the duration, commitment, and resource-holding potential of kōkako pairs (Molles et al., 2006).

1.7 Kōkako distribution and conservation

The widespread loss of the preferred habitat of kōkako – indigenous mixed-podocarp forest (Figure 1.4) – was historically implicated in population declines

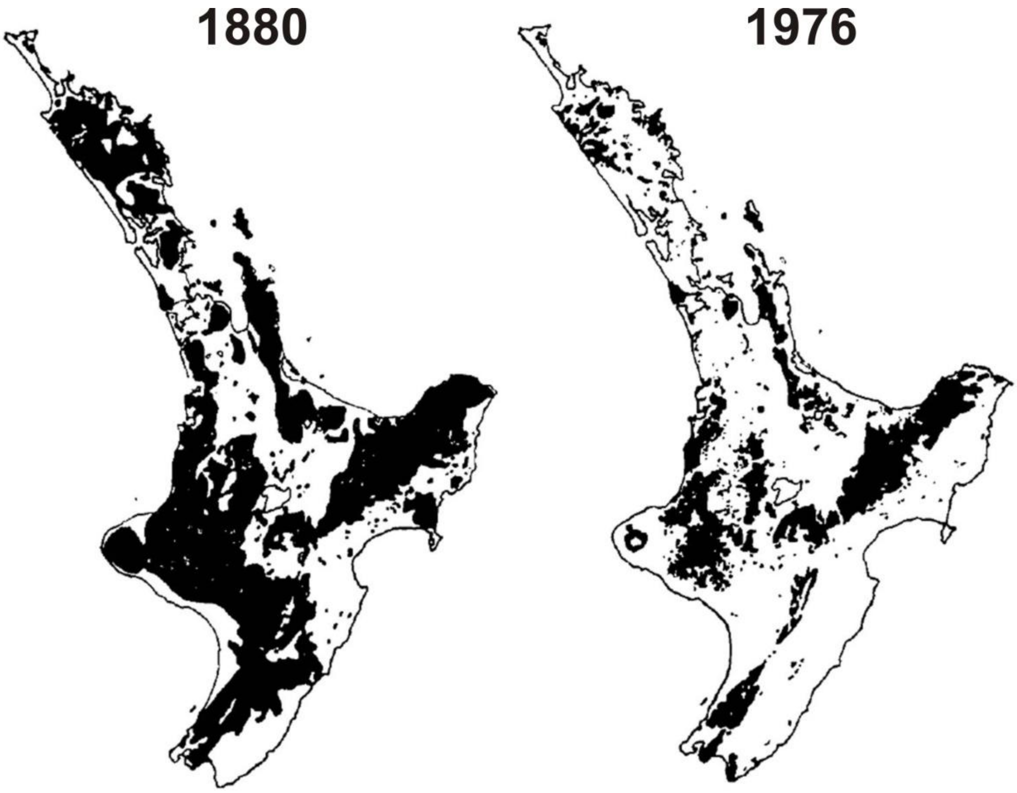

Figure 1.4 Extent of indigenous forest cover, North Island, New Zealand, in 1880 and 1976 (adapted from Lavers, 1978).

(Hay, 1981; Best and Bellingham, 1991). Kōkako have also been heavily impacted by introduced mammals, particularly the ship rat and common brushtail possum, which are major predators of eggs, nestlings, and adults (Innes and Flux, 1999). While sub-fossil remains indicate a widespread distribution before the arrival of European settlers in the late 18th century (Lavers, 1978), by the late 1800's kōkako were, "sparingly dispersed over the North Island" and were, "very local in [their] distribution." (Buller, 1882). Lavers (1978) reported that by 1978, kōkako were, "confined to either small, isolated pockets (where no long-term survival can be expected) or those parts of the more extensive podocarp/hardwood forests which contain suitable habitat" (Figure 1.5). Presently, kōkako are confined to fragmented and relatively undisturbed forests (Figure 1.6), patchily distributed throughout the North Island (Kōkako were also translocated to Secretary Island, South Island in 2008) in 15 remnant and 11 introduced

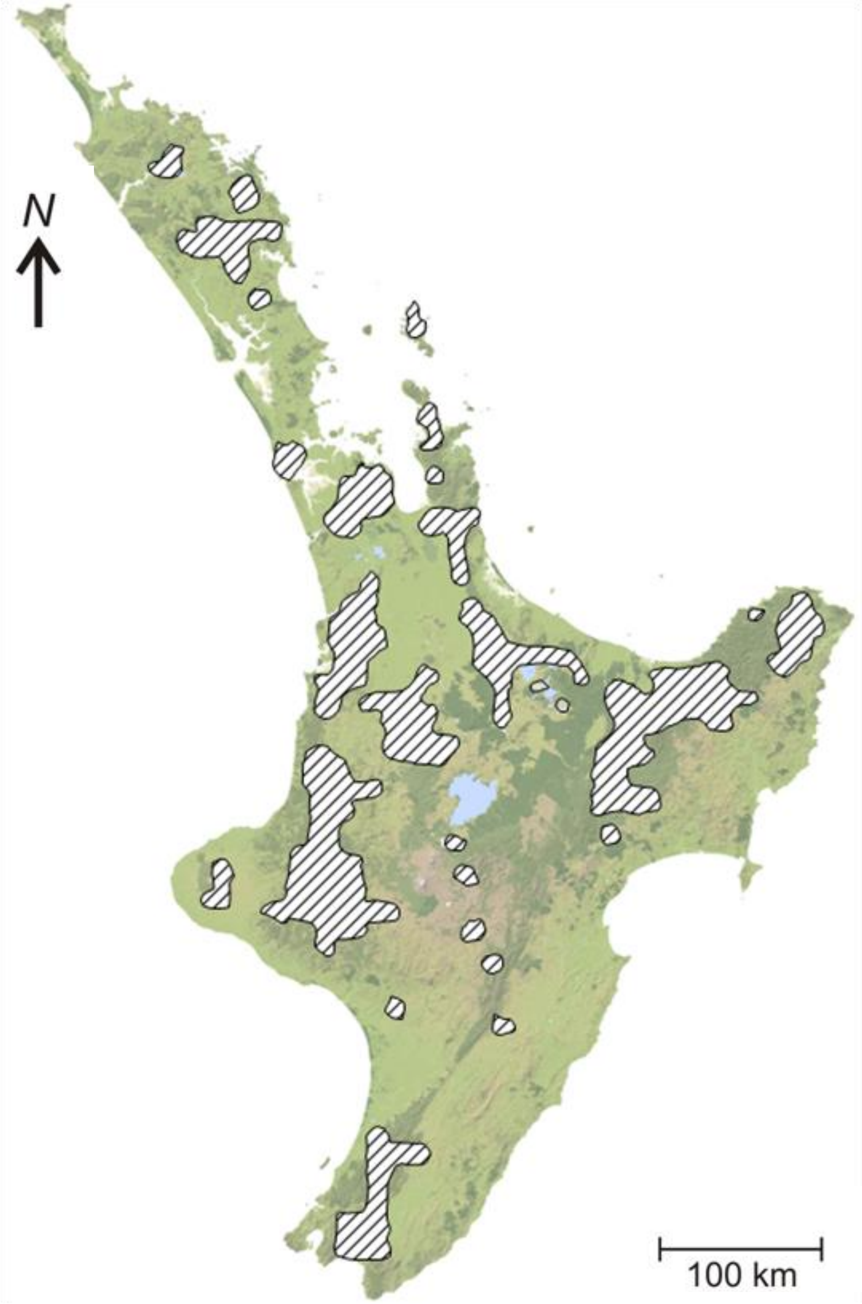

Figure 1.5 Distribution of kōkako sight records prior to 1978 on the North Island, New Zealand (adapted from Lavers, 1978).

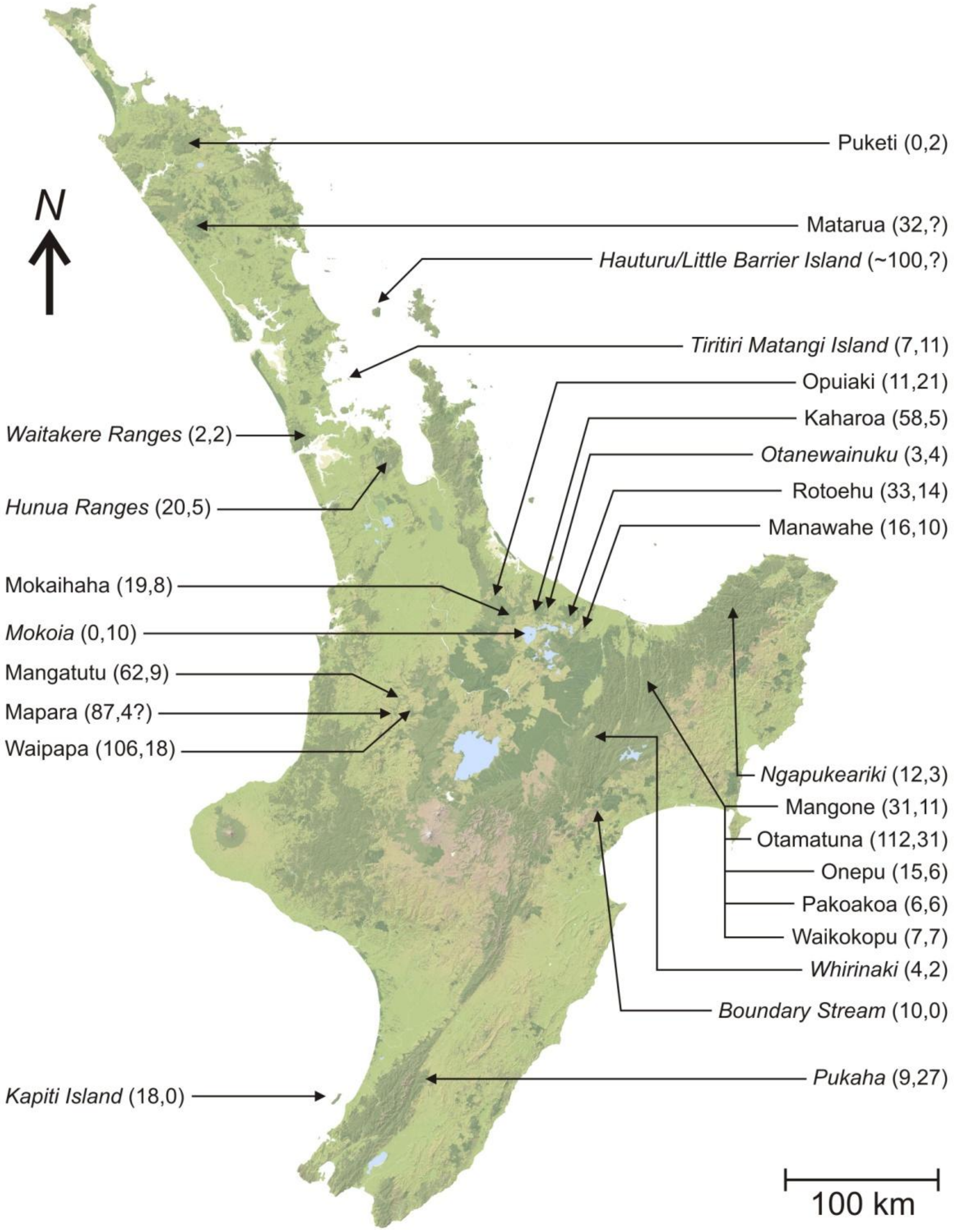

Figure 1.6 Kōkako populations on the North Island, New Zealand, as of 2010 (Kokako Recovery Group, personal communication). Numbers represent totals (pairs, singles), and translocated populations are represented in *italics*. Question marks indicate uncertain or unknown numbers.

populations, 4 of which are on islands. The entire current population is estimated at 1,728 (783 pairs and 162 singles; unpublished Kokako Recovery Group meeting report), and is listed as Endangered by Birdlife International (2010).

1.8 Aims of the thesis

This thesis presents an investigation of the biological significance and conservation implications of vocal dialects, using the North Island kōkako as a model system. The kōkako is an endangered New Zealand endemic songbird that is known to exhibit distinctive vocal dialects over its fragmented range (Hudson, 2001; Molles et al., 2006). To prevent the extinction of this species, conservationists in New Zealand have attempted to establish or augment populations in managed habitats by translocating kōkako either from relatively large, stable populations, or from declining remnant populations (catalogued in Molles et al., 2008). Effectively, this process artificially simulates secondary contact between previously allopatric populations, and provides a compelling example in which to examine potential barriers to gene flow and incipient speciation. Furthermore, immediate species conservation goals may rely on successful territory establishment, pair-formation, and ultimately reproduction of the founder stock, which may involve individuals originating from different source populations. In this thesis, I explore the above themes both experimentally and by harnessing long-term data sets, to examine how different degrees of vocal variation influence between-group pair formation and territorial behaviour.

In **Chapter 2**, I assess how local-scale vocal variation influences territorial settlement behaviour and pair-formation of kōkako translocated from two adjacent "song neighbourhoods". I employed acoustic techniques by broadcasting representative duet song at the release site during this translocation to additionally determine if territory settlement locations could be influenced by within-population variation in acoustic signals, and if acoustic anchoring could effectively be employed with this species. Under the *Social Adaptation Hypothesis* I predict that vocal origin should determine where birds settle in relation to each other and neighbourhood playback, potentially leading to a clustering of same-neighbourhood territories. These findings will also help determine the efficacy of using conspecific song playback to reduce long-distance post-release dispersal of translocated birds, and to determine the importance of the variability of those songs. With respect to post-release pair formation, I predict that birds should pair assortatively with respect to neighbourhood origin in accordance with the *Genetic Adaptation Hypothesis*. (**Status**: "In press" for *Biological Conservation*, 27 November 2011, as "Bradley DW, Molles LE, Valderrama SV, King S, Waas JR. Factors affecting post-release dispersal, mortality, and territory settlement of endangered kōkako translocated from two distinct song neighbourhoods").

In **Chapter 3**, I examine the function of broad-scale dialect variation by performing playback experiments to assess discrimination of local and non-local dialect duets by territorial kōkako pairs. If pairs distinguish between dialects, then I predict a stronger response to local dialect duets than to foreign dialect duets, in accordance with the *Social Adaptation Hypothesis*. Additionally, I use the findings of this experiment to test the relative importance of each sex's role in territory defence by presenting territorial pairs with synthesised mixed-dialect duets in a second experiment. If the male is the more important sex in territorial aggression, and responses to local duets were stronger in the first experiment, then I predict a stronger response to the mixed-dialect duets containing a local male component. (**Status**: Submitted for publication to *Behavioural Ecology* on 14 November 2011 as "Bradley DW, Molles LE, Waas JR. Local-foreign dialect discrimination and responses to mixed-dialect duets in an endangered passerine").

Preliminary evidence (Rowe and Bell, 2007) has suggested that, when kōkako are translocated from multiple source populations to a single destination, pair formation between members of different dialect groups may be delayed or prevented altogether, affecting the outcome of costly and risky conservation interventions. In **Chapter 4**, I examine this purported pattern by conducting a robust analysis on a long-term historical data set of post-translocation pair formation collected by the New Zealand Department of Conservation involving multiple dialects over 18 years. Under the *Genetic Adaptation Hypothesis* by which females select males with locally adapted genes, and the *Social Adaptation*

Hypothesis by which females select same-dialect males to better defend resources, I predict that following release, birds will pair assortatively with respect to population of origin and dialect group. (**Status**: In preparation for publication as "Bradley DW, Molles LE, Waas JR. Long-term data reveal dialect-based assortative pairing following translocation of an endangered species").

In **Chapter 5**, I summarize and build upon the main research findings of this thesis and discuss implications, both in terms of behavioural ecology and the conservation of kōkako. I also make recommendations for future research in light of my research findings.

In **Appendix 2**, I describe a pilot experiment conducted on the North Island robin (*Petroica longipes*) to determine the efficacy of acoustic anchoring in reducing excess post-release dispersal following translocation, and the strength of conspecific interaction on territory settlement decisions. Although methodological lessons from this study were used during the planning and execution of Chapter 2, this study was not within the scope of the thesis proper, and was therefore excluded from the main body of the thesis. (**Status**: Published as "Bradley DW, Ninnes CE, Valderrama SV, Waas JR, 2011. Does 'acoustic anchoring' reduce post-translocation dispersal of North Island robins? Wildlife Research 38:69-76)".

My research is of critical importance to increase the effectiveness of conservation interventions targeting kōkako, especially in the context of translocations, and yet is applicable to other species exhibiting marked vocal variation. Ultimately, this thesis aims to bridge the gap between behavioural ecology and species conservation, and highlight the utility of behavioural research in conservation.

The following chapters and Appendix 2 are presented as a series of stand-alone manuscripts suitable for publication. Although I am the primary author in these papers, the research was a collaborative effort, and so I use the term "we" rather than "I". Each chapter has been adapted slightly from the format of the manuscripts submitted for publication, so that the format is consistent throughout the thesis.

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North Island Kokako (*Callaeas wilsoni*)
Te Urewera Mainland Island
New Zealand

– Artwork © Sam Clark. Used with permission.

The kōkako was a grey bird, and didn't think it was beautiful enough, so it stole feathers from the huia. It had just enough for that black mask over its eyes when it got caught.

– Account of Maori oral tradition by Syd Morrison *in* Morris R, Smith H, 1988. Wild south: saving New Zealand's endangered birds. New Zealand: TVNZ in Association with Century Hutchinson.

Chapter 2: Factors affecting post-release dispersal, mortality, and territory settlement of endangered kōkako translocated from two distinct song neighbourhoods*

2.1 Abstract

Animal translocation success rate is generally low, with the causes of failure poorly understood without comprehensive and protracted monitoring. Here we examine the outcome of a translocation of endangered North Island kōkako (*Callaeas wilsoni*) from two adjacent song neighbourhoods in New Zealand, each with individual vocal traditions (c. 75% of phrases unshared), to a single release site. We conducted detailed radio-telemetry to monitor post-release dispersal over 50 days during four serial releases of 20 birds while broadcasting neighbourhood-specific song around the release site. The birds moved substantial distances after release, however overall short-term release site dispersal was not as great as predicted by a random walk model, suggesting an attraction to playback and/or a reluctance to explore areas away from the release site. This apparent attraction was not specific to a given song neighbourhood, however. Although the post-release mortality rate (22% over 31 days) was relatively high in this translocation, we did not detect an effect of sex, age, source origin, or duration of captivity on mortality. We show that habitat use during this acclimation period was disproportionate to availability – the birds' preferred habitat was similar to that at the capture site. At least four pairs formed, with two and three confirmed breeding in the first and second seasons post-release respectively. We found no evidence of assortative pairing with respect to song neighbourhood, revealing that reduced phrase sharing rates found in adjoining neighbourhoods are not a barrier to pair formation. We compare this example with other kōkako translocations and make recommendations for future translocations.

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2.2 Introduction

Animal translocations, defined as the "deliberate and mediated movements of wild individuals or populations from one part of their range to another" (IUCN, 1998), are an important wildlife management tool frequently used for biological conservation (Griffith et al., 1989; Fischer and Lindenmayer, 2000). Although some translocations, particularly in New Zealand, have met with spectacular success (e.g. Butler and Merton, 1992; Ortiz-Catedral and Brunton, 2010) it is generally acknowledged that translocation success rate is often low (Griffith et al., 1989; Dodd Jr and Seigel, 1991; Letty et al., 2007; but see Parker, 2008). While the causes of past translocation failures are at times poorly understood (Fischer and Lindenmayer, 2000), current research is enhancing our understanding of translocation science by detailed and prolonged monitoring of translocated animals, with the aim of improving future success rates (Hamilton et al., 2010; Devineau et al., 2011).

While the ultimate goal of an animal translocation is to establish a self-sustaining population, it is vital to examine behavioural responses immediately following release into an unfamiliar environment as these affect longer-term population processes such as breeding success and survival (Armstrong et al., 1999; Tweed et al., 2003; Armstrong and Seddon, 2008; Dickens et al., 2010). Tracking post-release movement (hereafter referred to as ‘dispersal’) is particularly crucial because knowing where animals go, which habitats they use or avoid, which conspecifics they settle near, and with whom they ultimately form social bonds will allow us to improve the success of future translocations (Tweed et al., 2003; Sutherland et al., 2010). Managers also need information on which individuals survive and which die, when they die, the potential causes of mortality, and ultimately which animals contribute most to establishing a successful population.

Animals are subjected to numerous physical and behavioural challenges during translocation (Letty et al., 2007). For example, there is a risk of injury during capture and handling, both in enclosures at the source and release sites, and in containers during transportation. Individuals are sometimes held in captivity at the source site while others are captured, and held again at the release site to acclimatise them before release, all of which may compound stress (Dickens et al., 2010). Once released, animals are faced with an unfamiliar environment with potentially unfamiliar conspecifics, and in which they must find food and avoid predation. Examining how animals cope with these overlapping challenges is important for optimising future translocation protocols (Teixeira et al., 2007; Dickens et al., 2010).

This study concerns the translocation of endangered North Island kōkako (*Callaeas wilsoni*), a large (c. 230 g) songbird endemic to New Zealand (Heather and Robertson, 1997; Birdlife International, 2010). Due to their conservation status, several re-introductions of kōkako have been attempted (catalogued in Molles et al., 2008), either to create ‘insurance’ populations and thereby preserve genotypic heritage (e.g. Brown et al., 2004), increase genetic diversity in small, inbred populations (Hazel Speed, Department of Conservation, personal communication), or return kōkako to their former range (e.g. Molles et al., 2008). In cases where kōkako have been successfully translocated to islands, or isolated forest blocks embedded within farmland, post-release dispersal opportunities were restricted, essentially confining the birds to the intended area. However, where kōkako have been translocated to mainland sites within a matrix of suitable habitat, some birds have wandered widely, resulting in the loss of potential founders. To mitigate this problem, playback of conspecific vocalisations to "acoustically anchor" kōkako has been attempted with some promising preliminary results (Molles et al., 2008). When kōkako have been sourced from multiple sites, assortative pair-formation with respect to source site has been documented (Brown et al., 2004; Rowe and Bell, 2007), suggesting that vocal variation resulted in social discrimination. How song variants affect where birds disperse to, with whom they form partnerships, or where birds establish territories are important questions, the answers to which will inform and improve future translocations.

From August to October 2009, kōkako from distinct song neighbourhoods in Te Urewera National Park were translocated to Whirinaki Forest, 53 km to the southwest, to establish a new population. This time period was chosen primarily as it coincides with high food availability and yet minimizes breeding season disturbance. We used the opportunity of this translocation to examine post-translocation movements of 20 kōkako (10 from each neighbourhood) while we broadcast songs representative of each group from multiple speakers near the release location. With the aim of improving the success of future translocations, we examined: (1) dispersal and mortality immediately following translocation in relation to sex, age, and holding time in captivity; (2) movements in relation to conspecific song playback representative of the two neighbourhoods (based on the hypothesis that birds will be attracted to conspecific songs, we predicted that dispersal movements away from the release site would be lower than expected by a random dispersal model; further, if birds are attracted specifically to local songs, we predicted that birds would tend to associate with speakers broadcasting songs recorded from their own neighbourhood); (3) habitat associations relative to source site habitat both during dispersal and once final territories were established (if kōkako exhibit a rigid preference for their natal habitat type, we predicted that they would occupy those habitats with the greatest similarity to their catch site); and (4) pairing success with respect to the origin of the birds, timing of release, and dispersal parameters. As assortative mating with regard to natal *song dialect* has been shown to occur in this species (Rowe and Bell, 2007), we also predicted that adults would pair assortatively with respect to *song neighbourhood*. We use our findings to develop recommendations that will aid managers in improving the success of future translocations.

2.3 Methods

2.3.1 Capture and release sites

The New Zealand Department of Conservation (DOC) captured for translocation 20 kōkako from within contiguous native forest (permit number DOCDM-185320). Birds were captured from two adjacent areas in the vicinity of the Otamatuna Hut (eight males, two females) and Te Mapou Hut (three males, seven females), Te Urewera National Park, New Zealand (lat. 38˚20´S, long. 177˚9´E; Table 2.1) using local song playback. The two capture areas are separated by a

Table 2.1 Kōkako translocated to Whirinaki Forest Park, New Zealand, days in captivity, and the expected and observed probabilities of within neighbourhood pair formation following release. *P*-values are 1-tailed and determined by Fisher's exact tests.

Capture-site neighborhood	Sex	Age	No. of birds released	No. of birds available to pair	Days held in captivity		Assortative pairing		
					Range	Average	P(exp.)	P(obs.)	P
Otamatuna	Male	Adult	5	5	2-7	4.20	0.29	0.33	0.71
		Sub adult	3	0	3-10	7.00	-	-	-
	Female	Adult	2	2	2-7	4.50	0.83	0.67	0.86
		Sub adult	0	0	-	-	-	-	-
Te Mapou	Male	Adult	3	1	1-5	2.67	0.71	1.00	0.75
		Sub adult	0	0	-	-	-	-	-
	Female	Adult	7	5	1-8	3.71	0.17	0.00	0.58
		Sub adult	0	0	-	-	-	-	-

wide, deep valley and individual capture sites were generally on ridges within those areas (Figure 2.1a). All birds were weighed, measured, banded, and fitted with radio transmitters (model: PD-2, Holohil Systems Ltd., Carp, ON, Canada) attached using a modified Rappole Harness (Rappole and Tipton, 1991). At capture, feather samples were taken from all birds for sexing, and blood, faecal, and cloacal samples from six birds in each neighbourhood were collected for disease screening. Birds were held in individual aviaries close to the catch site for a maximum of 10 days ($\bar{X}$ = 4.25, SE = 0.55, N = 20; Table 2.1; for husbandry details, see King 2010). In two cases, a male and a female, presumably members of the same pair, were caught at the same net site and were therefore held in the same aviary. Once either the maximum holding period was reached or the aviary contained eight individuals, the birds were transported by helicopter, and then by car, to the release site; there the birds were housed in an aviary overnight, provided with water and food, and released passively at dawn the following morning. As introduced mammalian predators such as brushtail possums (*Trichosurus vulpecula*) and ship rats (*Rattus rattus*) have been identified as the leading cause of nesting failure in kōkako (Innes and Hay, 1995; Innes and Flux, 1999; Innes et al., 1999), a release site was chosen within a 1000 ha core area in

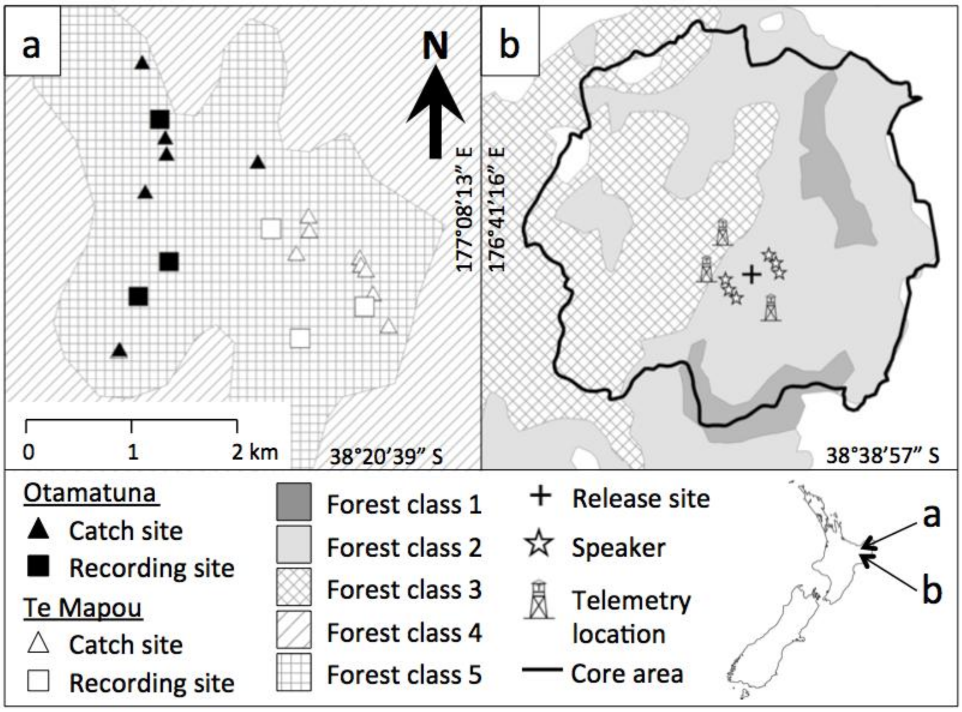

Figure 2.1 Map showing: (a) kōkako capture sites for the translocation and where songs were recorded for playback and (b) the release site, indicating speaker locations, telemetry positions, and the boundary of the core management area.

Whirinaki Forest Park (lat. 38˚65´S, long. 176˚41´E; Figure. 2.1b) where predator numbers were controlled with trapping and/or ground-based poison prior to, and following release.

2.3.2 Recording locations and playback preparation

Prior to capture, we recorded the duet songs of three kōkako pairs from each neighbourhood (none of which were translocated) to be broadcast to the birds during and following release. Recorded songs had a high signal-to-noise ratio and low background noise with little heterospecific acoustic interference. Focal pair recordings were made using a directional microphone (Sennheiser ME66 or MKH416) and a digital recorder (Marantz PMD 660 or M-Audio MicroTrack I), and saved as uncompressed monaural WAV files (16-bit, 44 kHz). When natural song became infrequent, small bursts of locally recorded song were used to stimulate singing. As we did not know during the recording period which birds would be caught for translocation, we assigned neighbourhood membership to pairs based on the distance between all catch locations and each recording location; the distance ($\bar{X}$ ± SE) was lower within a neighbourhood (937.16 ± 211.17 m) than between neighbourhoods (1931.54 ± 334.33 m; paired t-test, t_5 = 6.52, P = 0.001). Analysis of songs recorded from the three pairs from each catch area (Figure. 2.1a) confirmed that the two source locations represent distinct song neighbourhoods. Using the sharing formula $2N_s/R_1+R_2$ (Dice, 1945), where N_s is the number of shared phrases, and R_1 and R_2 are the repertoire sizes of the two pairs, phrase sharing was significantly higher between pairs from the same song neighbourhood ($\bar{X}$ ± SE; 65.5 ± 3.2%) than between song neighbourhoods (26.4 ± 5.9%; $p < 0.0001$, N = 6, t = 7.05, df = 11), although phrase sharing between the areas did occur. By comparison, disjunct populations not included in this study share few, if any phrase types (S. Valderrama, unpublished data). Our analysis used phrase repertoires of all six pairs whose songs were broadcast from the speakers, and whose repertoire curves were complete (i.e. an asymptote was reached), indicating that each pair’s full repertoire had been sampled (Botero et al., 2008). We created sets of nine different ten-minute tracks from each pair's recordings (Track 5; Appendix 1) and loaded each onto a separate iPod (model: Nano, Apple, Cupertino, CA, USA). Using the alarm function, we set tracks to play in a random order beginning at sunrise and continuing for 90 minutes. We did not play heterospecific song as a control for logistical reasons, and because it has been found in previous work that kōkako do not respond to heterospecific vocalisations (Molles and Waas, 2006).

2.3.3 Speaker setup

To simulate two song neighbourhoods, we arranged six speakers around the release location (Figure 2.1b), with each neighbourhood represented by three speakers, each 100 m apart and each speaker representing a pair; this design is appropriate as kōkako are typically close together (i.e. < 5m) when duetting. Each speaker (model: MW6902, Minwa Electronics Co. Ltd., Hong Kong) was suspended from a branch 10 m above the ground, and 250 m from the release location. Therefore, each song neighbourhood was 500 m apart, a comparable separation to that of the two groups at the source site. Each speaker was then connected to the iPod through an amplifier (model: CA115, TOA Corporation, Kobe, Japan), controlled by a battery timer and contained within a waterproof case which was wired to a 12 V battery.

Recording and playback was conducted with approval from the New Zealand Department of Conservation and the University of Waikato Animal Ethics Committee.

2.3.4 Release schedule

Birds were released over four separate transfers to Whirinaki Forest Park. To control for microhabitat heterogeneity near the release site, the location of each simulated neighbourhood was alternated for each new release of birds, and iPods rotated within each neighbourhood. Prior to each release the birds were held overnight in covered 4 m x 3 m aviaries located centrally among the speakers, and released 30 min after dawn the following day. This allowed the birds to hear the stimuli from all six speakers (each 250 m away) for at least 30 min prior to release. Birds from the Otamatuna area were released first (27 Aug, four males and two females; 5 Sept, four males), followed by birds from the Te Mapou area (24 Sept, one male and six females; 8 Oct, two males). Note that one Te Mapou female died prior to release (see below).

2.3.5 Telemetry

For a period of seven days following the each release, which we termed the ‘acclimation phase’ (sensu Moehrenschlager and Macdonald, 2003), observers conducted radio telemetry for three hours each morning beginning 30 min before sunrise, thereby encompassing the playback period, plus an additional hour. Bearings were taken by two to four observers situated on high points around the release location (Figure 2.1b) using TR-4 receivers (Telonics, Inc., Mesa, AZ, USA) and Yagi antennas (Sirtrack Ltd., Havelock North, New Zealand). Observers took bearings on signals according to a pre-determined schedule, thus ensuring simultaneous bearings on single birds to within five minutes. Following the acclimation phase for birds released in the fourth translocation, we tracked all birds using radio telemetry from locations further from the release site and at more protracted intervals (approximately once per individual or pair per week). During the first breeding season, while transmitters remained active, birds were tracked weekly until a visual sighting was made, after which the birds were followed to determine nesting locations and to determine nesting status. Nests were subsequently checked at important reproductive times (e.g. when eggs were estimated to have hatched).

2.3.6 Data analysis

Individual bird positions were determined using the computer program Location Of A Signal (LOAS; Ecological Software Solutions, Inc., Sacramento, CA), based on two bearings using the Best Biangulation method, or three or more bearings using the Maximum Likelihood estimator. To minimise error for biangulations, we calculated locations only when the inter-bearing angles were between 20° and 160° (Chu et al., 1989). Each bird-location record was separated by a minimum of 45 min. Although it has been suggested that consecutive locations on the same day are non-independent due to spatial and temporal autocorrelation (Swihart and Slade, 1985), we consider this inter-location time gap to be sufficient to be considered temporally and spatially discrete (Otis and White, 1999). This is because we were interested in the birds’ short-term movements, and as we expected that the birds would move over large distances, sometimes in the order of kilometres during the acclimation phase, it was necessary to frequently locate the birds. Additionally, translocated animals are not moving within established territories during the acclimation phase, and so we might expect short-term movements to be wider ranging.

To estimate the error of our telemetry system we placed 15 unused radio-transmitters in random locations within a 1 km radius of the release site, and determined signal bearings from the same high points as those used during the study. We then compared the resulting triangulated locations to the actual locations using the estimated error distance (EstErrDist) output variable in LOAS, which is analogous to the Location Error Method (Zimmerman and Powell, 1995).

We determined the location error ± SE to be 115 ± 15.4 m, with an average angular error of 12.7 ± 1.4°.

To assess the timing and extent of the birds' post-release dispersal we compared true dispersal to a random walk dispersal model using the Geospatial Modelling Environment extension (Beyer 2009) in ArcMap (v. 9.2, ESRI, Redlands, California, USA). In the model, we sampled turn angles between successive steps from a uniform random distribution between 0° and 360°. To realistically model movements between successive points we set the program to draw step lengths from an empirical distribution, defined by actual distances between successive bird locations. The program assigned distances randomly from each of 20 equally sized intervals within the range of true distances. The probability of assigning step-lengths from each of the intervals was equal to the proportion of true distances within that interval.

As we may have been unable to detect some actual bird locations due to the varied site terrain, we constrained the random model to 'move' within an area defined by a viewshed analysis in Arcmap (Bowyer et al., 1998; Bowyer et al., 1999; Bangs et al., 2005; Hopcraft et al., 2005). Restricting the random walk model to the observer-based viewshed by removing all points that fell outside it, allowed for a realistic comparison to the birds' true locations. To construct the viewshed GIS layer, we created a digital elevation model from contour lines, used observer elevations from a handheld GPS (model: 60CSx, Garmin International Inc., Olathe, KS, USA), and designated the height of the observers and birds at 2 m and 10 m respectively. We set the outer limit of viewshed to 5 km based on transmitter signal propagation distances in pilot trials in this terrain. The model produced 500 random walks, across which we calculated a mean distance to the release site at the end of each step. We ran the model for seven consecutive steps to compare with the birds' dispersal in the acclimation phase. When we located individual birds multiple times in a single day, we used the mean distance from release site to represent that bird's dispersal distance on that day.

2.3.7 Habitat use

We examined kōkako habitat use during the acclimation phase using vegetation maps produced from aerial photographs at a scale of 1:63,360 (Nicholls, 1966), and which were digitised by DOC and loaded into a GIS. Our vegetation maps consisted of discrete polygons of different vegetation classes according to the system in Nicholls (1966). To assess habitat availability we simulated 10 000 independent dispersal movements from the release location in random directions, with dispersal distances drawn from an empirical distribution defined by the true distances of each bird location during the acclimation phase. We then assigned habitat-use values as the proportion of locations in each forest class, pooling values from each bird to avoid pseudoreplication. We compared habitat-use with availability using chi-squared tests. We qualitatively compare the habitat of territories and nesting locations over two breeding seasons following translocation to those at the source site using the same forest class maps.

2.4 Results

2.4.1 Mortality

A single female was injured during transportation and subsequently euthanized at the release location. This bird had a 17% reduction in body mass compared to when it was captured two days earlier. A further three males and one female were found dead during the monitoring period, on average 12.25 ± 6.37 days after release (range = 3–31 days) and at a mean distance of 596.46 ± 76.71 m from the release site (range = 375.15–725.78 m). Predation was ruled out as a cause of death for 3 of these birds as they were found intact; the fourth was found partially eaten, though this may have occurred after the bird died. Necropsies failed to reveal the causes of mortality for the four birds. Using logistic regression we found no effect on mortality of sex ($\chi^2_1 = 0.80$, $P = 0.370$), age ($\chi^2_1 = 0.73$, $P = 0.390$), or the time spent in holding aviaries before translocation ($\chi^2_1 = 0.94$, $P = 0.330$), although these tests had low statistical power. One additional female dropped her transmitter 1260 m from the release site after three days, and was not seen again. Two of the remaining 14 birds were last detected 44 days after release, while the other 12 were still alive a minimum of 100 days after release. The loss of four of the eighteen birds equates to 22.2% mortality during the first 44 days following release.

2.4.2 Post-release movements

Birds moved extensively following release during the acclimation phase; the mean distance between locations on consecutive days was 433.66 ± 49.24 m. There was no difference between the movement rates of males (409.43 ± 64.09 m) and females (469.99 ± 81.70 m; t = 0.58, *P* = 0.570), or between adults (445.71 ± 55.99 m) and sub-adults (355.29 ± 54.71 m; t = 1.16, *P* = 0.320). Following translocation, birds dispersed from the release site, though not as far as predicted by the random walk model (Figure 2.2), although this analysis is potentially confounded by a decline in the number of birds detected throughout the 7 days.

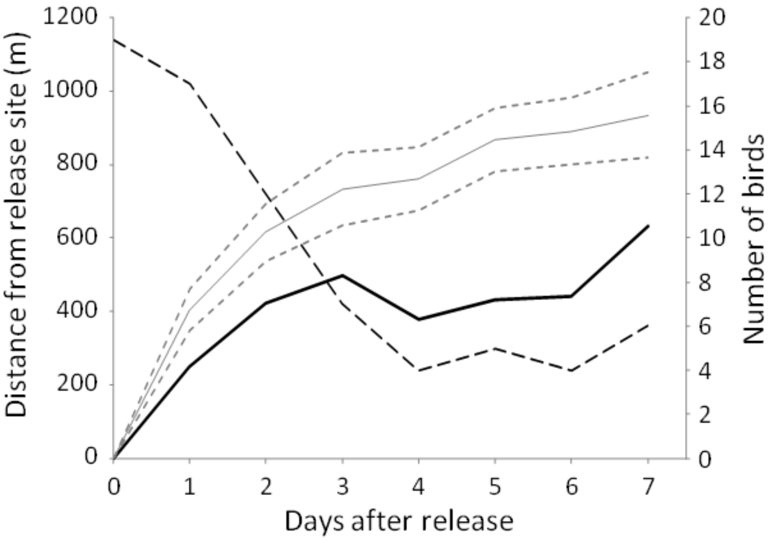

Figure 2.2 Mean post-release dispersal distances from the release site (black solid line) compared to a random walk model (grey solid line). 95% confidence intervals (grey dashed lines) were calculated from the means of 83 iterations of random sub-samples of 7 paths, representing a conservative approximation of the amount of variation in the random model with which to compare to the actual birds. The number of birds for which actual locations were determined (black dashed line) is presented on the secondary Y-axis.

However, we found that during the 7-day acclimation phase 11 birds (7 males, 4 females; 9 adults, 2 sub-adults) returned to within audible range (<750 m) of the speakers at least once ($\bar{X} = 1.55$, range = 1–3) after being detected beyond that range.

2.4.3 Bird positions relative to song neighbourhoods

During the 6 weeks of intensive radio tracking, we never heard a translocated bird singing, suggesting that birds did not become territorial over this time ("floaters" and dispersing juveniles usually remain silent until taking up a territory). However, we examined whether birds were associating with speakers broadcasting their own neighbourhood song. For this test we determined the distances from each bird location to the nearest speaker broadcasting their own neighbourhood song and the nearest speaker broadcasting song from the other area, and then calculated the mean distance for each bird. We found that during the acclimation phase when the birds were within audible range of the speakers birds were no closer to speakers broadcasting their own neighbourhood's songs (342.50 ± 27.30 m) than the other neighbourhood's songs (353.07 ± 33.41 m; paired t-test, $t_{16} = 0.21$, $P = 0.840$).

2.4.4 Habitat use following translocation

We assessed habitat use for 17 birds during the acclimation phase over three broad forest classes which varied in tree species composition and hardwood abundance (Forest classes 1–3 in Figure 2.3). Released kōkako occupied forest classes disproportionately when compared to availability ($\chi^2_1 = 18.47$, $P < 0.0001$; Figure 2.3). This was true when considering males ($\chi^2_1 = 10.51$, $P = 0.005$), females ($\chi^2_1 = 8.81$, $P = 0.012$), and adults combined ($\chi^2_1 = 20.13$, $P < 0.0001$), but not sub-adults ($\chi^2_1 = 0.28$, $P = 0.870$). Adult birds, males, and females, were located in Forest class 3 more often than expected by chance (crosshatched bars, Figure 2.3). This forest type has a relatively even mix of softwoods and hardwoods such as tawa (*Beilschmiedia tawa*), kamahi, and hinau (*Elaeocarpus dentatus*), and the vine supplejack (*Ripogonum scandens*), all of which are potential food sources for kōkako. In contrast, these birds avoided Forest class 2, which has a high proportion of softwoods such as rimu (*Dacrydium*

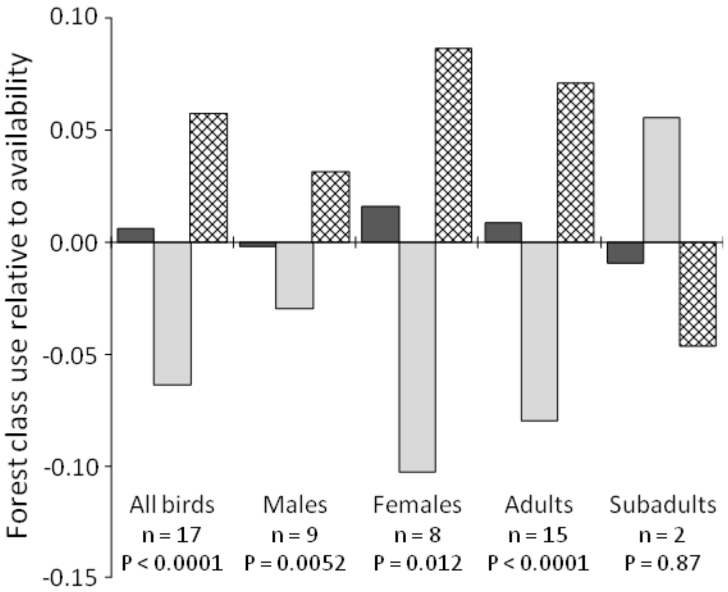

Figure 2.3 Forest class occupancy of kōkako during the 'acclimation phase' following translocation (the first 7 days) as determined by individual locations. Relative habitat occupancy is compared to the availability of pure softwood forest (Forest class 1, dark grey bars), softwood forest with a low proportion of hardwoods such as tawa (Forest class 2, light grey bars), and mixed softwood-hardwood forest with a proportion of tawa and kamahi (Forest class 3, cross-hatched bars).

cupressinum), kahikatea (*Dacrycarpus dacrydioides*), miro (*Podocarpus ferrugineus*), and matai (*P. spicatus*), and a low proportion of hardwoods such as kamahi (*Weinmannia racemosa*). These birds showed a relatively proportionate use of Forest class 1, which has an even higher composition of softwoods and very few hardwoods or vines.

2.4.5 Post-release territory locations

In the breeding season immediately after translocation (November 2009–March 2010) we successfully located three pairs and a single male that established territories (Figure 2.4). In the following breeding season (November 2010–March 2011), two of the pairs were still occupying the same territories and one pair had

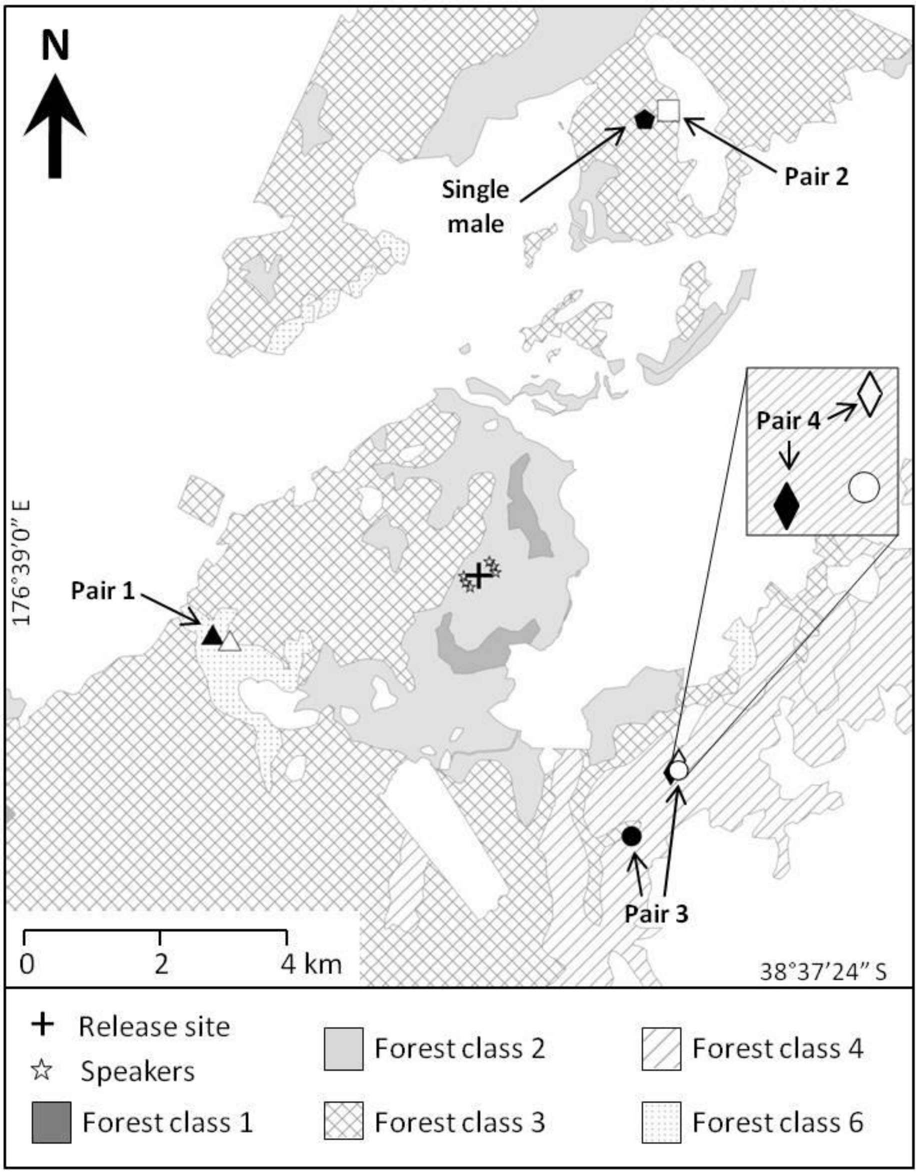

Figure 2.4 Forest-class distribution and post-translocation settlement locations in relation to habitat, release site, and playback speakers. Black shapes represent locations of pairs or single birds in the first breeding season following translocation (2009/2010), and hollow shapes represent locations of the same birds in the second breeding season (2010/2011).

moved its territory 1.26 km to the northeast. An additional pair formed a territory located close to the single male's territory from the first season, but this pair did not comprise that male. Territories over both seasons were located 5.18 ± 0.56 km (range = 4.03–7.86 km) from the release site (Figure 2.4). Habitat type for two of the territories (Pairs 3 and 4, Figure 2.4) in both breeding seasons was Forest class 4, a hardwood dominated mix of predominantly tawa and kamahi, with locally abundant tawari (*Ixerba brexioides*) and supplejack, and lesser amounts of softwoods such as rimu. The territories of one pair in the first season (Pair 2, Figure 2.3), and that of the single male in the second season (Figure 2.3) were located within Forest class 3 (see *2.3.4 Habitat use following translocation* for description of Forest classes). One pair's territory (Pair 1, Figure 2.3) in both seasons was within Forest class 6, which consists of re-growth dominated by young hardwoods such as kamahi and rewarewa (*Knightia excelsa*), with fewer and locally distributed tawa and hinau. The source site habitat in which the birds were captured was Forest class 5, which is dominated by hardwoods such as tawa, kamahi, tawari, and red beech (*Nothofagus fusca*), with a low softwood component.

2.4.6 Mate choice following translocation

Of the four pairs that established territories in the first breeding season following release, all involved birds released as adults. At least two of the pairs nested, one of which successfully fledged chicks (Pair 1, Figure 2.4). In the second breeding season, one pair was confirmed to have hatched a single chick (Pair 1, Figure 2.4), and two other pairs were confirmed to have nested (Pairs 3 and 4, Figure 2.4). The pairs that formed included one caught as a pair (i.e. the male and female were caught consecutively from the same location), one comprised of birds caught in the same neighbourhood area, and two between birds from different neighbourhoods. Excluding birds known to have died during the acclimation phase, assuming that only adult birds bred, and that all pairs had an equal opportunity of forming, revealed that birds did not pair assortatively with respect to neighbourhood of origin (Fisher's exact tests, all $P > 0.5$; Table 2.1).

2.5 Discussion

2.5.1 Mortality

Translocation exposes animals to a risk of mortality, and while care is taken to reduce the risk of injury to animals during transportation, one bird in this particular translocation had to be euthanized before release. Although we do not have data on additional birds with which to compare pre- and post-transportation reductions in body mass, necropsies of the four birds that died shortly after release suggested that weight loss was not substantial and thus was not the cause of death. Although one of the birds was found partially eaten, and may have died as a result of depredation, the other three bodies were found intact.

The combined consecutive acute stress events of capture and handling (e.g. Lynn and Porter, 2008), captivity (reviewed in Morgan and Tromborg, 2007), transport (reviewed in Fazio and Ferlazzo, 2003), and release in an unfamiliar location (e.g. Dickens et al., 2009) may lead to the chronic stress of translocated animals (Teixeira et al., 2007; Dickens et al., 2010). Chronically stressed animals have suppressed immune systems (e.g. in humans; Glaser and Kiecolt-Glaser, 2005) which may lead to increased susceptibility to pathogens (e.g. red deer, *Cervus elaphus*; Griffin and Thomson 1998). Of six birds screened for disease prior to release in this study, three tested positive for avian malaria, one of which died during the acclimation phase. A mortality rate of 22.2% within 44 days of release is unusually high when compared to other kōkako translocations. For example, during kōkako translocations to other sites in 2004 and 2005, 100% (10/10) and 85.7% (6/7) of birds survived to at least 6 months after release (Christian Sauermann, DOC, personal communication; Tony Silbery, DOC, personal communication). Post-release mortality in this study may have been a result of disease exacerbated by translocation-related stress.

2.5.2 Post-release movements

This study documents substantial post-release movement of kōkako following a serial translocation of birds from two adjacent song neighbourhoods. Although birds moved an average minimum distance of almost half a kilometre per day, this is probably an underestimation of the true distance moved by these birds. The distances moved were not unexpected, given that post-natal dispersal of several kilometres is typical before establishing a territory (Innes et al., 1996; Innes and Flux, 1999). As translocated birds have to establish a territory within suitable habitat, the context is somewhat analogous to post-natal dispersal. However, in a translocation context, chronic stress may instigate greater movement away from the release site as a form of stress avoidance behaviour (Dickens et al., 2010).

The random walk model, simulating individual steps over the initial acclimation phase, demonstrated that the actual birds' movements away from the release site were lower than expected. This effect could be explained by a reluctance to leave the release site itself, where individual birds last encountered other kōkako. Limitations in the random walk model, such as a lack of directional persistence, may have introduced a bias towards greater dispersal distances from the release site, however we have no data on which to base this value. Alternatively, a failure to detect birds that may have moved farther from the release site may have increased the chance that the 'random' birds remained closer to the release site and thus created the impression that the birds, as a whole, did not disperse great distances. Additionally, these explanations do not negate the finding that some birds remained closer to the release site than predicted and that they returned to the area around the release site during the playback period. Furthermore, signal detections were frequently made of birds located within the mean range of the random walk model (i.e. up to 800 m), thus validating comparison to the model.

2.5.3 Bird positions relative to song neighbourhoods

Broadcast of species-typical vocalisations at a release site to potentially reduce excessive post-release dispersal and encourage the use of protected habitat has been used in several avian translocations (e.g. Molles et al., 2008; Bradley et al., 2011). When animals are sourced for translocation from multiple sites social discrimination may occur, especially when source populations exhibit behavioural differences which may be crucial in mediating social interactions (Collins, 2004; Naguib, 2005). Although in our study persistent detections of birds close to the release site may reflect an overall short-term attraction to playback, this did not reflect the neighbourhood song being broadcast. It is possible that vocal variation between the two source neighbourhoods (c. 25% song sharing) was not sufficient to promote neighbourhood discrimination, although we have elsewhere demonstrated that kōkako show clear behavioural discrimination between "true" dialects (≤ 5% song phrase sharing; D. Bradley, unpublished data). Alternatively, translocation stress may have out-weighed any potential attraction to familiar vocalisations, or the attraction was transient and insufficient to retain the birds near the release site in the long-term. This may have been due to stimulus habituation, suggesting that a less persistent and more varied playback schedule may have been more effective. As the birds were transferred sequentially from the two song neighbourhoods, it could be argued that any effect of the speakers on birds that were released later was confounded by natural song produced by birds released previously. However, despite that kōkako naturally produce loud song at dawn, we did not hear any kōkako song following translocation during the acclimation phase, despite our proximity to the birds.

2.5.4 Habitat use following translocation

During the acclimation phase while adjusting to their new surroundings and potentially coping with translocation stress, we found that birds occupied habitats disproportionate to availability, avoiding the habitat at the release site (Figure 2.1b). This forest type (Forest class 2) grows over gentler terrain and is dominated by an unbroken, 40 m high canopy. In contrast, the birds preferred the forest on steeper terrain and on higher elevation ridges, similar to the habitat at the catch sites (Forest class 5, Figure 2.1a). This habitat is dominated by hardwoods such as tawa, kamahi, tawari, and red beech, with a low softwood component consisting mostly of rimu. In contrast to that at the release site, this forest type grows on relatively steep slopes and on ridges, and is characterised by a broken canopy and an abundant hardwood understory. The preference for this type of forest may therefore be a reflection of an underlying preference of this species for a forest with a diverse understory flora with asynchronous timing of fruit production, providing a constant food supply (Hay, 1975). Kōkako territories at the source sites formed a linear distribution along ridges perhaps as isolated, emergent trees on these ridges provide open perches from which to sing. The lack of this habitat type within Forest class 2 may explain the avoidance of this habitat during the acclimation phase when birds may have been establishing a territory and searching for a suitable mate.

2.5.5 Post-release territory locations

In the two breeding seasons following translocation we located the seven breeding territories of four pairs. The habitat in all cases is different to that at the release location, and bore similarities with the catch site habitat: steep terrain with an abundant hardwood understory component. The release location was originally chosen due to the intensive predator control measures that were undertaken there prior to translocation. As the territories were entirely located beyond management boundaries, DOC initiated a limited extension of rat, stoat, and possum control to cover the territories of pairs 1, 3, and 4 (Figure 2.3), to reduce the chances of predation.

2.5.6 Mate choice following translocation

Our study found that pair formation was not assortative with respect to source site (or song neighbourhood), in contrast to the outcomes of translocations to Kapiti Island whereby kōkako were taken from disjunct, remnant populations, each with presumably marked vocal differences (Brown et al., 2004; Rowe and Bell, 2007). The degree of cultural similarity between source populations is probably greater in our study than between the Kapiti Island founders, decreasing the likelihood of assortative mating. Indeed, several song phrases produced by the source population were shared between neighbourhoods, and post-natal dispersal between the capture areas and cases of pairings between neighbourhoods have been documented in the past (S. King, unpublished results). Nevertheless, further examination of pair formation and social discrimination following multi-source translocations is needed to understand the consequences of behavioural variation on translocation success, and ultimately on the establishment of a founder population.

2.6 Conclusions and recommendations

This study assessed the mortality and post-release dispersal of an endangered bird following translocation. We did not find that post-release mortality was related to sex, age class, or duration of captivity. Instead, the high mortality rate of this translocation may have related to translocation stress. Although neighbourhood-specific song playback near the release site may have contributed to short-term retention near the release site, it was relatively ineffective at controlling post-release dispersal in the long-term, potentially due to unfavourable habitat at the release site. An alternative explanation for the apparent lack of long-term attraction to the speakers is that playback actually indicated to the birds that the territory was occupied, and thus deterred them from establishing a territory nearby. Kōkako exhibited disproportionate habitat use both during the critical acclimation phase, and in their final territory choices, suggesting that inappropriate habitat at the release site may have been a stronger influence on dispersal. Distinguishing this possibility from the potential deterrent effect of playback (see above) is not possible given the experimental design we used. Nevertheless, our findings underscore the importance of considering habitat while selecting a release site. Behavioural variation among individuals sourced for this translocation was also insufficient to promote assortative pairing, indicating that, at least for this species, vocal variation must be greater to result in social discrimination while pairing.

Based on the findings of this study we recommend the following considerations for future translocations: (1) Mortality during and following translocation may be related to acute or chronic stress, which can be reduced by limiting capture, handling, and holding times, and conducting releases during mild weather to limit the impact of translocation stress; (2) Song playback at the release site may function as a short-term attractant to released animals, but may be ineffective at ensuring long-term site retention without additional attractants; (3) Detailed knowledge of each species’ behaviour is essential to anticipate post-release dispersal and reproductive success, including consideration of the degree of behavioural similarity between released individuals; (4) Habitat at the release site should be as similar to that at the capture site as possible, both in terms of vegetation and topography. (5) Prolonged and detailed monitoring of released individuals is an invaluable and critical process in assessing translocation success.

2.7 Acknowledgements

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The cry of the crow is indescribably mournful. The wail of the wind through a leafless forest is cheerful compared to it. Perhaps the whistling of the wind through the neck of an empty whiskey bottle is the nearest approach to it, and is sadly suggestive of departed spirits. Few people are aware that the crow is a song bird as it is only in the depths of the forest they can be heard to perfection. Their notes are very few but are the sweetest and most mellow toned I have ever heard a bird produce.

– Charlie Douglas (c.1890)

Chapter 3: Local-foreign dialect discrimination and responses to mixed-dialect duets in an endangered passerine*

3.1 Abstract

Social discrimination based on geographic variation in territorial signals is a taxonomically widespread phenomenon – most studies have found stronger reactions to local than to foreign signals. In birds with male-only song, this discrimination is thought to result in social exclusion, and has been suggested as a behavioural barrier to inter-population genetic exchange. However, little information exists on duetting species in this context, and nothing is known of how "mixed dialect" pairs are perceived, despite their confirmed occurrence. We addressed these deficiencies using a duetting, endangered passerine, the kōkako (*Callaeas wilsoni*). We used reciprocal stereo playback experiments between two fragmented populations to present duets from local and foreign dialects (Experiment 1). Additionally, we assessed responses to mixed-dialect pairs by synthesising duets, a novel technique, to determine which sex contributes the most salient duet components (Experiment 2). Territorial pairs responded to local duets with less delay, and produced more song phrases, with a lower diversity, compared to playback of foreign duets. Pairs responded to mixed-dialect duets with equal overall strength regardless of the sex of the local component. Responses to mixed- and pure local duets were qualitatively similar. From an evolutionary perspective this indicates that kōkako dialects might not prevent gene flow. Importantly, these findings also suggest that animals translocated for conservation need not necessarily exhibit homogeneous cultures to acquire and defend resources.

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3.2 Introduction

Biological diversification may be influenced by reductions in between-population mating (e.g. Podos, 2010) and gene flow (e.g. Huber et al., 2007) resulting from variation in mating signals and from social discrimination which limits access to resources (Andersson, 1994; Price, 1998; Irwin et al., 2001; Slabbekoorn and Smith, 2002; Coyne and Orr, 2004; Price, 2008). An ability to distinguish local from non-local signals is a necessary component of this process, and has been demonstrated in a wide range of taxa, from arthropods (e.g. Gray, 2005) and molluscs (e.g. Johannesson et al., 2008), to birds (e.g. Uy et al., 2009) and cetaceans (e.g. Filatova et al., 2011). Most avian studies have found that response by free-living males to local song is stronger than to non-local or "foreign" song (e.g. Milligan and Verner, 1971; Westcott and Kroon, 2002; Searcy et al., 2003; Podos, 2007; Parker et al., 2010; but see Baker et al., 1982 and Balaban, 1988). On a proximate level, observed response patterns can be seen as a by-product of species recognition whereby the more similar the sender's song to that of the receiver, the stronger the receiver response (McArthur, 1986). On an ultimate level, individuals with local experience, as revealed by local song, may represent a greater relative threat to pair bonds and/or other resources, such as a territory (Rothstein and Fleischer, 1987).

Despite advances in our understanding of the process and implications of recognition of geographic song variation in birds, research has been largely limited to those species that produce vocalisations as single individuals. Many birds coordinate their territorial songs as duets, whereby a pair of individuals combine their vocalisations with temporal precision (e.g. Thorpe et al., 1972). Duets present an intriguing juxtaposition of cooperation (e.g. Hall and Peters, 2008) and conflict-based functions (e.g. Sonnenschein and Reyer, 1983) between pair members. Nevertheless, discrimination of discrete geographic song variants, or dialects, in duetting birds has rarely been assessed, despite that duetting occurs in over 400 avian species (reviewed in Hall, 2009). Notable exceptions to this include the slate-coloured boubou, *Laniarius funebris* (Wickler and Sonnenschein, 1989), and the yellow-naped amazon, *Amazona auropalliata* (Wright and Dorin, 2001), that have been shown to produce duets with regional dialects, and the eastern whipbird, whose duets exhibit sex-specific patterns in geographic song variation (Mennill and Rogers, 2006). Wright & Dorin (2001) presented yellow-naped amazon pairs with duets recorded from local and foreign dialects and found that pair-response was strongest to local duets. However, the importance of each sex in dialect-based discrimination and territory defence has never been considered.

Although a stronger response to local compared to foreign song is widespread, in some species this pattern is not consistent among populations. Differential response patterns to sub-species song has been shown in *Henicorhina* wood-wrens (Dingle et al., 2010): Birds from one subspecies responded strongly to local song, but weakly to the other subspecies' songs, while the birds of the other subspecies responded with equal strength to both songs regardless of origin. Dingle et al. (2010) suggest that this may reveal (1) asymmetries in competitive ability or aggressiveness between the two taxa, or (2) differences in the ability to recognise variation in song across subspecies. Asymmetric response patterns of black-throated blue warbler (*Dendroica caerulescens*) populations to local and foreign song, detected by Colbeck et al. (2010), may be best explained by "asymmetric recognition errors". In both the wren and warbler cases however, a lack of discrimination in response to conspecific song variants in one population, but not another, was important in elucidating a potentially significant directional barrier to gene flow.

We examined recognition of song variation in pairs of endangered North Island kōkako (*Callaeas wilsoni*), a passerine of the endemic New Zealand family Callaeidae. Kōkako have declined due to introduced mammalian predators, and translocations to offshore islands and to intensively managed mainland sites have been critical to this species’ conservation. Kōkako defend year-round territories by producing lengthy duets (up to 30 s; Molles et al., 2006), with easily distinguishable dialects among populations (Hudson, 2001; Molles et al., 2006). We performed two reciprocal experiments on disjunct, isolated kōkako populations, both of which are frequently used as sources for translocations (catalogued in Molles et al., 2008). We employed stereo duet playback, a useful technique for investigating the functions of songs from the perspective of both pair members (reviewed in Douglas and Mennill, 2010), to present territorial pairs in two populations with: (1) local and foreign duets to examine inter-population dialect discrimination and, (2) simulated mixed-dialect duets consisting of vocal contributions from either a local male or a local female, combined with a foreign partner, to assess the relative importance of each sex in dialect recognition and any resulting discrimination. Both the ‘recognition’ hypothesis (McArthur, 1986) and the ‘relative threat’ hypothesis (Rothstein and Fleischer, 1987), while not mutually exclusive, predict that responses to local duets should be stronger than to foreign duets in both study populations (Experiment 1). Experiment 2 seeks to determine if the male component of a duet is a more salient signal in population recognition and territory defence than the female component. As males tend to sing more during duets (Molles et al., 2006), we predict that responses to the synthesised duets comprised of a local-male song should be stronger than to the stimulus comprised with a local-female song.

3.3 Methods

3.3.1 Study sites and field recording

The two populations in this study are located on the North Island, New Zealand. The larger Mapara Wildlife Reserve (hereafter "Mapara"; 1,300 ha, lat. 38˚32´S, long. 175˚16´E) comprises three near-contiguous forest blocks and has a kōkako breeding population of 87 pairs (density = 6.6 pairs/100 ha; M. Spearpoint & S. Govella, New Zealand Department of Conservation, personal communication). The smaller Rotoehu Forest (hereafter "Rotoehu"; 440 ha, lat. 37˚58´S, long. 176˚32´E) contains approximately 30 kōkako pairs (density = 6.8 pairs/100 ha; N. Spurdle, New Zealand Department of Conservation, personal communication).

Kōkako sing repeated, easily identifiable song sequences, known as ‘themes’, comprised of phrases of grouped notes, or elements (Molles et al., 2006). Pairs produce a moderately large repertoire of phrases ($\bar{X}$ ± SE; Mapara: 17.4 ± 1.4, authors, unpublished data; Rotoehu: 18.3 ± 0.6, Molles et al., 2006), and sing duets by combining phrases into sequences (Figure 3.1a), which are not usually sex-specific but are typically made by the same individual within a pair (Molles et al., 2006). A recordist can differentiate between the singers by positioning themselves between two duetting birds, and quietly dictating their identities into the microphone.

We recorded kōkako song (Mapara: Oct 2008–Apr 2010; Rotoehu: Mar–Apr 2010) by locating known territories in the early morning and either recording naturally singing focal pairs or by playing short bursts of recorded song to stimulate singing. Recordings were made using a directional microphone (Sennheiser ME66 or MKH416) and a digital recorder (Marantz PMD 660), and saved as uncompressed monaural WAV files (16-bit, 44 kHz). Recorded songs had a high signal-to-noise ratio and low background noise with little heterospecific acoustic interference. Where necessary, background noise was digitally removed from sound files using the lasso selection tool followed by a frequency bandpass filter between 300 Hz and 10,000 Hz using Audition (Adobe, San Jose, CA, U.S.A.).

As kōkako are sexually monomorphic in plumage, identifying sex of birds in the field is problematic (Flux and Innes, 2001). In some cases the New Zealand Department of Conservation had fitted birds with uniquely coloured bands prior to this study, making individual identification possible; at least one member of a pair was colour-banded in eight of nine pairs at Mapara, and two of six pairs at Rotoehu. In these cases, sex was known from genetic tests (two birds at Mapara, two birds at Rotoehu), or determined through body measurements (one pair at Mapara; see Flux and Innes, 2001 for details) or detailed behavioural observations during incubation when only the female tends the clutch (Flux and Innes, 2001; six birds at Mapara, ten birds at Rotoehu). Where birds were not banded, sex was inferred for two birds at Mapara and four birds at Rotoehu based on: (1) the amount of singing (males normally sing a greater portion of duets than females; Molles et al., 2006), and/or (2) the use of certain phrase types that are strongly sex-biased (i.e. 'E' phrases; Molles et al., 2006).

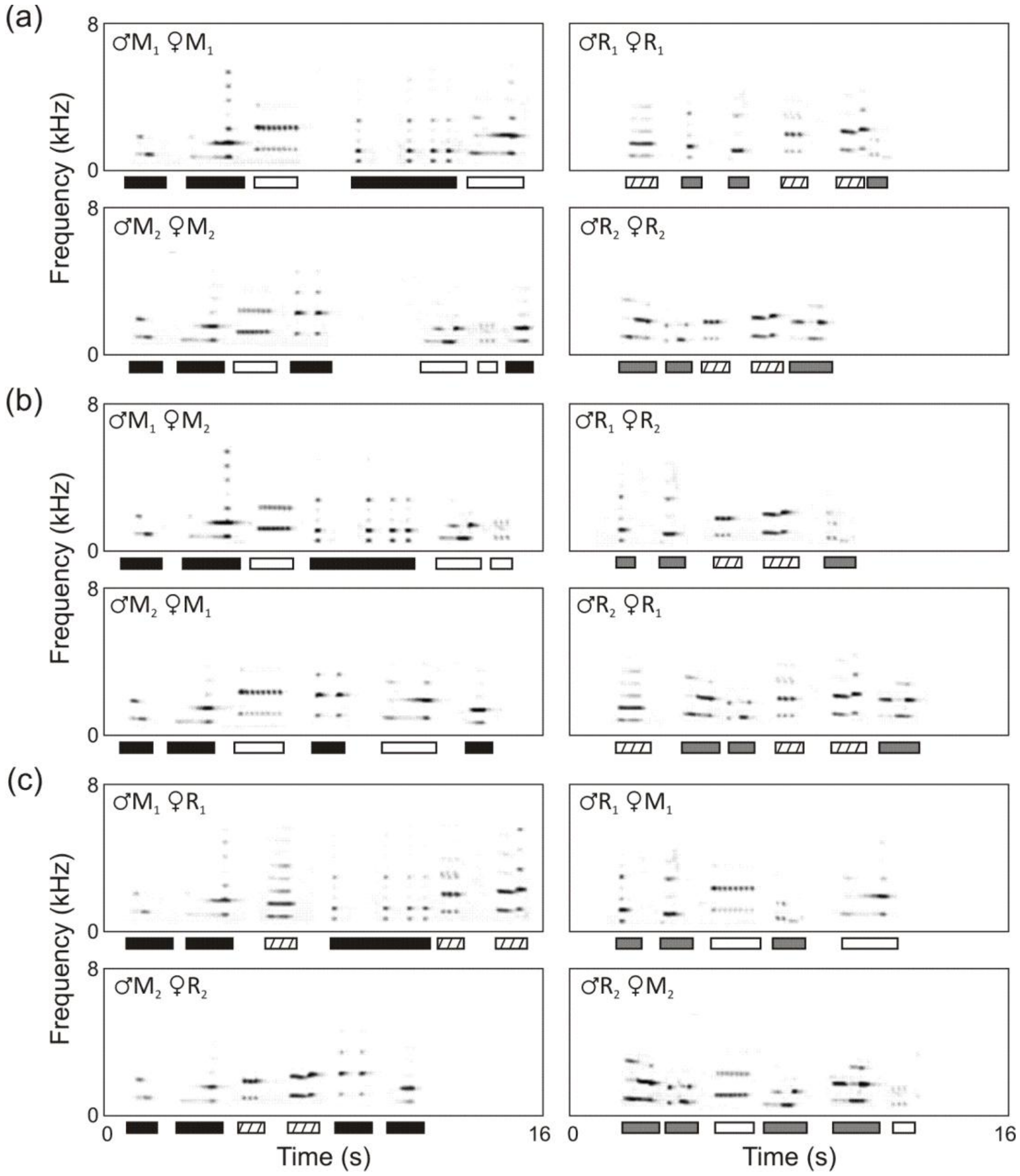

Figure 3.1 Sonographic examples of: (a) kōkako duets produced naturally by two pairs at Mapara (M1 and M2) and Rotoehu (R1 and R2); (b) synthesised local-local duet stimuli representing pairs at Mapara (M) and Rotoehu (R); and (c) synthesised mixed-dialect duet stimuli representing either a Mapara male and a Rotoehu female (left examples), or a Rotoehu male and a Mapara female (right examples). Duet components are indicated by shaded bars below sonograms: Mapara male (black) and female (hollow), Rotoehu male (gray) and female (diagonal lines). See Tracks 6–8 in Appendix 1 for examples.

3.3.2 Stimuli preparation

To generate playback stimuli, we used recordings of birds that were not neighbours of the playback subjects, but occupied territories sufficiently nearby to sing a similar geographic variant to that of the test pairs. The mean distance from test location to recording location for local stimuli was 703 m at Mapara, and 1,173 m at Rotoehu, which corresponds to the width of 2–3 territories in each population.

Our first experiment examined the birds' discrimination of duets produced by pairs singing either pure local or pure foreign dialects (Mapara, 22 August–2 September 2010, 7 pairs; Rotoehu, 11–20 September 2010, 8 pairs). We digitally separated the individual component phrases from the duet recordings from each population and synthesised novel cross-pair duets by recombining song phrases of the male from one pair with the female from another pair within the same population (Figure 3.1b; Tracks 6 and 7, Appendix 1). Where necessary, we modified the timing of the duet slightly to avoid overlapping contributions. We chose not to use true-pair duets in this experiment as artefacts necessarily introduced into the stimuli for the second experiment (see below) would prevent comparison across the two experiments. Normalising the amplitude of the male and female duet components is a common procedure in stereo speaker duet playback experiments (e.g. Logue and Gammon, 2004; Rogers et al., 2004; Mennill, 2006), ensuring that responses to the two speakers would not be influenced by variation in amplitude (Douglas and Mennill, 2010). We therefore normalised each channel in all synthesised duets to -1 dB using Audition.

In the second experiment we examined the birds' responses to duets comprised of local male or local female components, combined with foreign partner components (Mapara, 26 August–9 September 2010, 7 pairs; Rotoehu, 13–22 October 2010, 9 pairs). We synthesised hybrid, mixed-dialect stimuli of two kinds: (1) duets comprised of component phrases from a Mapara male and a Rotoehu female (Figure 3.1c, left sonograms; Track 8, Appendix 1); and (2) duets comprised of phrases from a Rotoehu male and a Mapara female (Figure 3.1c, right sonograms). We hereafter refer to the synthesised mixed-dialect duets as either local-male/foreign-female or local-female/foreign-male.

For both experiments, the synthesised stimuli were saved as 16-bit, 44.1 kHz stereo wave files with the individual contributions of each bird assigned to separate audio channels. The resulting same-dialect cross-pair duet stimuli (Experiment 1) were a length ($\bar{X}$ ± SE) of 9.22 ± 0.56 s for Mapara birds and 8.43 ± 0.47 s for Rotoehu birds; the mixed-dialect duet stimuli (Experiment 2) were 9.51 ± 0.68 s for Mapara male/Rotoehu female and 8.32 ± 0.37 s for Rotoehu male/Mapara female. An appropriate silent period was appended to each stimulus to standardise all stimuli to 30 s, and all stimuli were then repeated 6 times for a total playback period length of 360 s.

To create playback stimuli, we used recordings of the main duet themes of nine pairs from Mapara (three from each of the three adjoining forest blocks) and six pairs from Rotoehu. Although the use of the same recordings to test responses of multiple pairs constitutes pseudoreplication in the strictest sense (McGregor et al., 1992; McGregor, 2000), this concept has recently been debated at length (Freeberg and Lucas, 2009; Hurlbert, 2009; Schank and Koehnle, 2009; Wiley, 2009). Due to the difficulty in acquiring high quality recordings in which we had a strong degree of certainty of each bird's sex, we made repeated use of recordings in preparing playback stimuli (individual uses per experiment = 3.0 ± 0.21, range = 1–6). No individual's song was used more than three times at any site in the same experiment.

3.3.3 Experimental sites and playback procedure

Kōkako pairs defend their year-round territories by singing from song posts in the early morning, typically tall trees within the territory. We chose experimental sites based on song posts within territories detected during the recording period. At each site we marked a playback arena using coloured tape, bounded by two "end lines", 40 m apart, and divided by a "centre line" 20 m from each end of the arena (Figure 3.2). On each end line we marked two points, 15 m apart, at which we

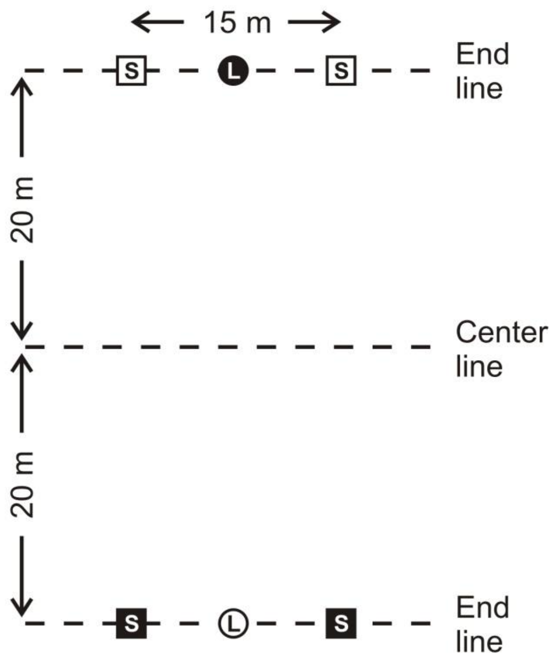

Figure 3.2 Experimental playback arena indicating lure ("L" circles) and speaker ("S" squares) locations during the first (white) and second (black) treatments in each trial. Flagged end- and centre-lines are represented by horizontal dashed lines.

raised amplified speakers (model: Mobile Cube, Roland Corporation, Hamamatsu, Japan) 3.5 m above the ground on extendable carbon-fibre poles. Prior to running trials we set the amplitude of each speaker to 80 dB measured at 1 m facing a Realistic sound level meter (model 33-2050, Radioshack, Fort Worth, TX, USA), which approximated natural song amplitude based on auditory comparisons in the field. Each identical half of the arena was used sequentially for the two stimuli playback treatments in each trial (see below). Where logistically possible, the same pairs were tested in both experiments using the same playback arena (5 times at Mapara, 5 times at Rotoehu).

Given that initial approach measurements are likely to be influenced by the chance location of the pair at the start of the trial, we used an acoustic lure to ensure that subjects were in a standardised position before commencing playback. To avoid prematurely influencing the focal pair with dialect-specific song, we broadcast a series of '*mew*' vocalisations (Molles et al., 2006) at a typical rate of one every minute, recorded from a non-neighbouring bird in the same population. *Mews* are an appropriate vocalisation type for a lure as they are thought to function in maintaining contact between birds and have a broadly similar acoustic structure across populations (authors, unpublished data). We broadcast the lure using a single speaker (model: mm32, Logitech Ltd., Hong Kong) from a location directly between the markers on the opposite end line of the arena, 40 m from the playback speakers. When both members of the focal pair approached to within 5 m of the lure, the lure was stopped and the first stimulus track started. Each 360 s stimulus presentation was then followed by a post-playback recording and observation period of 240 s, resulting in a total treatment period of 600 s. Immediately following the first treatment, the pair was lured to the opposite end of the playback arena to the first lure location (and between the first pair of speakers), and the second portion of the trial was performed. To reduce the influence of order effects on experimental outcome, playback order of the two stimulus types was balanced within experiment type at both sites.

3.3.4 Response measures

To characterise the physical response to each playback stimulus, we scored two variables: (1) *Approach latency*, defined as the time taken for the leading bird to cross the centre line from its starting position at the lure. We chose this variable as it is independent of the pair's experience of failing to find conspecific intruders upon speaker approach. When neither bird approached to within 20m, we assigned that trial a maximum latency value: the maximum approach time over all trials plus an additional 30 s (at 5 per cent of the total trial period, adding this amount to the maximum value provides a conservative indication of the low strength of response while not unduly biasing the data in favour of those values). The second measure, (2) *Pair attendance*, was a binomial variable where a value of 1 was assigned if the pair remained < 10 m apart for at least 90% of the treatment period, and a value of 0 was assigned otherwise. A 10 m distance approximates the separation of the pair if they were not in the same tree, and were thus not physically attending to each other (choosing a 90 % cut-off allowed for short periods when one bird may have flown ahead in approaching the speakers; kōkako travel in long leaps or glides, meaning that an immediately following partner could briefly be separated from the leading bird). During trials in Experiment 2 we also noted which speaker was approached first.

Two observers were present during the trials: The first observer, who was blind to the stimulus type used, operated the lure and dictated pair separation distances, while the second observer remained at the centre of the arena to record the time when the leading bird crossed the centre line. The second observer, who operated the playback unit and therefore could not be blinded as to the stimulus type, also recorded all vocalisations made by the pair (using the same equipment as used during stimuli recording; see above). From these we scored three vocal variables: (i) *Vocal latency* – the time taken for the pair to produce a song phrase; (ii) *Vocal output* – the total number of song phrases produced by the pair during the treatment period; (iii) *Vocal diversity* – the number of different phrase types produced by the pair divided by the vocal output. As we were interested in between-pair territorial signals, for all vocal measures we did not score *tooks*, which are produced during within-pair communication, or *mews* which are thought to maintain contact between pair members, and which we used for the lure.

3.3.5 Statistical analysis

We assessed the effect of independent predictor variables on the nominal response variable *pair attendance* using a logistic regression model. The remaining continuous response variables were analyzed using general linear mixed-models (GLMM). Including all variables is justified given there were no pairwise correlations above 70% (Table 3.1). In addition to balancing treatment presentation orders, we statistically accounted for any potential effect by including *stimulus order* as an ordinal variable in the GLMM. As territorial neighbours to the test pairs began to sing during some of the trials, potentially influencing our measures of the pair's playback response, we scored a binomial factor, *neighbour song*, to reflect this in the models. Neighbouring pairs were excluded from this study to

Table 3.1 Correlation matrix of continuous response variables

	approach latency	vocal latency	vocal output	vocal diversity
approach latency	-	0.30	-0.28	0.37
vocal latency	0.30	-	-0.45	0.36
vocal output	-0.28	-0.45	-	-0.68
vocal diversity	0.37	0.36	-0.68	-

remove the effects of habituation. We also tested for a possible interaction effect between *site* and *stimulus type* to detect whether there were any differences in stimulus discrimination between the two sites. In the full models we therefore included the effects of the fixed factors (*site, stimulus type*, *stimulus order, neighbour song*, and *site*/*stimulus type* interaction) on each of the dependent response variables (*approach latency*, *vocal latency*, *vocal output*, and *vocal diversity*). We corrected for multiple sampling of different test pairs by including *pair identity* as a random factor in the models, estimated using the restricted maximum likelihood (REML) method (Bartlett, 1937). All analyses were performed using JMP (version 9.0.2, SAS Institute Inc., Cary, NC, USA), all reported values are means ± standard error, and all *P*-values are two tailed.

3.4 Results

In 6 trials in Experiment 1 neither member of the pair approached to within 20 m of the playback speakers in response to at least one of the treatments. In 4 of the 5 cases at Mapara this was in response to the foreign-foreign stimulus, while at Rotoehu this was true in response to one of each of the two treatments. In Experiment 2 however, at least one member across all pairs at both sites approached to within 20 m of the speakers during the treatment phase, with the exception of one pair at each site that failed to do so after local-male/foreign-female stimulus.

We successfully conducted 15 playback trials in Experiment 1 (7 at Mapara, 8 at Rotoehu) and 16 playback trials in Experiment 2 (7 at Mapara, 9 at Rotoehu).

These experiments revealed that kōkako are sensitive to local versus foreign dialects in territorial duets, but respond similarly when both intruders are local as when only one of the intruders is local.

3.4.1 Physical responses

The overall logistic regression model for *pair attendance* was non-significant for Experiment 1 ($\chi^2_5 = 6.02$, $N = 32$, $P = 0.304$), whereas the whole model for Experiment 2 was significant ($\chi^2_5 = 13.13$, $N = 32$, $P = 0.022$). Parameter estimates for this test revealed that *site* ($\chi^2_5 = 7.57$, N = 32, P = 0.006) and *neighbour song* ($\chi^2_5 = 5.88$, $N = 32$, $P = 0.015$) were the only significant predictor variables in Experiment 2; all other *P*-values were > 0.4. In 11 of 14 trials at Mapara (76.8%) and 8 of 18 trials (44.4%) at Rotoehu, pairs remained together for at least 90% of the trial.

The GLMM for Experiment 1 also revealed a near-significant effect of the *site*/*stimulus type* interaction term on *approach latency* ($F_{1,12.7} = 3.58$, $P = 0.081$); we consequently ran the models again for each site independently. At Mapara, pairs approached local duet stimuli with significantly less delay than foreign duet stimuli (local duet = 171.21 ± 74.06 s, foreign duet = 423.64 ± 88.61 s; $F_{1,5} = 7.69$, $P = 0.039$), while at Rotoehu there was no effect of *stimulus type*, *stimulus order*, or *neighbour song* (all $P \geq 0.2$). Full models in Experiment 2 revealed no significant effects by any of the independent variables on *approach latency* (all $P \geq 0.3$). However, pairs tended to approach with comparatively less delay when the stimulus contained foreign-male and local-female components (*approach latency*; foreign-male/local-female = 131.02 ± 30.41 s, local-male/foreign-female = 70.50 ± 11.03 s; $F_{1,11.5} = 3.30$, $P = 0.096$). Additionally, test pairs were more likely to initially approach the speaker broadcasting the local dialect component (20/28 trials) compared to the foreign dialect component (8/28 trials; binomial test, $P = 0.036$).

3.4.2 Vocal responses

In Experiment 1, pair vocal responses to local duet song were significantly different than to foreign duet song (Figure 3.3), whereby pairs vocalised with less

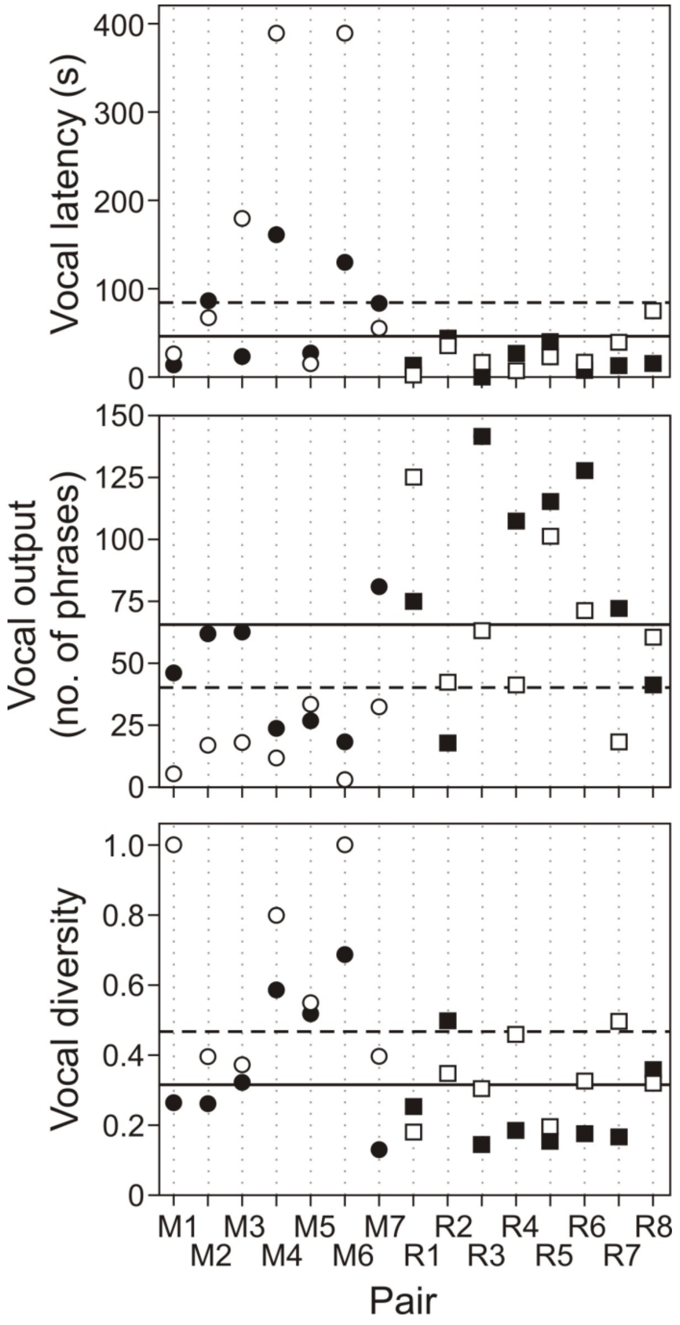

Figure 3.3 Individual test pair responses to playback of local (black shapes) and foreign duets (hollow shapes) at Mapara (circles) and Rotoehu (squares). Overall mean response values are represented by horizontal lines for local (solid line) and foreign duet stimuli (dashed line). Vocal diversity is calculated as the number of different phrase types divided by the total number of phrases produced.

delay (*vocal latency*: local duet, 45.65 ± 12.54 s; foreign duet, 89.90 ± 33.35 s; $F_{1, 12.9} = 5.19$, $P = 0.040$), and produced more song phrases (*vocal output*: local duet, 65.73 ± 10.46; foreign duet, 40.73 ± 9.19; $F_{1, 12.6} = 5.90$, $P = 0.031$) with lower diversity (*vocal diversity*: local duet, 0.32 ± 0.05; foreign duet, 0.48 ± 0.07; $F_{1,12.8} = 6.71$, $P = 0.023$). Playback *site* was the only other significant factor in all models (*vocal latency*: Mapara = 118.17 ± 33.86 s, Rotoehu = 23.58 ± 4.88 s; *vocal output*, Mapara, 29.50 ± 6.26; Rotoehu, 74.00 ± 9.89; *vocal diversity*: Mapara = 0.52 ± 0.07, Rotoehu = 0.29 ± 0.03; all $P < 0.05$; Figure 3.3).

In Experiment 2, pair vocal responses to the two mixed-dialect duet stimuli were not significantly affected by *stimulus type*, *site*, or the interaction of those two factors (all $P > 0.3$). Pairs vocalised with a similar delay (*vocal latency*; local-male/foreign-female = 72.42 ± 35.90 s, foreign-male/local-female = 46.48 ± 10.44 s), producing similar numbers of phrases (*vocal output*; local-male/foreign-female = 53.31 ± 8.23, foreign-male/local-female = 51.06 ± 7.44), with a similar diversity (*vocal diversity*; local-male/foreign-female = 0.28 ± 0.03, foreign-male/local-female = 0.35 ± 0.03). The model for *vocal output* showed significant effects of *stimulus order* ($P = 0.002$) and *neighbour song* ($P = 0.009$), whereby pairs responded with a greater number of phrases to the first stimulus and when their neighbours were also singing.

3.5 Discussion

Our first experiment showed that overall, local duets elicit a much stronger reaction than foreign duets when broadcast to territorial pairs of kōkako. When pairs perceived local territorial intruders they rapidly responded by producing a greater number, yet lower diversity of phrases, while responding to foreign duets with a fewer number, yet greater diversity of phrases. The pairs' physical approaches to local duet stimuli were also more rapid than to foreign duets stimuli at Mapara, although we did not find this pattern at Rotoehu. However, these general findings are congruent with both hypotheses for signal-based discrimination. Under the recognition hypothesis (McArthur, 1986), response to foreign song is diminished compared to local song as the non-local songs are not clearly perceived as conspecific signals, while under the relative threat hypothesis

(Rothstein and Fleischer, 1987), foreign songs are recognised as conspecific signals but responses are reduced due to signal dissimilarity, and are therefore less intimidating than local songs. Even though pair responses revealed a clear and significant difference between treatments, pairs do respond to foreign song, indicating that these songs were recognised as conspecific and thus supporting the latter hypothesis. While local duets may represent a strong threat, foreign duets represent birds that are less likely to usurp a pair or individual from their territory and/or breeding position.

Our results may have been confounded by incorrectly assigning sex to the recorded birds, and thus the playback stimuli. We feel that the effect of such errors would have been minimal as same-sex pairs are known to occur in both of the study populations in rare cases, and so would be familiar to test pairs. Additionally, if we did accidentally present pairs with same-sex local duet stimuli the response would still be to that of a local signal. Same-sex foreign duet stimuli are unlikely to be treated differently to male-female duets due to the test pairs' unfamiliarity with the structure of foreign dialect duets and inability to distinguish between male and female duet contributions.

Kōkako pairs produced a less diverse vocal response following local duet playback. In some species, a low-diversity song is associated with increased aggression (e.g. red-winged blackbird, *Agelaius phoeniceus*, Searcy and Yasukawa, 1990; dunnock, *Prunella modularis*, Langmore, 1997; banded wren, *Thryophilus pleurostictus*, Molles and Vehrencamp, 1999; but not song sparrow, *Melospiza melodia*, Kramer and Lemon, 1983). As kōkako engage in matched counter-singing (Molles and Waas, 2006), the pattern of lowered diversity may therefore indicate a stronger threat response in this species. This finding is consistent with the results for the other vocal response variables, *vocal latency* and *vocal output*. An alternative explanation is that, in producing more phrases in response to local duets, pairs may have utilised greater proportions of their repertoire compared to a low output response, and so necessarily re-use phrases with each additional one produced, thus diluting the overall vocal diversity of the response. In contrast, when responding to foreign duets, pairs produce fewer phrases with a higher diversity.

Although we found an effect of *stimulus type* overall, we also found that *site* was a significant factor affecting vocal response variables in Experiment 1. Pairs at Rotoehu were faster to respond, were more vocal, and produced a lower diversity of phrase types, when compared to pairs at Mapara. A potential explanation is the large discrepancy in the number of breeding pairs across the two sites (87 at Mapara versus 30 at Rotoehu). Dispersing juveniles at Mapara may be exposed to a greater diversity of songs compared to those at Rotoehu, which may expand the range of phrase types that they deem familiar (i.e. local). Alternatively, this pattern could be explained by the difference in temporal proximity of the trials to breeding at the two sites: 50 days before the mean incubation start date at Rotoehu (10 Nov; J. Innes, Landcare Research, personal communication) compared to 83 days at Mapara (25 November; I. Flux, North Island Kōkako Recovery Group, personal communication). Although aggressive territorial behaviours are thought to be endocrinologically mediated by high circulating levels of testosterone (Wingfield et al., 1987) and/or luteinising hormones prior to breeding (Levin and Wingfield, 1992), we suggest that this alternative is unlikely given that at both sites the trials were completed well before the breeding period. Similarly, explanations for across-site differences based on the demographic histories of the populations are unlikely; both populations declined to lows of < 5 breeding pairs prior to 1989 (Flux et al., 1994; Innes et al., 1996) and have comparable current population densities. Experiment 2 revealed that pairs at Mapara were also more attentive to their partner than those at Rotoehu, but this effect may have been confounded by the effect of *neighbour song*.

Overall, our second experiment showed that pairs respond similarly to both mixed-dialect duet stimuli, and initially approached the speaker broadcasting the local duet component. *Approach latency* however, was comparatively shorter in response to foreign-male/local-female duets. As we know that pairs are able to discriminate between local and foreign duets, and approach more rapidly to local duets (Experiment 1), a similarly rapid approach to foreign-male/local-female stimuli in Experiment 2 is best interpreted as a response to the local-female component rather than the foreign-male component. Either males were driving the response and approaching to assess the potential of a new same-dialect partner, or females were doing so to challenge a perceived same-sex intruder and prevent being usurped from the partnership (e.g. Rogers et al., 2007). However, as distinguishing males from females in the field is prohibitively difficult, we are unable to assess this result further. Although our measure of *vocal output* was compromised by *stimulus order* and *neighbour song* in Experiment 2, we can assess the relative strength of the vocal responses by qualitatively comparing *vocal latency* to those of the single dialect treatments in Experiment 1. Doing so suggests that pairs vocalised with a similar delay to both mixed-dialect stimuli (local-male/foreign-female, 72.42 ± 35.90 s; foreign-male/local-female, 46.48 ± 10.44 s) as they did to local-local stimuli (45.64 ± 12.54 s). These findings show that any familiar component of the stimulus, whether male or female, triggers a strong reaction from at least one of the pair members, equivalent to that of local-local duet stimulus.

Our results agree with those of Wright & Dorin (2001) and thus extend support for both the recognition and relative threat hypotheses for dialect-based discrimination to a territorial and endangered duetting species. Furthermore, from an evolutionary perspective our findings indicate that, in this species, successful territory defence by mixed-origin pairs, and thus the breakdown of a potential behavioural barriers to gene flow, may be possible between behaviourally distinct populations. With the arrival of humans in New Zealand, opportunities for natal dispersal in kōkako between disjunct dialect groups has been reduced, as appropriate habitat has become highly fragmented and embedded in a grassland matrix unfavourable for kōkako. However, multi-source translocations have led to artificial secondary contact between populations, which can result in mixed-dialect pair formation (H. Speed, Department of Conservation, personal communication). Our findings have implications for conservation science as they challenge the idea that cultural homogeneity in translocated animals is required for successful territory establishment and reproduction, although sourcing birds from the same dialect area is optimal where possible. As conservation managers of endangered species are faced with choosing birds from a limited number of populations for translocations, our findings suggest that knowledge of intra-population behavioural discrimination may be crucial for a positive translocation outcome. Assessing the outcomes of past and future multi-source translocations may highlight the evolutionary and practical consequences of behavioural variation on conservation outcomes. To our knowledge, our study is the first to synthesise duets using components from different song dialects. Further studies that replicate this design may additionally elucidate the influence of sex-specific dialect discrimination in duetting birds, which may be crucial to achieving the long-term conservation goals in duetting species such as kōkako.

3.6 Acknowledgements

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Chapter 4: Long-term data reveal dialect-based assortative pairing following translocation of an endangered species

4.1 Abstract

Animals translocated for conservation purposes may be sourced from a single location or multiple locations which may exhibit inter-site variability in reproductive behaviours. The influence that these differences can have on the propensity and pace of pair formation, and the ultimate impact this may have on the success of the translocation, is unknown due to the low sample sizes of many translocations. We address this knowledge gap by collating an existing 18-year data set documenting multi-source translocations of the endangered North Island kōkako, a species with known population-specific duets, to six sites from 11 source populations. We found that when all six sites are considered individually, kōkako pairs form assortatively with respect to dialect (like with like), significantly so at two sites. When data from all sites are combined, kōkako pairs form assortatively more often than expected by chance. However, mixed-dialect pairs did form at two sites, either when an existing "core" population was present at the time of translocation or following the release of a captive-reared sub-adult bird with potentially plastic song. Our findings make an important contribution towards understanding the impact behavioural variation can have on the conservation of endangered species, and highlights the value of combining long-term data from multiple sources.

4.2 Introduction

Endangered species conservation invariably involves the management of small populations within a small number of protected habitats. Intentional movements of animals to introduce, re-introduce, or supplement populations, collectively termed translocations (IUCN, 1998), are used extensively to achieve the goal of species persistence (Fischer and Lindenmayer, 2000). Translocation success, defined as the production of a viable, self-sustaining population in the wild (Griffith et al., 1989), hinges on pairs forming and reproducing successfully. To maintain genetic diversity, translocations are frequently sourced from two or more distinct populations (Innes and Flux, 1999), yet the behavioural implications of doing so are rarely considered, particularly with regard to mate choice. Therefore, in solving a genetic problem, a behavioural problem may be created which could limit successful reproduction in the founder population.

When translocated songbirds originate from culturally distinct populations, dialect differences may inhibit across-population pair formation at the release site, thus exacerbating the bottleneck effect. The conclusion that birds chose mates based on dialect as a proxy for population membership is based on the combined ideas that, (1) bird song generally functions in mate attraction (e.g. Eriksson and Wallin, 1986), and 2) birds are able to discriminate between dialects (e.g. Podos, 2010). Nevertheless, to our knowledge, song-dialects have rarely been documented to affect mate choice of free-living birds (see Table 1.1 in Chapter 1), particularly in duetting species. When dealing with endangered species, this conclusion may be informed by only a small number of observations with consequently little statistical power. This deficiency can be addressed with the use of long-term data sets collected by government agencies and conservation bodies, which should be harnessed to address key ecological and conservation issues.

We present a case study of the North Island kōkako (*Callaeas wilsoni*) to address the issue of how mate choice might impact translocation success in the face of low statistical strength associated with small sample sizes. Kōkako are endangered songbirds endemic to New Zealand that have been the subject of numerous translocations in the past 30 years (catalogued in Molles et al., 2008). Kōkako are known to exhibit population-specific song dialects (S. Valderrama, University of Waikato, unpublished data; see Chapter 3), in which mated pairs produce lengthy duets (up to 30s; Molles et al., 2006) by producing serial stereotyped phrases. Duetting is thought to be a cooperative behaviour between sexual partners in some species (reviewed in Hall, 2004), used for enhancing the pair-bond (Wickler and Seibt, 1980), maintaining contact (e.g. Mennill and Vehrencamp, 2008), jointly defending a territory (Seibt and Wickler, 1977), and achieving reproductive synchrony (Dilger, 1953). Learning to coordinate lengthy duets may be a costly exercise in terms of perfecting phrase timing and sequencing, which may occur more easily between birds from the same population that are both familiar with dialect-specific duet rules (Logue, 2006). Additionally, although in most birds it is the female who selects the partner, in duetting birds mate choice may be mutual (Tobias et al., 2011), increasing the importance of intersexual song familiarity. In this study, we take advantage of an existing 18-year data set involving multi-source translocations to six sites from 11 source populations to determine if kōkako pair assortatively with regard to source population and song dialect. Integrating long-term data such as these is crucial for informing the logical composition of translocation cohorts.

4.3 Methods

We collected unpublished post-release reports of 11 multi-source translocations of kōkako to six different sites (Figure 4.1) over 18 years (i.e. 1993–2011) completed by staff and associates of the New Zealand Department of Conservation (DOC). Although these reports varied in their level of detail, in all cases the released birds carried uniquely coloured leg-bands, and in most cases we were able to extract data from the reports including the date of translocation, the number, sex, and origin of translocated birds, and (if applicable) the number and sex of birds known to exist at the release site at the time of release (i.e. the "core" population). Additionally, if the release site supported a core population at the time of release, these reports contained pre-translocation survey data of the release site population, including known pair identity information.

At each release site in each breeding season (approximately Oct–April) for which data were available, we determined the number of permutations of potential pairs that could have formed given the number of unpaired birds in the population. In calculating pairing probabilities we made the following assumptions: (1) Birds caught and translocated as pairs were as likely to form new partnerships as those translocated as unpaired singles. This assumption is realistic as pairs typically

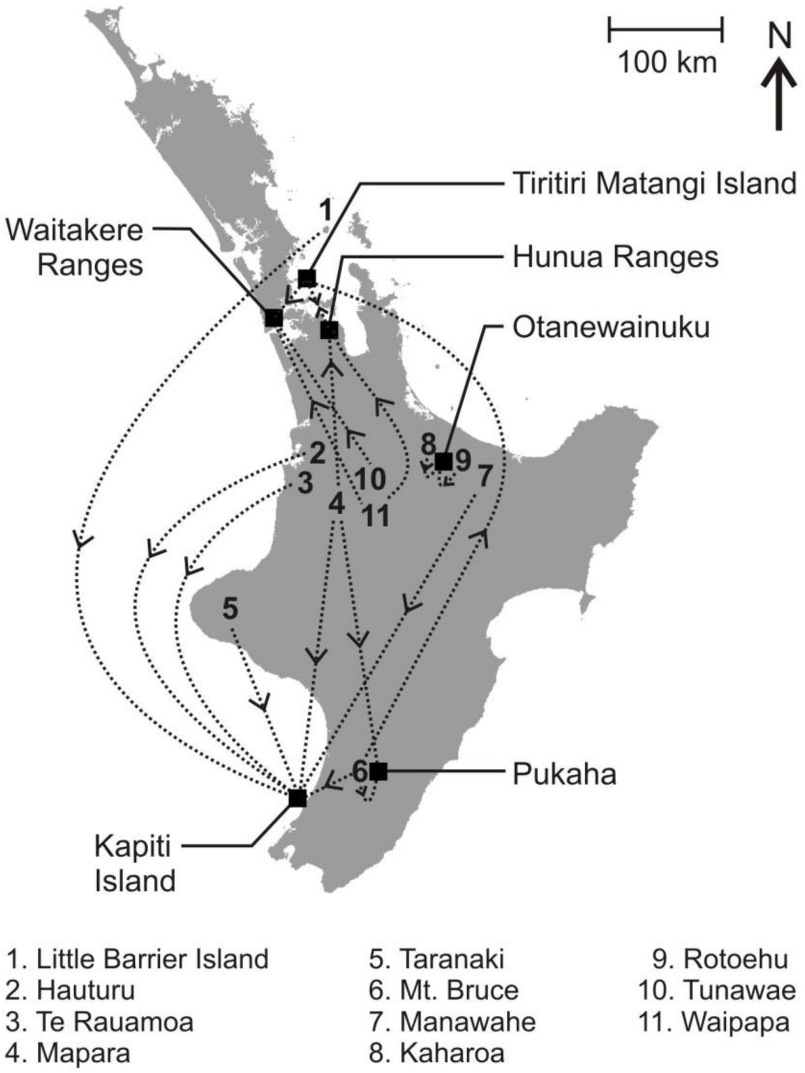

Figure 4.1 Map of the North Island, New Zealand, showing locations of source sites (numbers) and release sites (black squares) involved in multi-source translocations of kōkako (dashed lines).

divorce during translocation (S. King, DOC, personal communication; but see Chapter 2). (2) Pairs that formed after release remained stable. While divorce can occur naturally in kōkako, of the 35 pairs assessed in this study only 1 pair eventually divorced. Furthermore, at a site monitored by Higgins et al. (2006) between 1990–2000, only 7.4% of pairs changed mates for reasons other than the partner's death. (3) A bird whose partner died was as likely to form a new partnership the following season as an unpaired bird. (4) Birds in male-male partnerships in one season were "available" for pairing the following season. Male-male pairs do occur in kōkako (Innes et al., 1999), although this occurrence is rare and probably results from a strongly male-biased sex-ratio in declining populations (Innes et al., 1999). We also adhered to the following sampling rules: (i) Only birds seen on surveys or incidentally after 1st October of that season (i.e. the beginning of the breeding season) were counted in the totals, even though some birds are known to have been alive based on sightings in later years. (ii) When a bird's sex was unconfirmed, it was omitted from the analysis.

Given that kōkako produce population-specific song-dialects, we designated pair types depending in whether pairs were comprised of: (a) birds from same dialect populations (SD), or (b) birds from different dialect populations (DD). We excluded pairs where at least one bird fledged at the release site following translocation (FD), based on an assessment of the site and season with the highest ratio of FD pair formation. In this case, pair formation involving FD birds was much less frequent than SD and DD pairings, although we acknowledge that there are occasional contra-indications from seasons with less data (i.e. a single pair involving a locally-fledged bird; Kapiti Island, 1996/1997).

At each translocation release site we calculated the ratio of observed pairs to not-observed pairs (i.e. possibly-occurring) of the two types (i.e. SD and DD) in each season, hereafter termed "hit ratios"; this allowed us to assess which pairing type predominated and whether the direction of that pairing was assortative or non-assortative with respect to dialect.

We used the mid-p values of 1-tailed Fisher's exact tests for each season at each site to compare the chance of achieving the observed pairs given the possible pairs of the two pair types. Mid-p values, calculated as P(evidence **more** favourable to $H_a|H_o$) + ½ P(evidence **precisely** as favourable to $H_a|H_o$), were first proposed by Lancaster (1949, 1961) and have been suggested as a way to reduce Type-II errors by Routledge (1994) and Agresti and Gottard (2006). If the hit ratios indicated non-assortative pairing we used the complementary mid-value to account for a change in the direction of the dominant trend.

Under the null hypothesis of non-assortative mating, all SD and DD pairings are equally probable. Therefore in the seasons with low numbers of observed pairs we determined all possible pair combinations corresponding to the number of pairings observed in that season. Note that for the Hunua Ranges in 2008–2009, the number of pair combinations was too large for complete enumeration, so we randomly selected 100,000 runs of the appropriate number of pairings.

To calculate the overall significance of achieving the observed pairings given the possible pairings, we used a weighted Z-transform test to combine all mid-p values (or complementary values, see above) across seasons within sites using the *combine.test* function in the *survcomp* package (Haibe-Kains et al., 2008) in the program R (R Development Core Team 2011). We chose this method as it has been demonstrated to have more statistical power and precision than the Fisher's combined probability test, or the unweighted Z-transform test (Whitlock, 2005). For this test, we assigned a weighting value based on the number of observed pairs in each season. This procedure is appropriate as it emphasises each season proportional to the statistical power of the individual test in that season. To determine the overall significance of pairing patterns we performed a combined weighted Z-transform test using all independent site-specific P-values.

4.4 Results

We found that, on average, kōkako paired assortatively with respect to origin population and song dialect over most seasons at all six sites (Table 4.1). When sites and seasons were considered separately, this pattern was statistically significant in two seasons at two sites (Kapiti Island, 1997–1998, P = 0.036; Waitakere Ranges, 2010–2011, P = 0.017; Table 4.1), and at a level close to significance at one site in one season (Kapiti Island, 1993–1994, P = 0.083; Table 4.1). When combining across seasons for the two sites which we had data from multiple years we found that, overall, pairs formed assortatively more often than chance on Kapiti Island (P = 0.010, Table 4.1), but not in the Hunua Ranges (P = 0.223, Table 4.1). When seasons are combined within sites, Z-transform tests revealed that, overall, pairs formed assortatively with respect to origin population (P =0.007; Table 4.1). The only sites in which mixed-dialect pairs formed were

Table 4.1 Seasonally possible and observed pair numbers of kōkako translocated to six sites in New Zealand. Pairs are composed of birds originating either from the same dialect population (SD) or different dialect populations (DD). Hit ratios are calculated as the number of observed pairs divided by the number of possible pairs. Assortative pairings occur when DD hit ratios are lower that SD hit ratios. When pairings are non-assortative, we used complimentary mid-p values for combined tests to reflect a reversal of the dominant trend. Weight values represent the sum of observed pairings at that site and in that season, while combined weight values represent the sum of weights at that site. Sites combined across multiple seasons are indicated with site-specific *P*-values calculated using combined *Z*-tests.

Site	Season	Possible pairings		Observed pairings		Hit ratio (%)		Assortative pairing?	Mid-p	Weight	*P*	Combined weight
		SD	DD	SD	DD	SD	DD					
Kapiti Island	1993-1994	1	5	1	0	100	0	YES	0.083	1	0.010	6
	1995-1996	4	20	0	1	0	5	NO	0.417†	1		
	1996-1997	12	36	1	0	8	0	YES	0.125	1		
	1997-1998	8	20	2	0	25	0	YES	0.036	2		
	1998-1999	2	3	1	0	50	0	YES	0.250	1		
Pukaha	2005-2006	9	3	3	0	33	0	YES	0.125	3	0.125	3
Hunua Ranges	2007-2008	48	6	3	1	6	17	NO	0.222††	4	0.223	13
	2008-2009	26	73	4	5	15	7	YES	0.120	9		
Tiritiri Matangi	1997-1998	1	1	1	0	100	0	YES	0.250	1	0.250	1
Otanewainuku	2010-2011	16	8	3	0	19	0	YES	0.125	3	0.125	3
Waitakere Ranges	2010-2011	41	80	3	0	7	0	YES	0.017	3	0.017	3
											0.007	**Total**

† complimentary value of 0.583 used, †† complimentary value of 0.778 used

Kapiti Island, in the 1995–1996 season (1 pair), and the Hunua Ranges in the 2007–2008 (1 pair) and the 2008–2009 seasons (5 pairs; Table 4.1).

4.5 Discussion

When translocating animals for conservation, it is important to consider both the genetic and social consequences of combining animals at a release site from different source populations. In this study, we showed that kōkako pair assortatively with respect to source population once released. This pattern was evident in three individual seasons at three different sites, when combining all seasons at all sites, and when combining pooled values across each site.

Assortative pairing within source populations may result from a genuine homotypic preference for birds exhibiting similar vocal dialects (i.e. "like prefers like"). The adaptive benefit of such behaviour may be realised in the familiarity of a local mate to local conditions, which in turn may be expressed in the adaptations that offspring of same-dialect pairs will have to local ecological conditions (co-adapted gene complexes; Baker, 1982; Baker et al., 1982). However, in a finite population the pool of available birds with whom to pair may be limited, and individuals may pair non-assortatively by necessity rather than exhibiting a true heterotypic preference for a different source mate (Burley, 1983).

In kōkako, we found that pairs do not readily form between individuals from different dialect regions. This finding is not surprising given that in Chapter 3 we documented a low response to playback of non-local song by resident kōkako. In that study, we showed that foreign duet playback elicited a delayed approach and vocal response, and a low vocal output when compared to playback of a local duet. While the process of mate choice is very different from that of territory defence, a similar conclusion can perhaps be made regarding the effect of local and non-local song on pair formation; further, part of the responses observed in Chapter 3 may have reflected the assessment of extra-pair mating possibilities. We also found that responses to synthesised duets – in which we combined duet contributions from both local and non-local dialects – were similar to pure local duets, regardless of the sex of the local component (see Chapter 3). This suggested that any familiar signal component is sufficient to elicit a strong response. It is also plausible that duets produced by birds fledged at the release site elicits a response intermediate to local and non-local song.

Dialect-based assortative pairing has been previously suggested in kōkako on Kapiti Island by Rowe and Bell (2007). Their study assessed pair formation between 1992 and 2001, and indicated assortative dialect-based mate choice in this population, but could not statistically assess this pattern due to a low sample size. Rowe and Bell (2007) also claimed that the assortative tendency ceased following juvenile recruitment subsequent to release. Although we were unable to assess this pattern directly in this study, pairs comprised of at least one locally-fledged bird did form both on Kapiti Island and in the Hunua Ranges. As it is known that young songbirds undergo a sensitive learning phase during vocal development (Cunningham and Baker, 1983; Marler and Peters, 1987), it is thought that exposure to several song dialects during this learning phase may affect mate choice decisions as adults, resulting in a dilution of the preference for a same-dialect partners (e.g. MacDougall-Shackleton et al., 2001). Pairs involving a bird fledged at the release site following translocation could nonetheless be valuable for kōkako conservation, offering a way out of the same-dialect preference "trap".

Although this study reveals that overall, kōkako pair assortatively following translocation, during one season (1995–1996) on Kapiti Island, and two seasons (2007–2008 and 2008–2009) in the Hunua Ranges, pairs did form between birds originating from different populations. The mixed-dialect pair that formed on Kapiti Island involved a male from Hauturu and a captive-reared female from Mt. Bruce (Figure 4.1). Although we do not have detailed data with which to draw conclusions about the timing of song-learning in kōkako, we know that the female was released as a sub-adult (i.e. < 2 years old) and so may have been more flexible in song production than an adult, allowing it to adjust the timing of its song to duet with the male. This may in turn have promoted pair formation between these birds.

The other instance of mixed-dialect pair formation was in the Hunua Ranges. Notably, this was the only site with an existing core population at the time of release. The single mixed-dialect pair that formed in the 2007–2008 season was between an adult female recently translocated from Mapara (Figure 4.1) and a single, territorial, core population male. There were at least five other unpaired, translocated males with whom to pair. Possibly the female paired with the core male because he held a territory, in contrast to the translocated males who would be perceived as non-territorial 'floaters' following release. In support of this explanation is that all five available, translocated males that did not pair that season were successfully paired in the following season (2008–2009) by which time they had acquired territories. Those males paired with females from the core population (1 pair), same source population (2 pairs), and a different source population (2 pairs). However, for all these males there were only two "available" unpaired birds from the same population from whom to choose. Mixed-dialect pairs also formed in the Hunua Ranges in the 2008–2009 season, involving a mix of "core" birds and birds translocated from Mapara or Tiritiri Matangi Island (Figure 4.1). Four of those pairs involved males translocated from Mapara two seasons previously, three of which were unpaired the season before, indicating that these males may by then have had sufficient time to acquire a territory and thus attract a mate.

Although we regarded male-male pairs as available, single birds in our analysis, we are aware of at least one population (not included in this study) where male-male pairs persisted even in the presence of unpaired females. It is possible that the short-term value of territory occupancy is sufficiently high for survival to out-weigh reproductive benefits of divorcing a same-sex partner. Although not adaptive in the long-term, this behaviour may have become habitual in these individuals.

This study highlights the utility of long-term datasets for conservation. Based on our findings, translocation release strategies could be appropriately adapted to maximize translocation success. For example, the default and simplest strategy would be to simultaneously release birds from different source populations due to logistical constraints. However, given that cross-population pair formation is potentially enhanced by territorial resident singles, a better release strategy may be to allow individuals from a single source population to become established before supplementing the translocation with additional birds from a second source population.

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Chapter 5: Summary

Kōkako are endangered, duetting passerines endemic to New Zealand that exhibit distinct vocal variation across the species' fragmented range. Conservation of the species is mainly focused on the two complementary approaches of (1) ecosystem management through the control of exotic mammalian predators and herbivorous competitors, and (2) re-introduction or translocation programmes to offshore islands or managed reserves. Despite considerable effort on the part of the New Zealand Department of Conservation, community groups, and other non-governmental organisations, the demographic responses of kōkako have been slow, potentially due to cultural differences between populations sourced for translocation. Therefore, in this thesis I examined how varying degrees of vocal variation, both on a microgeographic neighbourhood level and macrogeographic dialectal level can impact two critical life history processes, mate choice and territory defence.

In Chapter 2, I described a novel translocation of 20 kōkako from two adjacent and vocally dissimilar song neighbourhoods (within neighbourhood phrase sharing of c. 65% versus between neighbourhood phrase sharing of c. 25%). I assessed post-release dispersal following translocation and found that although the birds moved substantial distances, dispersion distances over the first seven days after release were not as great as predicted by a random walk model. When I examined whether this effect was specific to speakers broadcasting locally-produced song I found the birds were no closer to their own neighbourhood speakers that those speakers broadcasting song from the other neighbourhood. This finding indicated that between-neighbourhood phrase sharing rates as low as 25% did not result in discrimination by the birds following release. The overall effect of the broadcast song was also transient and did not result in the birds establishing territories close to the speakers, which casts doubt on the utility of acoustic techniques in reducing post-release dispersal distances. A more likely explanation for the excessive distance over which the birds travelled before establishing territories was a lack of the birds' preferred habitat at the release site. I found that during the acclimation phase the birds disproportionately used available habitats and preferentially used the habitat type that was most similar to that at the catch sites. This pattern was confirmed by the final territory settlement choices that the birds made; the final territory locations were in a forest-type similar to that at the catch sites. These findings are important from the perspective of conservation managers as they can inform decisions regarding the choice of translocation release sites. In this study I also examined pair formation over two seasons following release, and found that mate choice was non-assortative with respect to song neighbourhood. From this it is evident that the reduced phrase sharing rate found in adjoining neighbourhoods is not a barrier to pair formation. Under the definitions given by others (see section 1.5 in Chapter 1), this degree of vocal variation is better described as a gradual or clinal variant (as in Figure 1.2b, Chapter 1), rather than a true dialect. I therefore do not use the term "dialect" in this case, and instead refer to these groups of individuals as "song neighbourhoods" (see a and b in Figure 5.1).

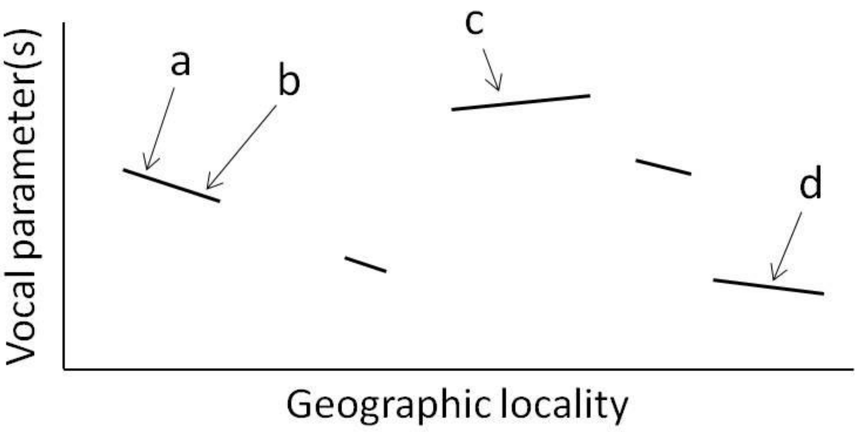

Figure 5.1 Schematic representation of variation in kōkako song. Points 'a' and 'b' correspond to two song neighbourhoods within a single population with gradual variation in song, while 'c' and 'd' represent isolated populations with different song dialects.

Although the context is very different, the lack of discrimination of vocal variants shown by kōkako translocated from adjacent song neighbourhoods (Chapter 2) are in contrast to the markedly different behavioural responses of birds to local- and foreign-population playback reported in Chapter 3. In this study I performed two reciprocal playback experiments in two fragmented populations with discrete dialects (i.e. ≤ 5% phrase sharing) to assess responses of territorial pairs to local and foreign duets. I found that pairs responded to local duets with less delay, and produced more song phrases, with a lower diversity, when compared to playback of foreign duets. These findings clearly indicate the salience of inter-population dialect variation in kōkako, with a stronger and more urgent response to local song. Presumably, local song represents a greater threat to either the pair as a whole or to each member of the pair independently. I explored this finding in a second experiment by presenting pairs with synthesised mixed-dialect duets comprised of either a local male or a local female combined with a foreign partner. I found that pairs responded with equal overall strength regardless of the sex of the local component. Additionally, responses to the mixed-dialect duets were similar to responses to pure local duets I found in the first experiment. This indicates that any local component is sufficient to elicit a strong response during territorial intrusion. From an evolutionary perspective, this indicates the degree of vocal variation between kōkako populations may not be sufficient to promote discrimination or territorial exclusion if mixed-dialect pairs are able to form. The IUCN guidelines for re-introductions recommends that source populations show similar behavioural characteristics (IUCN, 1998). However, overall the present study suggests that animals translocated for conservation may not need to exhibit homogeneous cultures in order to acquire and defend resources as pairs.

To assess patterns of mate choice decisions of birds exhibiting different dialects, in Chapter 4 I examined pair formation over eleven breeding seasons at six sites to which kōkako were translocated during an 18-year period. I found that when each site was considered individually, the statistical power of the tests were low. However, when the sites were taken together, the test revealed that kōkako pair assortatively with respect to source origin, and therefore with respect to the dialect that the birds produce. In spite of this, I also found that mixed-dialect pairs do form in this species in limited numbers when an existing "core" population was present at the time of translocation or when the mixed-dialect pair involved a translocated sub-adult bird. The results suggest that even when vocal variation is large, behavioural isolation is not complete, and therefore genetic exchange at translocation release sites between previously isolated populations is possible. The findings also make an important contribution towards understanding how behavioural variation can impact upon efforts to conserve endangered species, and highlights the value of combining long-term data from multiple sources.

Taken together, my research shows that the 'degree' of vocal similarity between groups may dictate social discrimination, both during territory defence and mate attraction. Although the contexts of the two experiments I presented in Chapter 2 and Chapter 3 are different – the first involves playback to non-territorial pairs immediately following translocation, and the latter to established territorial pairs in remnant populations – they nevertheless suggest that distinct cultural boundaries may promote territorial exclusion of non-local pairs. However, results from Chapter 4 strongly suggest that dialects are important to birds during pair formation.

I have shown in this thesis that different degrees of vocal variation can affect behaviour in different ways, yet obvious questions arise from these findings: How does vocal variation affect post-natal dispersal in the short term, and genetic differentiation in an ultimate sense? In kōkako, the fact that dispersal could not occur between the allopatric populations I studied in Chapter 3 and Chapter 4 (as a result of human induced habitat modification of the intervening landscape), makes assessment of correlated vocal and genetic variation problematic. If song variation is maintained through some form of dispersal aversion to areas with dissimilar song, then we would expect genetic variation to follow similar spatial patterns to vocal variation. This has been suggested to occur in the white-crowned sparrow by Baker and Mewaldt (1978), who analysed band-recapture data to show that across-dialect dispersal was inhibited, although not completely, by song dialects. However, the finding of Baker and Mewaldt (1987) was subsequently challenged by Petrinovich and others (1981) who claimed that without knowledge of the exact natal areas of dispersing juveniles it is not possible to reach conclusions regarding the function of dialects as barriers to dispersal. Recent research by Yoktan et al. (2011) has also failed to find a relationship between song dialects and genetic structure in the orange-tufted sunbird. Other studies in our research group have revealed that dispersal between areas within contiguous forest, such as those at Mapara and Rotoehu (Chapter 3) and Te Urewera National Park (Chapter 2) is not inhibited by vocal differences intermediate to those found between populations (S. Valderrama et al., University of Waikato, unpublished data). At those sites, females dispersed c. 50% further than males (c. 1.6 km versus 2.5 km at Mapara), and that the site of post-natal territory settlement was not restricted by dialect region (S. Valderrama et al., unpublished data). Genetic studies have revealed that genetic variability is low within these populations (Hudson et al., 2000), a finding that could be explained by sufficient within-population dispersal. The question then arises: Is inter-population dialect variation sufficient to promote genetic differentiation in the long-term at sites where secondary contact between allopatric populations has been artificially created through translocation? I present evidence showing that dialect variation in kōkako influences both territorial behaviour (*Social Adaptation Hypothesis*, Chapter 3) and mate choice decisions (*Genetic Adaptation Hypothesis*, Chapter 4), which supports a model of incipient speciation through reproductive isolation. However, such differentiation appears to be short-lived as crossing of dialect "boundaries" by second generation juveniles seems not to be reduced. This pattern could be explained by a combination of dispersal behaviour and delayed vocal learning, as suggested by the *Epiphenomenon Hypothesis* (Andrew, 1962; Slater, 1986). If physical isolation of kōkako populations were to persist, and conservation efforts involving the mixing of multiple poplulations were to cease, then it is possible that short-term behavioural variability, and consequently long-term genetic variability, would increase.

5.1 Recommendations for future research

Given my findings in this thesis, there are several avenues for future research on this species that warrant attention. To assess vocal change or plasticity in kōkako, it would be useful to collect song recordings of banded birds prior to future multi-source translocations. If those same birds are then tracked over a number of years and recorded at a later date, detailed analysis could be made concerning song change following contact with birds from different dialects. The offspring of those birds could then be marked and followed to determine song learning trajectories when exposed to multiple dialects.

The duetting behaviour of kōkako is intriguing, and understanding the process by which duet "codes" are established in pairs is another exciting avenue of future research. A comparison of the duet-formation process by long-term monitoring of same- and mixed-dialect pairs would yield great insight. As there presumably is a significant time cost associated with learning a duet, I would predict that the order of phrases in the duet sequence (i.e. duet syntax) would take longer to learn in mixed-dialect pairs compared to same-dialect pairs. The importance of such a difference from the perspecticve of the birds could be tested by manipulating playback stimuli to represent different levels of duet-syntax consistency.

Habitat differences among translocation source and release sites may lead to vocal change in kōkako. Although most source sites have a similar vegetative structure (i.e. tall, mature, and relatively moist forest), some release sites, particularly those on islands, are noticeably different (i.e. relatively short and dry regenerating forest). Additionally, the ambient noise profiles may differ between sites based on the composition of the biotic community. Based on the *Acoustic Adaptation Hypothesis* for the evolution and maintenance of vocal variation in birds (Morton, 1975; Wiley and Richards, 1978; Bowman, 1979; Gish and Morton, 1981; Nottebohm, 1985), clear predictions can be made concerning the direction and strength of vocal change in kōkako. In several bird species, songs have been found to be a lower frequency at vegetatively denser sites compared to those in more open sites (reviewed in Slabbekoorn, 2004). The frequencies at which kōkako sing may, over time, become modified for optimal transmission through the forest at the release site. Such a study will shed light on the role that habitat alteration may have on the trajectory of vocal change in kōkako, and further our understanding of the plasticity of species to adapt to human impacts on the environment.

As I was somewhat constrained by a lack of banded birds in the populations I studied, extensive colour-banding, combined with vocal recording of known-sex birds both at natal sites and at the site of territory establishment following juvenile dispersal, would be particularly useful. Detailed song recording of immature birds throughout their first two years of life is also crucial to understanding the song-learning process in this species. For example, one could determine the length of time over which an individual can modify song phrases or incorporate additional sounds into its repertoire, essentially detemining where and how the kōkako song-learning program fits into the open-ended/closed-ended continuum (Brenowitz and Beecher, 2005). Knowing how a young kōkako learns locally-produced song beyond the boundaries of its natal neighbourhood, whether immediately after fledging or later in life, is important for determining how dialects form and the functional role that they can play in the life of a bird. Long-term data documenting the stabilty or fleixibility of vocal repertoires following dispersal would also greatly contribute to our knowledge of the forces driving the change or maintenance of cultural variation in this species. Such studies will reveal detail on the limits to which cultural boundaries can constrain genetic exchange, and ultimately the role of culture in evolution.

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Appendix 1: Supplemental CD

Track 1 Kōkako duet from Mapara Wildlife Reserve, New Zealand (2:57).

Track 2 Kōkako duet from Rotoehu Forest, New Zealand (3:03).

Track 3 Kōkako duet from Waipapa, Pureora Forest Park, New Zealand (8:52).

Track 4 Kōkako duet from Onepu, Te Urewera National Park, New Zealand (7:44).

Track 5 Example of a kōkako duet stimulus recorded from the Otamatuna neighbourhood, Te Urewera National Park, and broadcast as 'acoustic anchors' at Whirinaki Forest Park, New Zealand (1:30).

Track 6 Example of a kōkako duet from Mapara used as a stimulus type in Chapter 3. The male portion of the duet is on the left channel, the female portion is on the right channel (0:12).

Track 7 Example of a kōkako duet from Rotoehu used as a stimulus type in Chapter 3. The male portion of the duet is on the left channel, the female portion is on the right channel (0:09).

Track 8 Example of a synthesised mixed-dialect kōkako duet used as a stimulus in Chapter 3, comprised of a Rotoehu male component on the left channel and a Mapara female component on the right channel (0:10).

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Figure A2 Journal cover image of a North Island robin © D. Bradley.

Appendix 2: Does 'acoustic anchoring' reduce post-translocation dispersal of North Island robins?*

A2.1 Abstract

Animal translocations are an important conservation tool, however post-release dispersal can hinder successful population establishment. Playback of conspecific song attracts dispersing individuals in some species, although its application following animal translocation has yet to be rigorously investigated. To determine if conspecific song can be used as an 'acoustic anchor', we adopted an experimental approach during the translocation of 60 North Island robins (*Petroica longipes*). At one of two release locations, we broadcast song at natural rates from four speakers (four hours per morning), for nine days following release; we set the second release location as a control where identical conditions were established but no playback occurred. To assess the impact of playback, we monitored speaker and control locations, surveyed tracks around the release areas, and radio-tracked robins over nine playback days and an additional nine days. The majority of robins left both immediate release areas, however our results showed that: (1) more robins (6 birds on 14 of the 18 days), in particular females (3 birds), approached the playback location than the 'flagged' control location (3 male birds on 5 of the 18 days), (2) individual robins returned to the playback location repeatedly, unlike those at the control site, and (3) robins also visited the playback location longer post-playback than silent control locations. In contrast, radio telemetry data from five robins suggested that general dispersal was not influenced by playback. Two radio-tracked females moved over large distances (some to more than 3 km from their release location), while two radio-tracked males remained relatively close to the release sites. We demonstrate a short-term attraction effect of playback over a period of several weeks for some birds, particularly females. In contrast, we detected fewer birds over a shorter period at

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the silent control release site, where no females were detected. However, long-term monitoring at both sites suggests that the effect of playback on reducing post-release dispersal was transitory. The lack of a clear and lasting effect of acoustic anchoring on dispersal in this study provides information on the limited utility of song playback as a conservation management tool. Consideration of the species' ecology and suitability for 'acoustic anchoring' must be made before playback is employed as a conservation measure to reduce excess post-translocation dispersal.

A2.2 Introduction

An animal translocation is the deliberate and mediated movement of wild individuals or populations between parts of their range (IUCN, 1998). Translocations are frequently employed as a conservation tool (Griffith et al., 1989), and have been used to rescue species from the brink of extinction (e.g. South Island saddlebacks, *Philesturnus carunculatus*; Atkinson & Bell 1973), to establish 'insurance' populations on predator-free offshore islands (e.g. kakapo, *Strigops habroptilus*; Powlesland and Lloyd 1994), or to restore crucial ecosystem processes (e.g. wolves, *Canis lupus*; Mao et al. 2005). However, despite the high-profile successes of many animal translocations onto islands, translocations to mainland sites have met with limited success, potentially due to high post-release dispersal (Armstrong and Seddon, 2008). This has resulted in a loss of animals to unsuitable surrounding habitat, which is both unethical and increases the numbers of animals that need to be released. A small effective population size of the translocated animals may lead to an Allee effect, or render the new population susceptible to stochastic events, reducing the likelihood of long-term population establishment (Courchamp et al., 2008). This effect is most evident when the release site is a 'mainland island' managed for conservation purposes within a larger area of unmanaged habitat, as is increasingly the case in New Zealand (Saunders and Norton, 2001).

The presence of conspecifics is known to attract animals of some species and influence territory settlement decisions (Stamps, 1988, and references therein). Simulating the presence of conspecifics at a release site has the potential to promote the success of a translocation by attracting individuals shortly after release, thus facilitating ‘social networking’ between animals that may otherwise have never encountered each other (potentially promoting pairing success), and therefore mitigating the negative influence of high post-release dispersal on population establishment. This approach has been used previously to acoustically ‘anchor’ North Island kōkako (*Callaeas wilsoni*) to a site with exotic predator control (Molles et al., 2008). However, as kōkako are an endangered bird species and a simultaneous non-treatment release was not possible, this prevented conclusive support for the utility of this technique in a management context. Additionally, the broad-scale transferability of this technique to other species, with differing ecologies and territorial behaviours, is unknown without further experimentation.

In this study we tested the utility of broadcasting conspecific song, an acoustic ‘anchor’, following a translocation of North Island robins, *Petroica longipes* (sensu Holdaway et al., 2001; Miller and Lambert, 2006; hereafter referred to as ‘robins’). Robins are small (26–32 g), insectivorous forest passerines endemic to New Zealand’s North Island and several offshore islands (Heather and Robertson, 1997). Although robins are considered to be of Least Concern (Birdlife International, 2009) and are widespread on the North Island, they are absent or patchily distributed throughout much of their former range (Robertson et al., 2007), having declined since European settlement (Heather and Robertson, 1997). Decline is thought to be due to the combined effects of habitat degradation, and the introduction of mammalian predators (Heather and Robertson, 1997). Previous attempts to translocate robins to predator-managed sites have met with limited success when release sites are adjoined by suitable, yet unmanaged robin habitat (Hoverd, 2000; Empson, 2001; Lovegrove and Stephenson, 2001; Gilbert, 2004; Lewis et al., 2006; Mason et al., 2008). In these cases it is likely that individuals dispersed out of the managed areas, which is supported by distant re-sightings beyond management boundaries (Gilbert, 2004; Mason et al., 2008). Conversely, instances where larger proportions of robins remained in management areas, paired, and bred have largely been when the management areas are bordered by coastline or farmland (Howard, 1998; Lovegrove and Stephenson, 2001; Mason et al., 2008). These translocations appear to have resulted in the establishment of new populations, supporting the hypothesis that post-release dispersal is a compromising factor, however poor recruitment due to juvenile dispersal beyond the managed areas has limited population growth in some cases (e.g. Lovegrove and Stephenson, 2001; Mason et al., 2008). Therefore, management tools such as 'acoustic anchoring' have the potential to prevent excessive post-translocation dispersal, which may promote translocation success.

Robins are a suitable species on which to perform an experimental test of 'acoustic anchoring' for several reasons. They show a high level of site-fidelity (Richard and Armstrong, 2010), and occupy year-round territories (Armstrong et al., 2000), which they defend as a pair in the breeding season (September–March; Heather and Robertson, 1997) and partition between the sexes at other times (Armstrong, 1995). Robins therefore have the potential to be attracted to, and show lower aggression towards, familiar conspecific song cues (Armstrong, 1995; Powlesland, 1997; Richard and Armstrong, 2010). Robins are also a highly vocal species, and would be predicted to be sufficiently attentive to song playback in the period immediately following release (Richard and Armstrong, 2010). The limited juvenile dispersal abilities of robins (Flack, 1976a; Jamieson et al., 2009; Richard and Armstrong, 2010) may also translate into a tendency to avoid immediate dispersal, providing the opportunity for song playback to have an attraction effect. However, as noted by Richard and Armstrong (2010), translocated animals may not behave in the same way as dispersing juveniles as the context is markedly different. The overall goal of our study was therefore to determine if song playback can act as an attractant to birds, and to establish if playback can reduce post-translocation dispersal and improve release site retention. We predicted that (1) if song playback attracts robins following release then a greater number of individuals would be seen approaching playback speakers over an extended period than to similar silent locations at a control release site; and (2) if conspecific song acts as an 'acoustic anchor' then birds would settle closer to the release site where playback was used, ultimately establishing territories nearby, when compared to the control locations.

A2.3 Methods

A2.3.1 Field sites

The New Zealand Department of Conservation (DOC) and the Moehau Environment Group translocated 60 robins to the Moehau region of the upper Coromandel Peninsula, New Zealand in April 2009. For 51 birds, DNA was extracted from contour feathers and tested for the presence of the W-linked gene CHD1-W to establish the bird's sex (see Griffiths et al., 1998). For the remaining nine birds we used a combination of morphometric measurements and plumage (Armstrong, 2001) to determine sex. Approximately equal numbers of males (28) and females (32) were captured and subsequently released at two sites within similar regenerating forest. The simultaneous release of 30 birds at each of the two locations allowed us to conduct an experimental test of the utility of song playback at one site (hereafter referred to as the playback site) while keeping the other site as a control (hereafter referred to as the control site). The playback site (lat. 36˚32´S, long. 175˚28´E) is adjacent to the community of Port Charles and received 16 males and 14 females, while the control site (lat. 36˚30´S, long. 175˚25´E) is adjacent to Stony Bay and received 12 males and 18 females. For purely logistical reasons we designated the Port Charles location as the playback site (i.e. it provided easier access for the installation and maintenance of playback equipment), and the Stony Bay location as the control site. The playback site is within regenerating native forest ranging in elevation from 0–350 m, whereas the control site is within a larger block of both regenerating native forest between 0–400 m and mature native forest at elevations between 400–800 m (Mason and Chambers, 1950). The two release locations were at an elevation of 60 m and 100 m respectively, and are approximately 6.5 km apart, separated by a contiguous matrix of grassland, regenerating, and mature native forest.

A2.3.2 Field recordings

To simulate the presence of territorial robins at the playback site, we collected sound recordings at the capture site in the Pureora Forest, New Zealand (lat. 38˚27´S, long. 175˚30´E). Prior to capture, we located two singing males and visited them between 0645 and 1100 hours NZST (sunrise occurred at approximately 0700 hours) on two consecutive mornings (3–4 March). We followed these target birds around their territories and continuously recorded all vocalisations produced; no playback was used to elicit songs. We also recorded from the same site the vocalisations of several groups of whitehead (*Mohoua albicilla*); a non-aggressive, non-competitive, yet familiar species to the robins (Flack, 1976b), which is absent from the release area. We used these recordings as a playback control to determine if the robins' response at the playback site was independent of whether the song being broadcast was conspecific or heterospecific. We made all recordings with directional microphones (Sennheiser ME66 or MKH416) and solid-state digital recorders (Marantz PMD 660), saving the recordings as uncompressed monaural WAV files (16-bit, 44.1 kHz).

A2.3.3 Stimulus preparation

From field recordings we selected 50 robin vocalisations (25 from each bird) and 50 vocalisations from all whitehead groups combined, each with a high signal-to-noise ratio with low wind noise or heterospecific song interference. From these recordings we prepared four playback sets: one from each of the two robins, and two from all whitehead songs. The recorded robin vocalisations consisted of both 'song' and 'downscale calls' (Hay, 1975), and are hereafter referred to as song. Recorded song bouts varied between 1.7 and 30.9 s (mean = 8.1 s; SE = 0.9 s), while whitehead song length varied between 0.5 and 50.3 s (mean = 8.4 s; SE = 2.0 s). Using the software Syrinx-PC (J. Burt, Seattle, WA, USA), we filtered background noise of all songs using a frequency bandpass filter between 1000 Hz and 16000 Hz followed by a 1.0 s sound ramp at the start and end of the song. All sound files were then normalised to -1 dB in Audition (Adobe Systems, San Jose, CA, USA). We identified natural song breaks from our source recordings, and used these values to construct silent tracks in a ratio equal to that of natural dawn chorus conditions (song to silence ratio of 1:4). To ensure that we played the same total amount of song from both the robin and whitehead speakers, we inserted an equal amount of the silent tracks into all four playback sets. We thus had a selection of four sets of stimuli, each with 25 song bouts and appropriate silent tracks.

A2.3.4 Speaker setup and playback regime

At the playback site we mounted four speakers (model: MW6902) on poles 1 m above the ground, facing upwards. At the control site we marked locations in an identical spatial arrangement with flagging tape. Each speaker was connected with speaker wire to a waterproof case (model: Peli-Case, Pelican Products Inc., Terrance, CA, USA) containing a battery timer (model: SWC-033, Rainbow Power Company Ltd., Ninbin, NSW, Australia or Flash 16720 clock switch), an amplifier (model: CA115, TAO Corporation, Japan), and an iPod (model: Nano, Apple, Cupertino, CA, USA). The case was then wired to a 12 V battery (model: G12-40, Synergy Power Solutions, Suwanee, GA, USA), which powered the amplifier. Speakers were set up in pairs, each 20 m apart, with pairs 40 m on either side of the release location.

The volume of all speakers was set to a sound pressure level similar to natural song (80 dB at 1m horizontal distance from the forward-oriented speaker using a Realistic sound level meter model 33-2050). We programmed the iPods to turn on at the same time as the battery timer using the alarm function. As robins at the source location began to sing approximately 30 min prior to sunrise during the recording sessions, we set both the timers and the iPod alarm to turn on at this time, and adjusted them periodically as sunrise became later throughout the playback period. Songs were set to play in a random order to avoid stimulus habituation, for four hours each morning, beginning on the day of the release (8 April) and continuing for an additional nine days.

A2.3.5 Banding and transmitter attachment

All robins were banded with a unique combination of two to four coloured bands and one metal leg band to allow individual identification. To six of the robins (2 males and 4 females), we also attached 1.05 g radio transmitters (Model BD-2, Holohil Systems Ltd., Carp, ON, Canada) using a Rappole Harness (Rappole and Tipton 1991). This harness attachment system allowed for rapid processing, therefore reducing stress to the birds, and allowed for normal movement and behaviour of the birds after release.

A2.3.6 Monitoring

Following the releases we employed three techniques to monitor the robins, both at the playback and control site. Monitoring encompassed two 9-day periods for practical reasons, both when playback was employed, and after it was removed. We attempted to keep monitoring effort as constant as logistically possible between the two sites to facilitate legitimate comparisons.

1) *Speaker monitoring* – Each morning, 1–2 observers at each site walked pre-marked loops with a 10 m radius around each of the speakers (or flagged control locations), both during the playback period when the speakers were on, and for an hour immediately following the end of playback each day. Using binoculars, the observers recorded the identity of any robins noted within 10 m of the speaker.

2) *Track walking* – During the 18 day monitoring period, observers surveyed established tracks, spaced at 100 m intervals, throughout the two release sites. By walking slowly and pausing briefly every 50 m, observers noted the identity and location of each robin detected. The amount of walking track available from which to mount surveys varied across sites (playback site, 380 ha; control site, 780 ha) but search duration was always equivalent (playback site, 138.29 h; control site, 128.78 h). Each time a robin was encountered the position of the bird was recorded with a handheld GPS (Garmin GPS 60CSx, Garmin International, Inc., Olathe, KS, USA).

3) *Radio telemetry* – We conducted radio-tracking using TR-4 receivers (Telonics, Inc., Mesa, AZ, U.S.A.) and Yagi antennas (Sirtrack Ltd., Havelock North, New Zealand) to determine the locations of the birds carrying transmitters. When the birds could not be tracked to an exact position, we noted the bearing direction of the signal from two or more points on high elevation ridges within a one-hour period. Robin locations were then determined via biangulation or triangulation methods using Location Of A Signal (LOAS) software (Ecological Software Solutions, L.L.C., 2009). Minimum convex polygons were created for each bird using the Hawth's Tools extension (Beyer, 2004) in ArcGIS version 9.2 (ESRI, Redlands, CA, USA).

A2.4 Results

Following the translocation of 60 robins to the two sites, 33 (55%; 18♂, 15♀) were re-sighted at least once in the 18-day monitoring period. We re-sighted 14 (47%) of the birds released at the playback site, and 19 (63%) of the birds released at the control site. At the playback site, we detected as many males (8/16, 50%) as females (6/14, 47%; $\chi^2_1 = 0.08$, $N = 14$, $P = 0.78$); while at the control site we detected more males (10/12, 83%) than females (9/18, 50%), although this trend was non-significant ($\chi^2_1 = 1.26$, $N = 19$, $P = 0.260$). These general findings reflect all detections made during track-walking, radio telemetry, and speaker monitoring.

Speaker monitoring revealed that birds approached the speakers and at times produced territorial vocalisations (‘full song’; sensu Hay, 1975), seemingly in response to the stimulus sound. However, at the playback site, robins were seen a similar number of times within 10 m of the speakers broadcasting whitehead song (5 birds over 12 days) than speakers broadcasting robin song (4 birds over 6 days). We pooled all data collected at the playback site for the remaining analyses, similarly pooling all comparison data at the control site. Twice the number of birds, across a greater number of days, was detected at the playback site (6 different birds on 14 of the 18 days) than at the control site (3 different birds on 5 of the 18 days; Figure A2.1). Although 3 males were seen at each site, 3 females were additionally seen approaching the speakers at the playback site (Figure A2.1), and no female birds were detected and no additional birds were seen after the first 6 days of monitoring (cumulative counts on Figure A2.1). Robins were also detected more consistently (i.e. repeat sightings of each individual were more common) at the playback site than at the control site both during the 9 days when daily playback was occurring (playback site, 4 birds over 7 days; control site, 3 birds over 3 days), and for the 9 days after playback had ceased (playback site, 3 birds over 7 days; control site, 1 bird over 2 days).

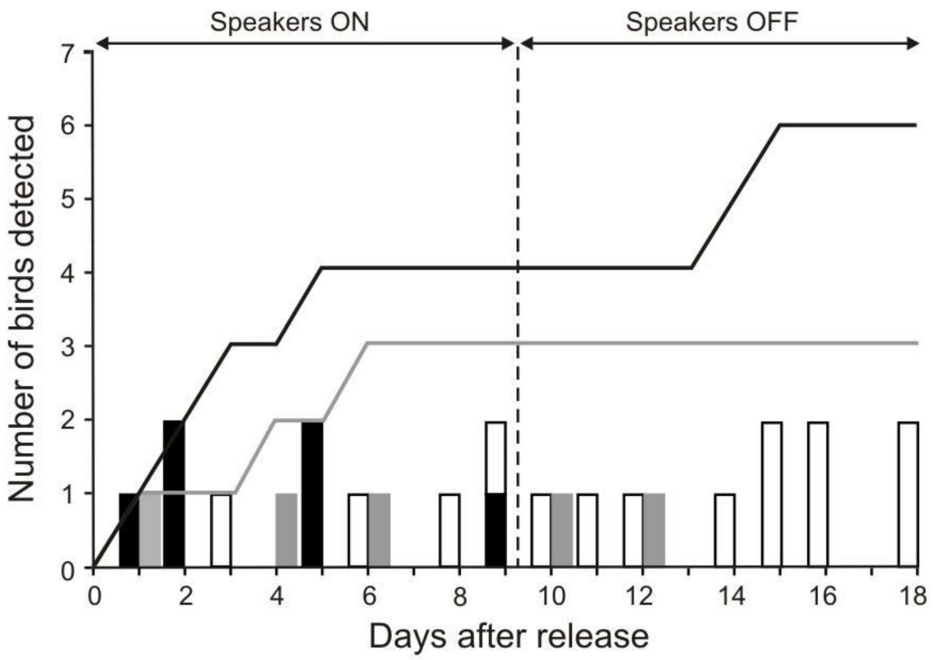

Figure A2.1 Robin detections within 10 m of speakers (or flagged control locations) during the periods when the speakers were on or after they had been switched off. Vertical bars represent the number of male (black) and female (white) visits detected at the playback site, while gray vertical bars represent male visits to the flagged control locations; note that no females were seen at the control site. Lines represent the cumulative count of birds at the playback site (black) and control site (gray).

We radio tracked the six robins over variable time periods ($\overline{X}$ = 13.2 d, range = 4–18 d) depending on the length of transmitter attachment (data from one female was excluded as the transmitter fell off after one day). Overall, radio telemetry revealed similar dispersal patterns between robins released at the two sites (Figure A2.2). However, these data reveal variation in dispersal patterns between sexes (Figure A2.2). Female robins ‘Control 1’ and ‘Playback 1’ moved widely over large distances in a relatively short time period; the minimum convex polygons (MCP) representing the area traversed by each of the birds were 480 ha and 797 ha respectively. In contrast, the male robins ‘Control 2’ and ‘Playback 2’ were more sedentary and remained relatively close to the release location (MCP areas =

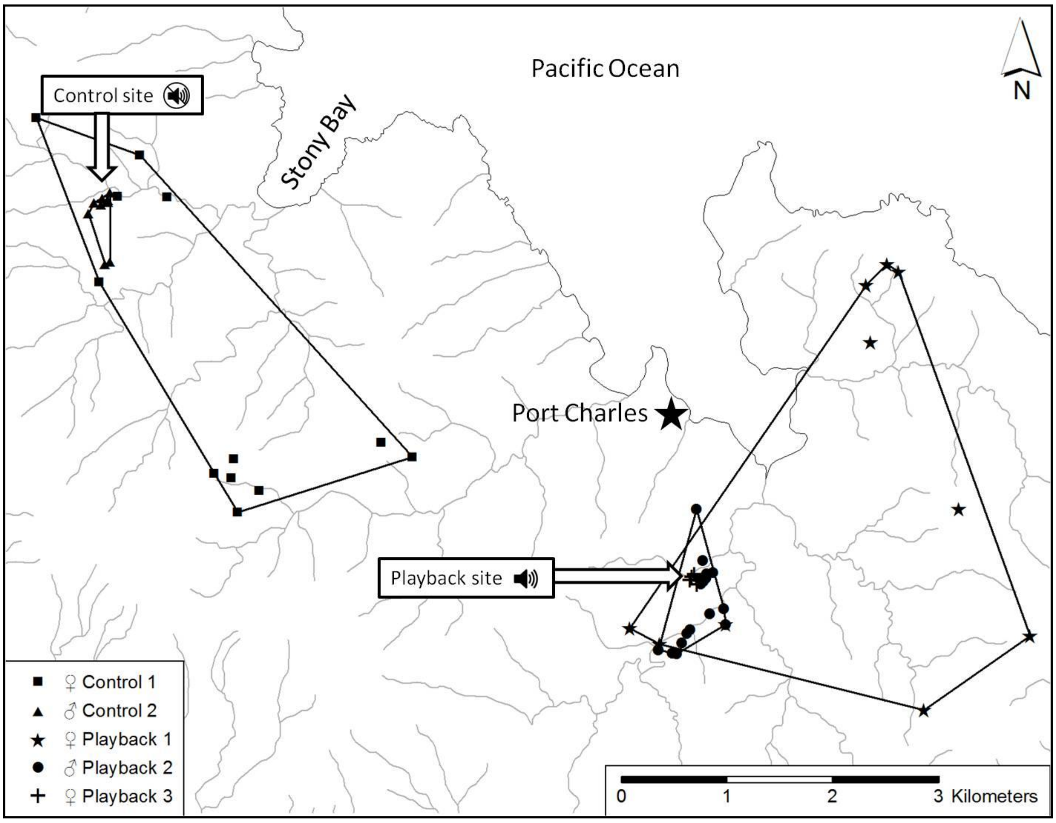

Figure A2.2 Locations of five robins released at two sites as determined by radio telemetry or radio-tracking to actual location over the 18-day post-release period. Bounding lines represent minimum convex polygons for the four birds for which transmitters remained attached for longer than 3 days (therefore excluding ♀ Playback 3).

9 ha and 43 ha respectively, Figure A2.2). Additionally, some robins repeatedly returned to the release site after previously moving away, notably birds ‘Control 1’ and ‘Playback 2’ (Figure A2.3); however, birds at the two sites did not appear to differ in terms of these movements.

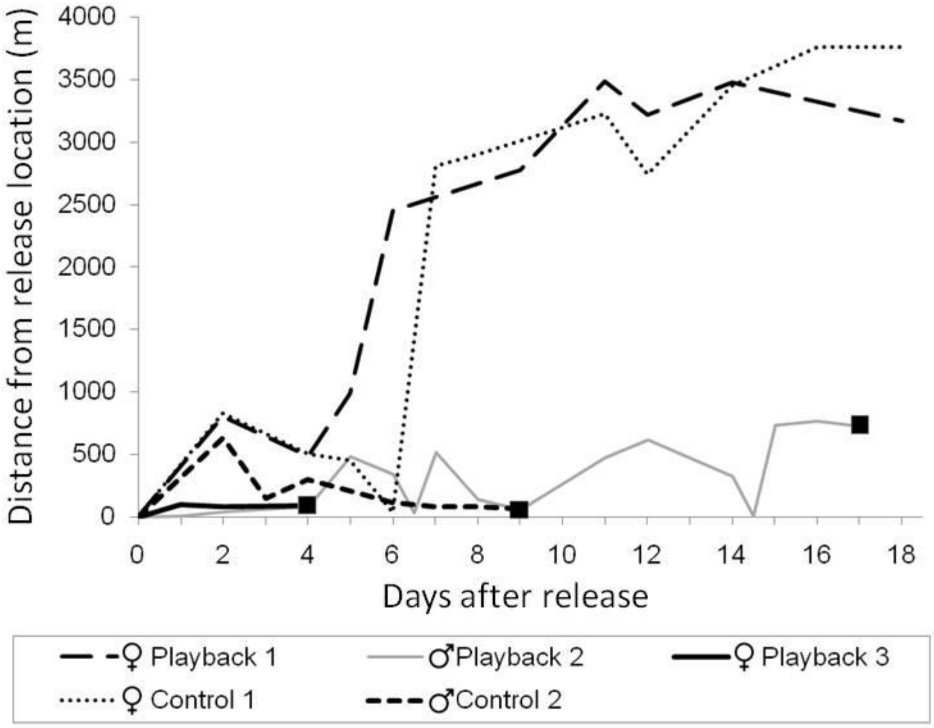

Figure A2.3 Distance from release location over time for five radio-tagged robins. Solid squares indicate the point at which the transmitter was dropped from the other birds.

A2.5 Discussion

We addressed the efficacy of broadcasting conspecific song in attracting and ‘anchoring’ translocated robins following release. Fewer birds were attracted to the control site than the playback site, where birds approached speakers almost three times more often. Females were sighted at the speakers both during the playback period and after playback ceased; in contrast, no females were seen approaching the flagged control locations. These results suggest that, at least for some individuals, short-term attraction (up to 18 days) to the playback location occurs; conspecific vocalisations may provide birds with clues about suitable settlement locations and/or future breeding opportunities (Eriksson and Wallin, 1986; Mountjoy and Lemon, 1996). Heterospecific sounds may also be attractive for species with overlapping habitat requirements (Mönkkönen et al., 1999;

Mönkkönen and Forsman, 2002; Slabbekoorn and Bouton, 2008). As whiteheads occupy the same habitat as robins at the capture location this may indicate suitable territory.

Despite the short-term attraction to playback, a long-term ‘anchoring’ effect was not apparent. Radio telemetry did not reveal evidence for release site retention at either location. In the breeding season following this study, only a single female was detected in a survey of the playback site (January 2010; L. Williams, MEG, pers. comm.), whereas five (2♂, 3♀) birds released at the playback site were detected near the control site, over 6.5 km away (N. Priddle, DOC, pers. obs.). Studies of species with different breeding ecologies to robins have found a longer-lasting positive effect of broadcasting conspecific sounds. For example, colonial-nesting seabirds have been encouraged to nest when colony calls have been played at previously unoccupied sites (Kress, 1983; Podolsky, 1990). Song playback also influences settlement decisions of migrant songbirds (Ahlering et al., 2006; Ward and Schlossberg, 2004). Both long-distance migrants and colony-nesting seabirds locate mates, and select breeding territories or nest-sites, after long periods away from breeding sites. Robins however, are sedentary and non-colonial, and may therefore be less susceptible to long-term attraction to conspecific song. Additionally, the robins were likely under considerable physiological stress as a result of translocation (Work et al., 1999), creating a markedly different context than that of natural dispersal. Playback may have initially attracted birds seeking foraging opportunities; however a lack of additional intraspecific cues from established territorial birds may explain the absence of a long-term ‘anchoring’ effect.

Radio-tracking of a limited number of birds suggested a sex-biased post-release dispersal pattern: females moved over large distances while males were more sedentary. In many bird species, greater post-fledging dispersal is sex-biased toward females (Pusey, 1987), a presumed inbreeding avoidance mechanism. However, robins may not avoid incestuous pairings (Jamieson et al., 2009), and a previous study of post-fledging dispersal in robins has not shown a sex-bias, although daily dispersal steps of females tended to be fewer and longer than those of males (Richard, 2007). Armstrong (1995) found that a higher, though non-significant proportion of males than females remained in their original release locations following translocation; however, the translocation was onto a small island where post-release dispersal was constrained. In the present study, female robins that moved extensively may have been seeking males with whom to pair, as unmated males are known to ‘adopt’ and feed dispersing females (Flack, 1973). Female locations were almost entirely at higher elevations within mature, native forest patches within regenerating forest (D. Bradley, pers. obs.), which highlights the needs to replicate the study in more homogeneous habitat.

A2.6 Conclusions

Conspecific song playback had a short attraction effect for some individuals, yet no ‘anchoring’ effect on post-release dispersal of robins following translocation. The applicability of this potential conservation tool should be investigated further. Future research should determine which species are appropriate subjects based on behavioural features such as territoriality and mating system (e.g. species using localised and site-specific resources and breeding opportunities may be better candidates). Studies should assess, with appropriate controls, the influence of playback on birds of each sex and age class, as individual requirements and consequent responses to song may vary. Given that females may be more prone to excess dispersal than males, and that females appeared to be attracted to conspecific song in our study, future translocations may benefit from differently timed release strategies, whereby females are released once males have established territories. Most importantly, all future studies should be replicated with thorough post-release monitoring in an experimental context (e.g. Armstrong et al., 1995 ; Seddon et al., 2007), which is essential for advancing the science of re-introduction biology.

A2.7 Acknowledgements

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