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Effects of translocation on Kokako (*Callaeas cinerea wilsoni*) song and its application to management.



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Abstract

This thesis fills a research gap in our knowledge of kokako song by looking at how song evolves in multi-dialect areas. Kokako only exist in small remnant populations separated by large tracts of unsuitable land. Kokako are very poor flyers, only able to fly for approximately 100 metres at a time. In order to prevent inbreeding and a loss of genetic diversity in the remaining kokako populations, managers are carrying out translocations to establish new populations, maintain gene flow and prevent inbreeding. However, these translocations have the potential to be unsuccessful because kokako exhibit macrogeographic variation in their dialects, and tend not to breed with individuals who do not share the same dialect as them. If the purpose of the translocation is to enhance genetic diversity by having kokako from different areas breed then song is an important factor that must be dealt with. Song is extremely important to kokako for a number of reasons. Chiefly, it is hypothesised that song is their primary means of territory defence. A kokako gains all its resources from its territory, so it is imperative that they successfully defend it. Their duet song functions in territory defence, but also acts to form and maintain pair bonds.

In order to try and address the problem that song causes in translocations I studied if and how song evolves in a multiple dialect area. I conducted research at Pukaha Mount Bruce, where there is a population of kokako originating from two different source populations, and thus two different dialects, Northern Mapara and Mangatutu. I looked at the Northern Mapara dialect, and recorded kokako belonging to three groups; kokako currently living in the source population, kokako that were translocated to Pukaha and kokako that were born at Pukaha. In order to determine how the song may be changing I looked at element repertoires, the levels of sharing between groups, the number of unique elements in repertoires and the syntactical and temporal characteristics of phrases.

This study shows that translocation into multiple dialect areas can affect kokako song. Translocation did not affect the size of the kokako repertoire, but it seemed to affect the amount of sharing within and between different groups of kokako. Currently the level of

sharing within the groups at Pukaha is lower than the level of sharing within the source Mapara population, indicating that the song may be diverging. There also seem to be more unique elements found at Pukaha, which in part explains the lack of sharing. There appears to be microgeographic variation at Pukaha, with birds clustered around the second (Mangatutu) dialect sharing less with the source population than do those kokako whose territories are lower down in the reserve. The phrases which are used are also evolving, with only one phrase truly shared among all groups. There are other phrases which show additions or deletions of elements, and so are evolving. The main change found in the phrases is the timing between elements, with six out of seven phrases examined showing changes.

These results have repercussions for future kokako translocations, and the future of the Pukaha kokako. A low amount of phrase and element type sharing combined with changes of intra-phrase timing could lead to the Pukaha kokako's inability to successfully defend their territories. This research shows how kokako song can give conservation managers information on the status of their populations in regards to interbreeding and raises questions which can be answered by further research, both at Pukaha and in other mixed-dialect kokako populations.

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Chapter One: General Introduction



Romeo: a Pukaha-born kokako.

1.1 Introduction to Bird Song

Song plays an extremely important role in the lives of many bird species, and is used in a variety of ways. It is an indicator of male quality, a tool for territory or resource defence and it can be used as an identification signal.

1.1.1 Evolution of Song through Sexual Selection

Bird song has been shown to play a role in mate attraction and male-male competition, so it is possible that bird song has arisen through sexual selection (Read and Weary 1992). Male song in some species has the ability to drive back rivals and catch the attention of females (Slater 2003). Song has also been found to be an indicator of male fitness. For example, female canaries (*Serinus canaria*) are particular to certain song phrases (Vallet and Kreutzer 1995). Slater (2003) hypothesised that these phrases may be ones the females heard frequently as young birds or alternatively that these phrases are more difficult to master, indicating that the males singing them are of a higher quality and thus would be better mates. Read and Weary (1992) suggested that the level of song output is set by the relative costs and benefits of advertising, and that sexual selection favours increased output. For example, greater song diversity and larger repertoires are exhibited in species where males play a greater role in the care of the offspring (Read and Weary 1992).

Another way female canaries look for suitable mates is to eavesdrop on male-male interactions. During these interactions male canaries sing, with the song timing providing information on the singer (Amy et al. 2008). Overlapping song suggests the male is willing to escalate the verbal confrontation, and females seeking mates will choose the overlapping male (Amy et al. 2008). Ability to learn has been shown to be an indicator of fitness in budgerigars (*Melopsittacus undulatus*). Female budgerigars prefer mates that are able to learn new vocalisations, and failure to be able to do this means a male is likely to be unable to find a mate (Hile et al. 2005). In blue tits (*Cyanistes caeruleus*) males that sing earlier gain more mates (Poesel et al. 2006).

1.1.2 Use of Song in Territorial Interactions

Song has been shown to play an important role in territorial and aggressive interactions between members of the same species (Mennill 2006; Molles and Waas 2006; Searcy and Nowicki 2006). A song may indicate the territory boundaries, and that the territory holder is prepared to defend its territory against any intruders. In song sparrows (*Melospiza melodia*) when males sing their soft song it is a sure sign that an attack is imminent (Searcy and Nowicki 2006). Male and female rufous-and-white wrens (*Thryothorus rufalbus*) not only use their song in territorial defence, but the males will go so far as to distinguish between male and female playback and direct their aggressive response to the male playback (Mennill 2006). Female stripe-backed sparrows (*Aimophila r. ruficauda*) play a leading role in territory defence, and have been shown to initiate more song bouts and sing before the males of the species (Illes and Yunes-Jimenez 2009). The females maintain a strong territorial response for a long period of time and exhibit a stronger response to pair and same-sex intrusions than males (Illes and Yunes-Jimenez 2009). Female bellbirds (*Anthornis melanura*) participate frequently in vocal interactions with their female neighbours, and will respond more strongly to the song of their neighbour than the song of a stranger (Brunton et al. 2008). During courtship and chick-rearing the female bellbirds will respond very aggressively to speakers playing neighbours' song, approaching very fast and getting very close to the speaker (Brunton et al. 2008). It is hypothesised that this aggression is a form of mate and/or food defence (Brunton et al. 2008).

1.1.3 Use of Song in Identification of Individuals

Bird song is often an indicator of species membership (Alcock 2005). Song has been found to inform the listener about the identity as well as the social, genetic and physiological status of the singer. Territorial birds need to be able to recognise their neighbours in order to avoid any costly confrontations towards birds that are not a threat (Molles and Vehrencamp 2001). Individual signatures within songs are well documented not only in territorial male song birds, but also female song birds and non-territorial song birds (Lehongre et al. 2008). Variations in song often indicate kinship (Slater 2003). In some species, one sex often learns their song from the same sex parent; for example males may learn from their dads (Slater 2003). Birds may be able to take

the information they receive from song to make decisions, for example females can use this knowledge to recognise kin and avoid mating with them (Slater 2003). Song can also be used to determine group membership, as in the case of the stripe-backed wrens (*Campylorhynchus nuchalis*) (Price 1999). Stripe-backed wrens are co-operative breeders and use song to discriminate between members of different patriline, even though members of the same patriline may belong to different breeding groups.

1.2 How Bird Song Develops

Song learning begins from birth with a sensory acquisition phase (White and Mooney 1999). Young birds are born with a rough idea of what their song is supposed to sound like, a “template”, and it is in this way that the extent of their learning is limited, so that they produce only their particular species’ song (Slater 2003). Songs that do not match the rough version imprinted in the young birds are not learnt, but those that do are matched with the juvenile’s own template when they begin to sing. The receptive stage lasts different lengths of time in different bird species, ranging from before the juvenile’s first winter into adulthood (Slater 2003). It appears to be fairly unanimous among writers that for young passerine birds to be able to learn their song properly, they need to be able to hear the song of an adult of their own species (Catchpole and Slater 1995; White and Mooney 1999; Slater 2003). Adult birds may influence the songs of younger birds by singing only certain vocalisations, or singing more often when the juvenile is around (Slater 2003).

The sensory acquisition phase is followed by sensorimotor learning (White and Mooney 1999). This is effectively a trial period for the birds, in which they perfect their song, often called a ‘subsong.’ Subsong is followed by ‘plastic’ song, in which the bird’s ‘subsong’ is matched with its innate template (White and Mooney 1999). This gives the final song, which often still requires auditory feedback from other members of the species to ensure the song does not degrade (Leonardo and Konishi 1999).

The completion of the bird’s song and its development is often referred to as crystallisation (Leonardo and Konishi 1999). After crystallisation the song usually varies little in adult birds, with feedback from other adults maintaining song stability.

Leonardo and Konishi (1999) carried out an experiment in which they looked at singing in adult zebra finches whose song had already crystallised. They used computer programs to disturb the birds during singing, which in turn caused the birds' song structures to deteriorate. After they started playing the normal song again the birds' song structure quickly returned to normal. They managed to show that, although birds may not be able to learn new songs, they are certainly able to retain plasticity in the brain.

However, changes in song of adult birds may not be due to hearing changes in song of other birds. Catchpole & Slater (1995) noted that juvenile birds may have a large repertoire of song types, and changes in song during adulthood simply reflect the birds calling on their extensive song repertoire and bringing new vocalisations out.

1.2.1 Song Structure and Organisation

There are four main ways in which signal information can be encoded within song (Lehongre et al. 2008); in the repertoire composition, in the sequence of occurring phrase or song types, in the structure of the vocal system, or in differences in the way the elements are produced. These forms of variation also aid in species identification, as different species encode their identities in different facets of their song. For example, in canaries it is the sequences which convey an individual's identity, with sequences longer than three phrase types being unique to single individuals (Lehongre et al. 2008). Male banded wrens (*Thryothorus pleurostictus*) recognise each other using individual versions of shared song types (Molles and Vehrencamp 2001). How a bird learns its song is perhaps dependent on that particular species' method of encoding individual identification within the song.

The typical song structure and repertoire size learned by young birds varies among different species. Some species are very phrase-focussed and will learn many different phrase types but no songs. For example, the unit of learning for the Anna's hummingbird (*Calypte anna*) is the phrase, and the phrases are made into songs which are commonly shared between neighbours (Yang et al. 2007). Other species are very song-type focussed and will learn whole songs, such as great tits (*Parus major*)

(Franco and Slabbekoorn 2009). Great tits have repertoires of varied sizes, made up of stereotypically produced song types, the composition of which may vary from year to year (Franco and Slabbekoorn 2009).

There can be a large amount of variety in the extent that song is shared between members of the same species (Catchpole and Slater 1995). In some species with large song type repertoires the whole repertoire may be shared, but individuals sing different song types out of that repertoire. For example village indigobird males (*Vidua chalybeate*) learn whole song repertoires, and share more than 20 song types with their neighbours, but do not necessarily share song types with non-neighbours (Catchpole and Slater 1995). Some species only have one song type, yet this is not necessarily shared between all individuals of the species. Male Costa's hummingbirds (*Calypte costae*) have a monosyllabic song, yet there are still differences between individuals (Williams and Houtman 2008). Differences can be seen in maximum frequencies, and in the durations of elements that make up the phrase. The most common pattern of sharing is when adult males share some of their song types with each other so that they are able to sing together (Catchpole and Slater 1995).

1.3 Local Dialects in Birds

In many bird species, song is similar to human languages, in that it has dialects. When the song of a species varies from one location to another, this is termed geographic variation (Searcy et al. 1997). There are two types of geographic variation, microgeographic and macrogeographic (Catchpole and Slater 1995). Microgeographic variation occurs between birds which live in the same area, and have the ability to interact or potentially interbreed with each other. Macrogeographic variation refers to song differences among populations which are many miles apart and are unlikely to ever interact.

Birds are able to discriminate between the local dialect and a foreign one, and will react differently to each song (Searcy et al. 1997). Males will usually, but not always, respond to local song more aggressively than they would foreign song. Song sparrows are able to discriminate local from foreign song (Searcy et al. 1997) and will respond more powerfully to local song. Saddlebacks (*Philesturnus carunculatus*) use different

geographic dialects to avoid mating with close relatives (Jenkins 1978). Jenkins (1978) demonstrated that male saddlebacks will move outside their parental dialect area to breed, indicating that it is possible they use dialect as a cue to avoid mating with kin.

Song dialects do not necessarily prevent gene flow between populations. Orange-tufted sunbirds (*Nectarinia osea*) exhibit strong microgeographic differences in their song (Leader et al. 2008). Most young do not cross the dialect boundary; however there is a high amount of gene flow between populations (Leader et al. 2008). So the persistence of dialects in this species may be explained by dispersal across dialect boundaries followed by vocal matching (Leader et al. 2008). A study on a population of white-crowned sparrows (*Zonotrichia leucophrys oriantha*) showed that song dialects are related to the genetic structuring of the population. However the proportion of genetic variability found in groups of birds belonging to each song dialect is similar to that found in populations or subspecies of other non-colonial song species, demonstrating that the effect of song dialect on genetic population structure in the sparrows is not strong (MacDougall-Shackleton and MacDougall-Shackleton 2001).

1.4 Continued Evolution of Bird Song

Bird song is continually transforming through multiple mechanisms, including sexual selection as mentioned earlier. The ability of young birds in their sensory acquisition phase to perceive small differences in song structure may lead to change of the structures, and variation in the elements (Podos et al. 2004). Ongoing geographic differences in song are likely to be caused by cultural drift; the phenomenon of random cultural change with exposure to different cultures (Searcy et al. 1997). Through exposure to different dialects song is liable to be readily changeable throughout time (Searcy et al. 1997). Small changes in phrases and their order in the song are likely to be results of listening to other birds sing as songs change gradually over a geographical gradient and are more variable within populations (Searcy et al. 1997). Isolated, defined changes in song are more likely to be based in strong selection pressures and female choice (Searcy et al. 1997). Large changes in phrase and song structure, and changing complexity are probably a result of the actual evolution of the bird and its song (Searcy et al. 1997).

Random changes in genetic loci may modify a bird's vocal potential, potentially changing the song (Podos et al. 2004). For example, syrinx mass determines the minimum vocal frequencies a bird can produce (Podos et al. 2004). If this were to change through a random genetic mutation some frequencies may not be able to be sung, or a bird may be able to produce new frequencies not previously heard in the population.

Cultural selection is different than cultural drift in that habitat differences may affect the songs' ability to transmit through the environment, and thus evolution of the song may occur to benefit transmission through the new environment (Podos et al. 2004). A study on 30 species of *Phylloscopus* and *Hippolais* warblers showed that timing characteristics of song, but not frequency characteristics, change with habitat structure (Badyaev and Leaf 1997). So as species colonise new areas their song characteristics may change through necessity rather than choice.

1.5 Duetting

1.5.1 What is a duet?

Duetting occurs when two birds combine their voices to produce a song (Hall 2004). There is a large amount of diversity amongst duetting species, both taxonomically and in the structure and function of their duets (Hall 2004). There are at least 222 species worldwide that duet, which is less than 3% of all bird species (Farabaugh 1982). There are two kinds of duets, antiphonal and simultaneous (Molles et al. 2006). Antiphonal duets are when the pair members alternate their vocalisations, often co-ordinating them so well that listeners may think they are listening to a single song (Power 1966; Mays et al. 2006). The Eastern whipbird (*Psophodes olivaceus*) is an antiphonally duetting species, and duets in this species are solely initiated by the male bird (Rogers 2005). Simultaneous duets occur when both birds sing in unison, and also can be co-ordinated so perfectly that they can be thought of as one bird singing (Power 1966; Mays et al. 2006). Among the species that participate in simultaneous duets are the bokmakierie (*Telophorus zeylonus*) and the African forest weaver (*Ploceus bicolor*) (Wickler and Seibt 1980; Hall 2004). Interestingly, white-crowned sparrow weavers (*Polcepasser*

mahali) sing both antiphonally and simultaneously (Voigt et al. 2006). There are some common characteristics of duetting species. They are generally territorial all year round, exhibit prolonged monogamous pair bonds and they most commonly occur in the tropics (Farabaugh 1982).

There are three main hypotheses for the functions of duetting, which appear to be related to the characteristics of duetting species. Formation and maintenance of the pair bond is the first of these hypotheses (Hall 2004). Some birds exhibit differences in local dialect, and if two birds are able to sing together this may be an indication that they would be able to form a good pair. This is especially true as some duets may require a large investment in order to do it correctly (Hall 2004). Another hypothesis for the function of duetting is resource defence (Molles and Waas 2006). Two birds singing may represent a greater threat to a predator or potential competitor than one bird singing by itself (Hall 2004). It will indicate to the predator or competitor that there are two birds willing to defend the resource. The third hypothesis is mate guarding. A duet could warn any single birds that the pair members are in fact a pair, and to look elsewhere (Hall 2004). There are two main ways this may work. Firstly an individual may prevent same-sex rivals copulating or pairing with its partner (Hall 2004). Second it may avoid being usurped itself by preventing its mate from taking another partner (Hall 2004).

Duetting is present in a number of New Zealand species. For example North Island brown kiwi (*Apteryx mantelli*) duet, and may use auditory feedback to change the timing characteristics of their calls during these duets (Corfield et al. 2008). Saddlebacks also perform a duet, which tends to be antiphonal but they will overlap occasionally (Jenkins 1978). Fernbird (*Bowdleria punctata*), tui (*Prosthemadera novaeseelandiae*), bellbird and weka (*Gallirallus australis*) are all duetting species (Heather and Robertson 1996; Lindsey and Morris 2000; Chambers 2007).

1.5.2 Non-avian duets

Birds are not the only species to duet. Duetting is present in a vast number of non-avian species, and the types and purposes of these duets are highly varied. In white-wing vampire bats (*Diaemus youngi*) antiphonal duets aid the bats in finding and identifying

individuals at long distances (Carter et al. 2008). Carter et al. (2008) found that antiphonal calling was common amongst bats which were isolated, and that when these bats were brought together this antiphonal calling decreased. This suggests that antiphonal calling is used to mediate social exchanges which may occur outside of the roost (Carter et al. 2008). Sperm whales (*Physeter macrocephalus*) also use duets to mediate social interactions. Sperm whales live in matrilineal groups where adults share care of offspring (Schulz et al. 2008). Their antiphonal vocalisations, termed codas, are shared within groups, and groups tend to interact primarily with other groups that have similar coda dialects (Schulz et al. 2008).

In other species, duets serve important roles in interactions between mates. All gibbons (Hylobatidae) produce long and loud song bouts, but siamangs (*H. syndactylus*) are known for their very complex duet structure (Geissmann 1999). If siamangs gain new partners they re-learn their duet, this investment suggesting that pair-bond formation and maintenance are important functions of siamang duets (Geissmann 1999). This is backed up by a study which suggested that those siamangs which groom more, behave synchronously and stay close together exhibit much higher levels of duetting activity than those that do not (Geissmann and Orgeldinger 2000). The bushcricket (*Leptophyes punctatissima*) uses duetting to form pair-bonds, where the male first vocalises and the female responds by moving towards the sound (Rheinlaender et al. 2007). The Australian bushcricket (*Caedicia*) duet is slightly different to other duets in that it only produces a short term pair bond, with the duet only used by males looking for females to mate with (Hammond and Bailey 2003).

These examples show us that duetting is not just for birds, and that the functions of duetting extend to non-avian species also. Whales show geographic variation in dialects despite the huge distances they travel. Siamangs use their duets to create and maintain pair bonds. This is an example of parallel evolution, where duetting has evolved multiple times in different groups of animals, with similar mechanisms and functions.

1.6 Study Species

The kokako, *Callaeas cinerea*, belongs to an ancient endemic New Zealand bird group, the wattlebirds (Family: Callaeidae). There are two other members in the group, the now extinct Huia (*Heteralocha acutirostris*), and the currently threatened Saddleback (Hay et al. 1985). Recent research has placed the hihi's (*Notiomystis cincta*) family close to the wattlebird family, as both are far removed from other families, however the branch size separating the two is so large that they cannot be considered closely related (Ewen et al. 2006). There are two subspecies of kokako, primarily differentiated by the colour of their wattles. The North Island kokako, *Callaeas cinerea wilsoni*, has bright blue wattles, whilst the South Island kokako, *Callaeas cinerea cinerea*, has orange wattles. The South Island kokako is assumed to be extinct, with the last sighting in 1967 in Mount Aspiring National Park (McBride 1981).

The North Island kokako (henceforth: kokako) is well known for its hauntingly beautiful song, commonly used in advertisements, and it is the face of the current Genesis Energy tree-people campaign (GenesisEnergy 2009). The kokako inhabits complex healthy native forest, both mature and regenerating (Clout and Hay 1981). It weighs approximately 230g, and shows no sexual dimorphism; sexes can only be separated unequivocally when DNA testing is carried out, or a female is observed incubating, as only the female of the species incubates the eggs (Innes and Flux 1999). They are long-lived birds, some reaching up to 20 years or more (Innes and Flux 1999). The kokako has short, round wings, making it a poor flyer (Sibson 1982). To move through the forest the kokako relies on its powerful legs to run or leap amongst branches, being only capable of a downwards glide or a short level flight (Hay et al. 1985). They are generally silent when moving through the canopy.

1.6.1 Kokako Ecology

Kokako are territorial birds that form pair-bonds. Their habitat is generally of an altitude below 750masl (Hay et al. 1985). The territories they hold are usually 4-20ha in size, and are maintained by singing (Innes and Flux 1999) and by boundary interactions, which consist of chasing accompanied by soft twittering noises. This sometimes leads to

fighting between birds, in which case they will grapple on the ground and peck at each others' wattles (Hay et al. 1985). Maintaining territories like this is particularly important as a territory is the source of all their resources.

Territories may be held by female-male pairs, male-male pairs or a solitary male (Innes and Flux 1999). There have also been reports of female-female pairs forming (Laura Molles, pers. comm.). Very rarely is a territory held by a single female, and if it is it is only for a very short time. Interestingly, kokako are among the very few bird species in the world to form male-male pair bonds in the wild. This was thought to be because of the decimation of the female numbers, but has also been shown to occur in juvenile males, even in the presence of an abundance of females (Innes and Flux 1999). Kokako song can be heard year round being used for within-pair communication, maintaining pair bonds and territorial interactions (Molles et al. 2006).

Best and Bellingham (1991) showed that the diet of kokako changes with season and with available food sources. Kokako gather all their resources from their territory, and thus as the composition of the vegetation within the territory changes so does the diet (Best and Bellingham 1991). Pigeonwood (*Hedycarya arborea*) leaves and fruit are an important food source for kokako, as are hanging spleenwort (*Asplenium flaccidum*) fronds (Flux et al. 1995). Rewarewa (*Knightia excelsa*) flowers are also taken (Innes et al. 1996). Leaves from hound's tongue (*Microsorium pustulatum*) and puka (*Griselinia lucida*) are eaten, as are fruits from mangeao (*Litsea calicaris*) and supplejack (*Ripogonum scandens*) (Innes et al. 1996). Puriri (*Vitex lucens*), five-finger (*Pseudopanax arboreus*), pate (*Schefflera digitata*) and broadleaf (*Griselinia littoralis*) leaves and fruit have also been known to be consumed by kokako (Hay et al. 1985). Invertebrates are mostly eaten during the breeding season, as a high protein diet is needed for egg development and rearing of chicks (Powlesland 1987). Fruit is an important part of the diet, particularly in years of intense fruit production (Powlesland 1987).

Kokako usually breed from October through to February (Hay et al. 1985). During a 'good' season, where weather conditions are fine and food is plentiful, breeding can start as early as September and continue through to as late as April or May (Flux and Innes 2001). Nests are built on average 16m above the ground, and are approximately

half a metre across (Flux and Innes 2001). The nest is usually built by the female, but in the case of male-male pair bonds it is likely only one of the males will build the nest, as one male generally takes on the role of the female (Hay et al. 1985; McLeod 1998). The nest is composed of a base of loosely woven twigs with moss and fern scales woven in to form the nest cup. Lianas are often added to the nest for added support. The female is the only one who incubates the eggs. The male feeds the female whilst she is incubating and brooding, and both parents feed the chicks (Flux and Innes 2001). Clutches of 1-3 eggs are laid; incubation takes approximately 18 days, and the nestling stage lasts about a month until the chicks fledge. Some kokako will have two clutches per season, although this only occurs in 'good' seasons (Tony Silbery, pers. comm.).

1.6.2 Distributions within New Zealand.

Sub-fossil remains show that kokako were widely distributed before the arrival of European settlers (Innes and Flux 1999). Once found throughout the forest tracts of the North Island (Gaze 1994) kokako are now found naturally occurring only in a few remnant stands of forest. Kokako were noted for their somewhat erratic distribution (Gaze 1994) which we now know is caused by the species' habitat demands. With logging occurring throughout 1880-1930, large tracts of forest were destroyed, confining the kokako to small remnants as this species is unable to fly between stands that are even 100m apart (Hay et al. 1985). Kokako played a major role in anti-logging campaigns during the 1970's and early 1980's, as a flag-ship species (Innes and Flux 1999). At present there are approximately 680 pairs of kokako (Kokako Recovery Group, 2007) spread throughout approximately 20 places all over the North Island (Figure 1.1) (Flux and Innes 2001). The isolation of these populations makes gene flow difficult, given that kokako are not able flyers. Translocations are required to prevent the degradation of genetic lineages among populations (Flux and Innes 2001).

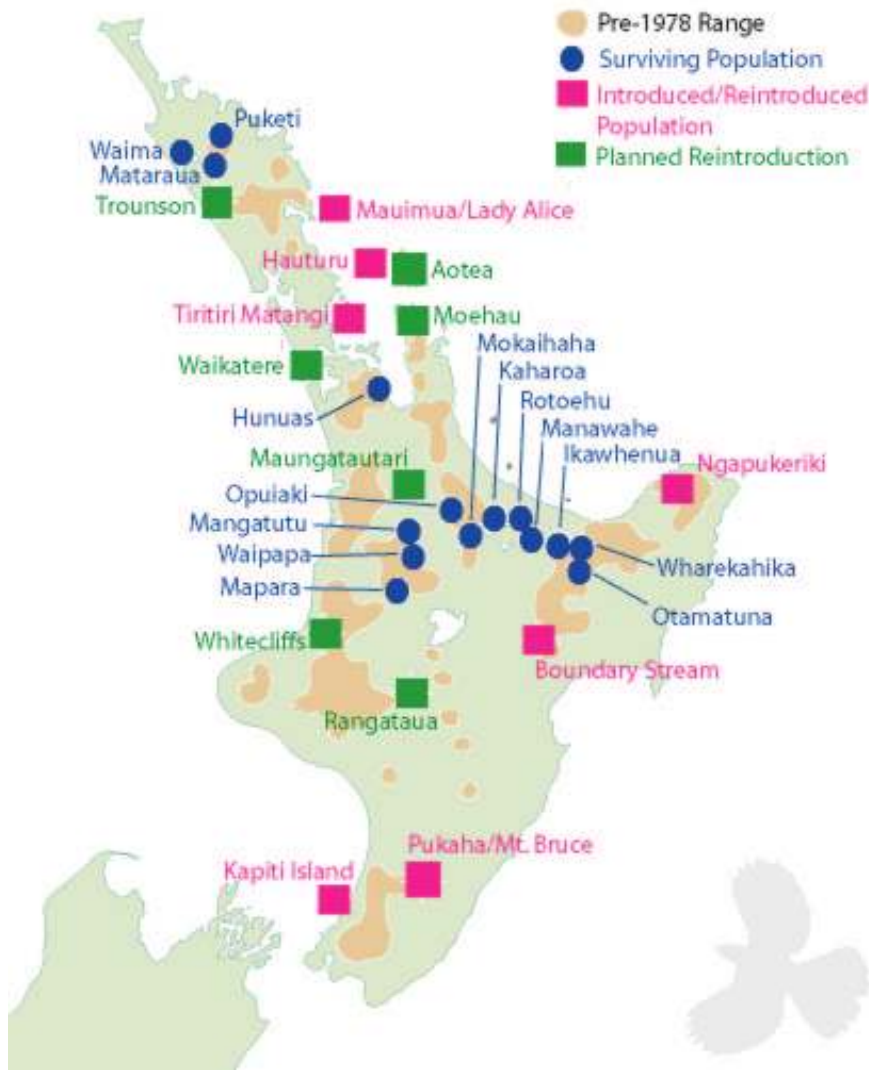


Figure 1.1: Map showing the current distribution of kokako populations. Map from Kokako Recovery Group.

1.6.3 Main Causes of Decline.

The causes of kokako decline may vary in different areas (Hay et al. 1985). However, the main cause of decline is predation at nests by possums (*Trichosurus vulpecula*), stoats (*Mustela ermina*) and ship rats (*Rattus rattus*), leading to a decline in recruitment (Innes and Flux 1999). Predation of females on nests also leads to skewed sex ratios, reducing breeding capacity of populations and slowing recovery once predator control is in place. In addition, rats and possums disturb kokako nests at night, leading to the chicks leaping from the nest prematurely in fright (Gaze 1994). Harriers (*Circus approximans*) are also known to prey on chicks and in rare cases even adults. Loss of habitat is also a reason for the fall in kokako numbers. One of the key features of

kokako habitats is the complex forest structure and wide variety of plant species (Hay et al. 1985). Logging, selective or otherwise, decreases this variety and complexity and can exclude some of the elements of the forest they require (Gaze 1994). While this may not directly affect the kokako, it may affect their ability to breed successfully (Gaze 1994).

Competition for food may be another reason for decline in some areas (Hay et al. 1985). With the introduction of cats, stoats, possums and rats, not only is there an increased risk of predation, but possums in particular will eat the same foods as kokako. However, kokako have a broad diet and can consume a wide range of foods (Hay et al. 1985) and in some areas this may have allowed survival as they can adapt to changes in food sources easily.

1.6.4 Current Management and Conservation

The aim of current management, set out by the Department of Conservation (DoC), is to bring the kokako back from its endangered status by restoring self-sustaining populations, with an average of 50 pairs per population and a total of 1000 breeding pairs (Innes and Flux 1999). It is envisioned that there will be kokako in all regions where they were previously. The North Island kokako recovery plan (Innes and Flux 1999) has four strategies they recommend to help maintain and expand populations of kokako:

1. Pest control and monitoring at current and potential mainland sites for kokako.
2. Translocations to potential mainland sites once they are able to safely support kokako.
3. Some translocations to offshore islands to ensure the continued viability of the species.
4. Continuation of captive breeding of the species for release into these pest-controlled sites, to provide something tangible for the public advocacy of kokako management and for preservation of extremely rare genetic lineages.

With these aims in mind the Department of Conservation released a kokako management folder (Flux and Innes 2001). Ongoing pest control, with the aim of reducing possum and ship rat pressure during the breeding season, is the key to kokako

conservation (Basse et al. 2003). This means that predators in kokako areas are kept to very low numbers at the start of breeding season, making it unlikely they will have any substantial effect on the kokako. As predator numbers increase over winter intensive trapping is carried out to decrease their numbers back to low levels before breeding begins again. There are also strict monitoring regimes, where the numbers of potentially breeding territorial adults in the populations are counted annually. The techniques for all the surveys are set out in this management folder.

1.6.5 Translocation History at Pukaha Mount Bruce

Pukaha Mount Bruce Scenic Reserve and National Wildlife Centre (henceforth: Pukaha) was one of five potential mainland reintroduction sites noted by the 1999 kokako recovery plan (Innes and Flux 1999); it was one of the sites where kokako were last seen in the southern North Island. Pukaha is a government owned reserve, and is a native hardwood-podocarp-broadleaf forest remnant.

A captive breeding programme for kokako was implemented at Pukaha between 2001 and 2004, but was not particularly successful as the captive kokako did not breed. After a successful release of wild Mangatutu (Figure 1.1) birds in 2003 it was decided to terminate the captive breeding programme and the two captive pairs of Mangatutu birds were released into the forest (Tony Silberry, pers. comm.). The captive breeding programme that was focused on breeding the rare Taranaki genetic lineage was initiated in 1999. This finished in 2008 and all Taranaki birds have been translocated onto Tiritiri Matangi Island, so that they can continue the lineage in the wild as there is currently no safe reserve for them in Taranaki. In 2005 there was another translocation of kokako into Pukaha, this time from Mapara (Figure 1.1).

Mangatutu Translocation: There were two translocations from Mangatutu to Pukaha. Six birds (four females and two males) were captured in Mangatutu Ecological Area in July 2003 and subsequently released at Pukaha following disease screening, banding and transmitter attachment (Hancock and Silberry 2004). Monitoring was carried out daily for the first three weeks after release, then weekly until October, after which a more intensive breeding season monitoring regime was implemented (Hancock and

Silbery 2004). No pairs were captured, and only two of the females, Pumpkin and Petal, were caught in the same net site at Mangatutu. There was a single mortality, Petal, approximately five months after the release, probably resulting from an attack by an Australasian harrier (Hancock and Silbery 2004). Two of the birds, Turk and Gale, built a nest which was identified in December 2003. This nest successfully fledged two chicks which were banded in January 2004. Another pair, Whakatere and Rain were thought to have paired but did not breed.

Two more birds from Mangatutu, a male and a female, were also released in October 2004. The female died whilst the male was not sighted at the start of the 2005/2006 breeding season or thereafter.

Mapara Translocation: In September 2005 seven birds (three pairs and a single bird) were translocated from Mapara (Silbery and Studholme 2006). The three pairs that survived remained paired at Pukaha. Two of these pairs established territories on the slope just behind the visitor's centre, whilst the previously-released Mangatutu birds and the third Mapara pair set up territories at the summit. Refer to Appendix 1 for census data on birds currently at Pukaha.

1.6.6 Kokako Song and Mate Choice

The kokako produces one of the world's longest non-repetitive bird songs (Molles et al. 2006). As yet, there is not a great deal of research that has been carried out on kokako song. Kokako's long song is sung either as a duet, or as a solo. The duets consist of four to six phrases, with pauses of approximately 0.6-21s between phrases (Molles and Waas 2006) (Figure 1.2). Kokako in Pongakawa Ecological Reserve have an average of 18.27 ± 0.59 phrases per pair, with a phrase consisting of, on average, three elements (Molles et al. 2006) (Figure 1.2). In contrast, kokako in the Hunua ranges have a repertoire of approximately 9-10 elements (Miner-Williams 2007). Mapara birds which have been translocated into the small Hunua population have been shown to have 10 unique elements, although it is unlikely that a full repertoire has been recorded in this instance (Miner-Williams 2007).

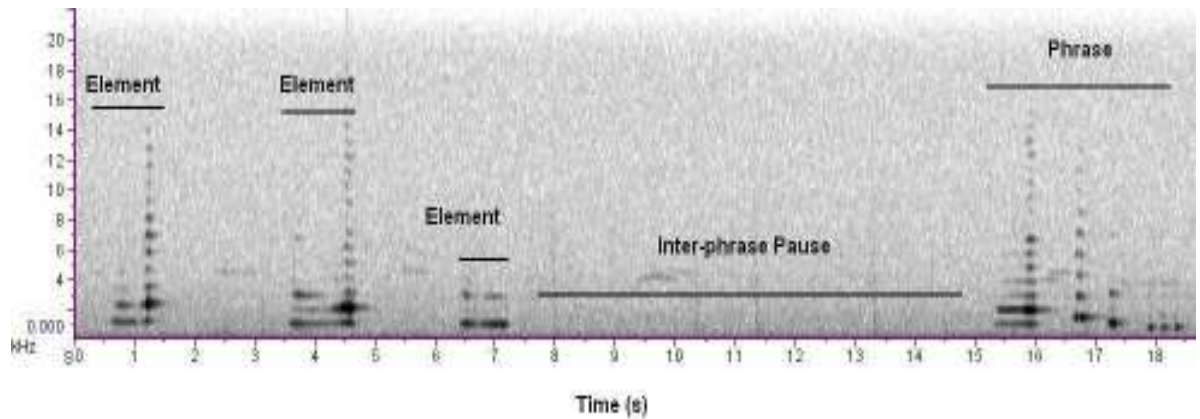


Figure 1.2: Spectrographic representation of an element, a phrase and an inter-phrase pause.

Kokako are well known for their highly co-ordinated duets. Neighbouring birds' duets typically consist of the same phrase sequences, indicating dialects are present both in phrases and the overall song (Molles et al. 2006). Both sexes are able to play the same part in a duet, with males tending to sing slightly more of the duet than females, although this is not a clear cut rule. They may anticipate or imitate the phrases sung by their neighbours (Molles and Waas 2006). It is thought that the inter-phrase pauses allow the kokako to listen for neighbouring pairs that may be singing so that they may respond accordingly (Molles et al. 2006). However, it is also possible that inter-phrase pauses allow pairs to listen for each other, so they are able to sing the next part of the duet. Often one bird of the pair will start singing but the other bird will be feeding, or not hear, and will not respond (Tony Silberry, pers. comm.). It may take a pair several tries before a pair is coordinated enough to sing the whole duet together.

Solo kokako are able to perfectly perform the same “duet” sequence as paired birds (Molles and Waas 2006). The way that kokako assemble their duets suggests multiple functions interact as the reason behind the duet. The duet is particularly evident as a territorial signal, as shown by Molles and Waas (2006). They used a one and two-speaker playback experiment to show that imitation duets indicate a greater threat to kokako than solo song, and thus trigger a more aggressive territorial response.

Kokako are among those birds that exhibit geographic variation in their dialects, and they tend to not mate with birds who do not share the same dialect as them. Kapiti Island kokako are particularly interesting, as they have one of the few recorded incidences of mixed-dialect pairings. Translocations from several different kokako

populations to Kapiti Island occurred in the 1990's (Rowe 2001; Rowe and Bell 2007). Initially, the kokako paired with birds which shared the same dialect as themselves. However, in later breeding seasons birds born on Kapiti paired with those translocated birds that had not paired initially (Rowe 2001). Two of the Kapiti Island-born birds did not have the option of pairing within their dialect as there were no unpaired birds from their parents' source area, and so these two young birds paired with translocated birds from a different area (Rowe and Bell 2007). There are some other cases where mixed dialect pairings have occurred. For instance, a female kokako transferred from Mapara to the Hunua Ranges in 2007 paired with a resident Hunua male and successfully fledged a chick in the first breeding season following her release. This pairing occurred even though there were translocated Mapara males in the area as well (Laura Molles, pers. comm.).

The kokako in the Hunua Ranges also have an interesting history (Hazel Speed, pers. comm.; Figure 1.1). The Hunua Ranges are a DoC managed area approximately 40km from Auckland, and have an area of 17,000ha; 1,000ha of which is managed for kokako. In 1994 a survey located 5 kokako pairs and 20 singles; however the pairs consisted of one male-female pair and four male-male pairs. Intensive pest control was carried out, and in 1996 another survey showed nine pairs and one single. These birds were all inbred as they came from one female. In 2006 there was a release of 8 males and 6 females from Mapara, and one Hunua-Mapara pair formed. In 2007 4 Tiritiri Matangi females were released along with 3 females and 1 male from Waipapa. In 2008 another release was carried out with 2 males and 2 females from Tiritiri Matangi. Since these releases the territories have decreased in size and have become bunched, despite there being plenty of room within and outside the managed area. Late in 2008 another survey was carried out; this time 5 of the 17 pairs found were mixed-dialect pairs. This is indicating an increase in mixed-dialect pairing as density is increasing.

Kokako have shown the ability to learn new songs. There have been multiple instances both on Kapiti Island and Tiritiri Matangi Island where kokako have been reported to add new songs to their repertoire (Rowe 2001; Campbell 2004). These birds ended up sharing fewer phrases with the birds from their source dialect than they did with their neighbours. On Kapiti Island neighbours share more phrases with each other than with birds that have territories further away. Kokako often participate in counter-singing

bouts where they match or anticipate the song of another pair, so we would expect them to share song with their neighbours in order to allow them to counter-sing (Molles and Waas 2006).

1.7 The Existing Problem and Aims of this Study

Song is very important to kokako for a number of reasons. Their duets are thought to function in the formation and maintenance of the pair-bond and mate-guarding. Perhaps the most important function of the kokako duet is for territory defence as a kokako's territory contains all the resources the bird will need. Because kokako only exist in forest remnants which are spread throughout the North Island and they are poor flyers, translocations are used to maintain gene flow and prevent inbreeding.

As shown in Rowe (2001) and Campbell (2004) kokako show song macrogeographic variation; birds from different areas have different dialects. When placed into a population with multiple dialects kokako will preferentially mate with those birds that share their own dialect. If the aim of translocations is to enable breeding between kokako from different areas, then these translocations have the potential to be unsuccessful, as the birds may not breed with each other. This is particularly important at low densities, as shown in the Hunua translocations. This assortative breeding coupled to small population sizes can lead to inbreeding and inbreeding depression, just the problem translocations are trying to repair. There is also microgeographic variation, for example in Mapara there are three different dialects, which exacerbates this problem.

This thesis fills a research gap in our knowledge of kokako song by studying variation of songs in kokako at Pukaha and between Pukaha kokako and kokako present in one of the source populations (Northern Mapara) and by looking at the song makeup of kokako born in an area where there is more than one dialect present. In this study I aim:

- To determine whether the repertoires of the adults translocated from Mapara North to Pukaha five years ago have changed in any way compared to their Mapara source population repertoires.

- To describe the makeup of the repertoire of the Pukaha-born birds, and to see if this repertoire is a copy of their parents' natal dialect, or if it is a mix of the two dialects present at Pukaha.
- To use elements of the song and song repertoires as a tool for managers to determine the likelihood of interbreeding between birds from different areas.

To do this I will look at song recordings in order to determine: repertoire size, sharing and phrase characteristics for *source*, *translocated* and *Pukaha-born* birds. These three measures will form the basis for the three following chapters.

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Chapter Two: General Methods



Song playback and recording.

2.1 Study Sites

2.1.1 Pukaha Mount Bruce

The area in which I carried out the majority of my research is Pukaha Mount Bruce Scenic Reserve and National Wildlife Centre Reserve, hereafter referred to as Pukaha. The reserve covers 945ha of land, and changes in elevation from 310masl to 710masl at the summit (Hancock & Silbery, 2004). The area is separated from privately-owned tracts of native forest by grassland and shrubland all around, apart from one grazed forest remnant of about fifty hectares on the north-east corner of the reserve. The park lies approximately three kilometres away from the extensive native forest of the Tararua Ranges.

The park contains a wide variety of plant species, a distinguishing feature of kokako habitat, allowing them to settle successfully there. Tawa (*Beilschmeiedia tawa*), supplejack, bush lawyer (*Rubus cissoides*), hangehange (*Geniostoma ligustrifolium*), pigeonwood, rewarewa, kamahi (*Weinmannia racemosa*), horopito (*Pseudowintera axillaries*) and hinau (*Elaeocarpus dentatus*) are all abundant species at Pukaha, along with hardwood podocarp broadleaf forest species. Many other important kokako food sources are also found in the reserve, such as hanging spleenwort and hound's tongue (Hancock & Silbery).

A map of the current kokako territories at Pukaha was provided by Tony Silbery (DoC; Figure 2.1), and a list of all kokako and bands by Tom Studholme (DoC). This information was used to find and identify the kokako in the reserve.

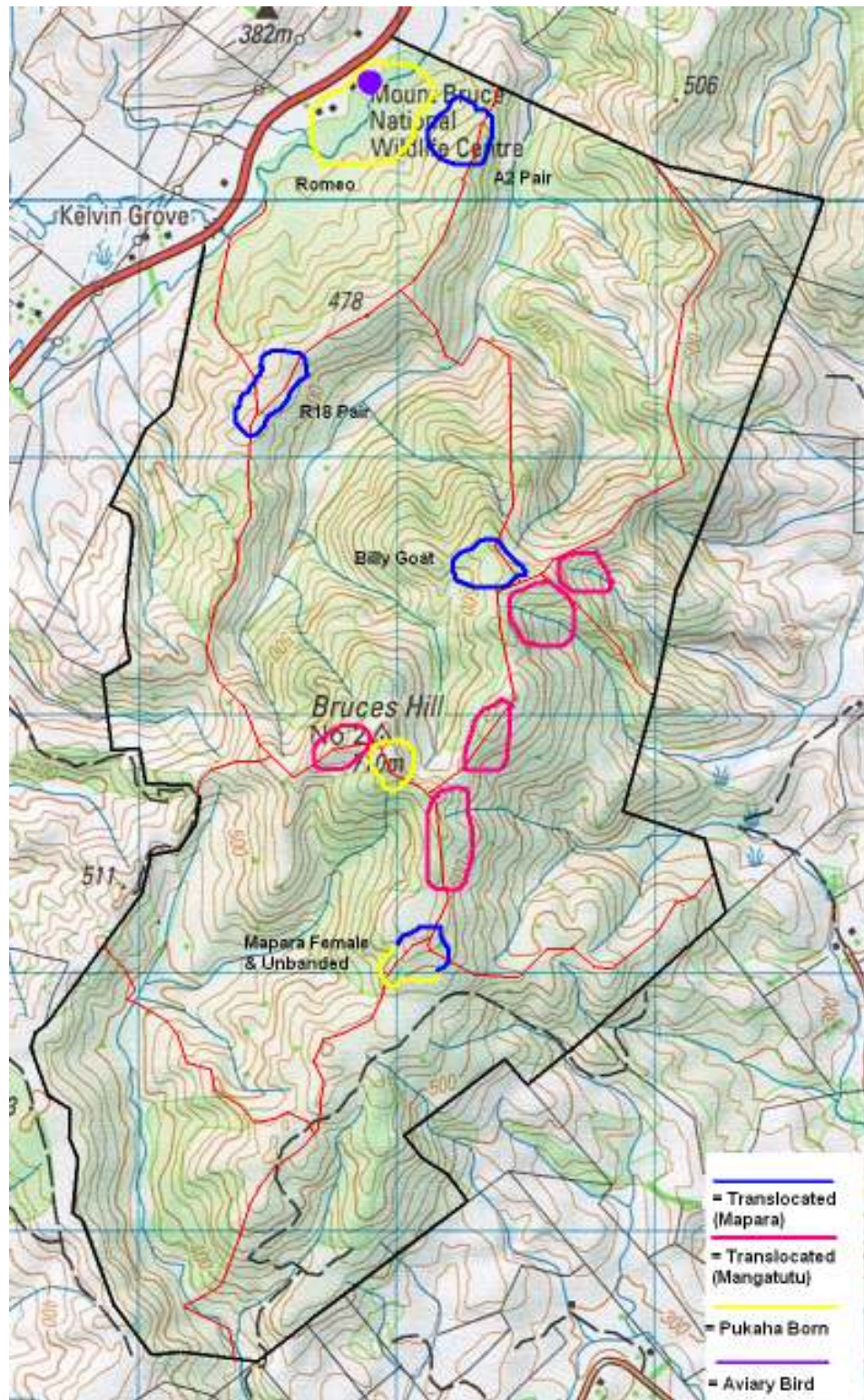


Figure 2.1: All Known Kokako Territories at Pukaha during 2007-2008 Breeding Season. N.B. Only the kokako whose calls were recorded for this thesis are named on the map. Mangatutu bird's territories remain unnamed.

2.1.2 Mapara

Mapara is a 1400ha reserve situated just south of Te Kuiti in the Waikato (Figure 1.1). The reserve is broken up into three blocks, North, South and Central. All the recordings undertaken for this study were done in the North block (Figure 2.2), because this was where the capture of kokako for the translocation to Pukaha was carried out. Mapara has been subject to intensive logging in the past, and is now surrounded by farmland and pine plantations. Vegetation is dominated by tawa, with a mixture of podocarp species also present. There have been intensive pest control operations carried out in the reserve, and kokako in Mapara have been the object of numerous studies and monitoring (Leathwick et al. 1983; McLeod 1998; Innes et al. 1999). For further details on topography, climate and history of Mapara please refer to Leathwick et al. (1983).

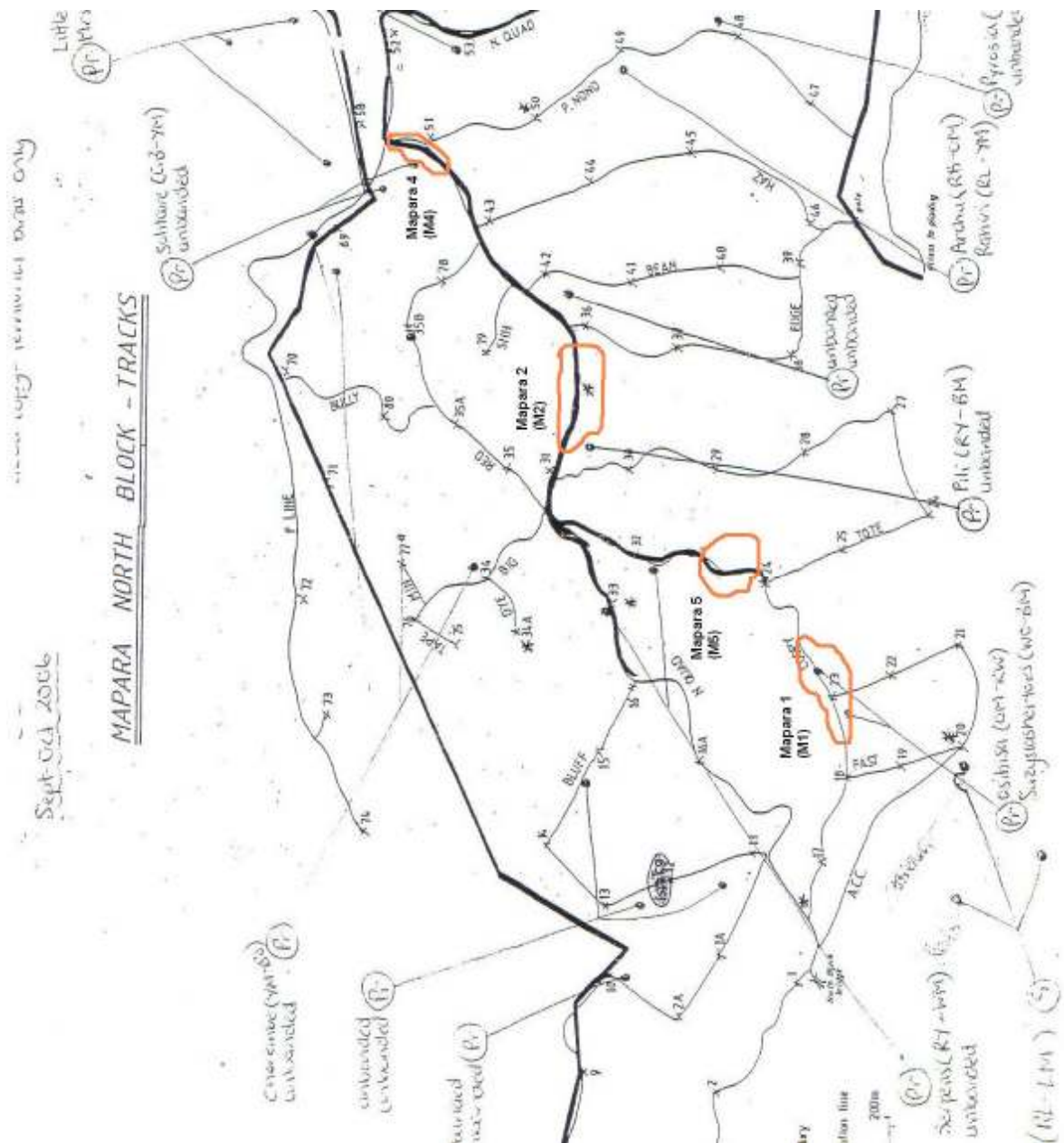


Figure 2.2: Map of Northern Mapara kokako territories. Map provided by the DoC Te Kuiti Area Office, only territorial birds marked on map. Orange named circles represent kokako pairs recorded.

2.2 Study Species: *The kokako*

Four categories of bird were recorded.

- Recordings were done at Mapara North to gain an idea of the original song of the translocated birds. (*Source birds*).
- The pairs translocated from Mapara to Pukaha were recorded. (*Translocated birds*).
- The Pukaha-born birds that have set up territories were recorded. (*Pukaha-born birds*).
- An aviary bird which sung consistently was recorded. I did this because one of the Pukaha-born birds tended to be found around this aviary, and I wanted to determine if any unique elements found in the Pukaha-born bird were attributable to the aviary bird. This bird, Poutama, will be referred to as the *aviary bird*.

At Pukaha four pairs and two individuals were recorded, of these five were males, four were females and one was of an unknown sex (Table 2.1). At Mapara four pairs were recorded, of these one was male, one was female and six were of an unknown sex. I expected to be able to detect changes in the kokako song following translocation by comparing the song of these four categories of kokako.

Four pairs were recorded at Mapara (Figure 2.2). Of these, two were able to be identified. Mapara 1 pair was positively identified as a male, Osibisa (OM-RW) and female, Suzyslashertoos (WO-BM). Mapara 4 pair was positively identified as Solitaire (GB-YM) and an unbanded bird. The other two pairs, Mapara 2 and Mapara 5, were unable to be identified. Mapara 3 was not analysed as I had only one five minute recording from the pair.

Table 2.1: Recorded pairs and individuals from Pukaha.

Bird	Bands	Territory	Sex	Born	Parents	Year Born (B)/ Released (R)	Paired With
Translocated							
M2(Billy Goat pair)	G-MB	Billy Goat/Hotel	♂	Mapara	?	R2005	M3
M3(Billy Goat pair)	B-ML	Billy Goat/Hotel	♀	Mapara	?	R2005	M2
M4 (A2 Pair)	Y-ML	Highway Block - BS	♂	Mapara	?	R2005	M5
M5 (A2 Pair)	Y-MW	A2 - A4 Highway Block - BS	♀	Mapara	?	R2005	M4
M6 (R18 Pair)	O-MR	A2 - A4 Highway Block - BS	♀	Mapara	?	R2005	M7
M7 (R18 Pair)	G-MR	R16 - R19 Highway Block - BS	♂	Mapara	?	R2005	M6
Mapara Female ^ (Mixed Pair)	W-GM	R16 - R19 Echo - Public Track - 620	♀	Mapara	?	R2005	Unbanded
Pukaha-born							
Romeo	M-WR	Highway Block - Aviaries - C-line	♂	Pukaha	M4 & M5	B 2005/ 2006	
Unbanded (Mixed Pair)		Echo - Public Track - 620	?	Pukaha	?	?	Mapara Female
Aviary Bird							
Poutama*	M-RB	In Aviary	♂	Pukaha Aviaries	Tamanui and E131052	B 06/03/ 2001	Bianca, Mihitai, Te Rae, Mapara, Kahurangi

^ Mapara female was wild caught at Mapara as an adult. She was brought into captivity at Pukaha on 26/07/2003. She was paired with Tamanui, Mihitai, Porkchop, Tamanui and Poutama. She was released on 22/11/2007 into the Pukaha forest. She was first seen with the unbanded male mid-2008.

* Poutama was born to a Taranaki male, Tamanui. He was shifted to Otorohanga to pair with Bianca on 20/08/2001. He was brought back to Pukaha on 19/07/2005 to be paired with the other females.

2.3 Recording Methods

I travelled to kokako territories at dawn. When I reached the focal territory I stopped to listen for ten minutes. If no birds could be heard I played a five minute recording of Mapara South dialect (recorded by Jeff McLeod). If the first playback did not draw the birds into the area I played the same song twice more, in two different areas of the territory. If they still did not respond I moved on to a different territory, so that a maximum of fifteen minutes of song was played to a pair per day. At Pukaha, if the Mapara South recording drew the birds in but they did not sing I would then play a Pukaha recording, as this may have been more likely to get a reaction from the birds because this is what they would be used to hearing. This recording was not used to draw birds in because it was too quiet to be heard from a distance of more than approximately twenty metres. At Mapara I gained all recordings either using no playback or the Mapara South recording, there were no instances in which I drew birds in but they did not sing.

I recorded any song using a Roland Boss Micro BR digital recorder and an Audio Technica 815b shotgun microphone. I also listened to the song as it was being recorded using headphones to ensure it was actually being recorded and that the birds were audible. I stopped recording either when the birds left the area and it was impractical to follow them, or when there had been no song for at least three minutes.

Recordings of each focal pair were collected on at least two different mornings to ensure that any rarely sung song elements had a greater chance of being recorded. All recordings were collected between 0600-1600hrs, with the majority occurring between the hours of 0800-1000. Recordings were gathered from the 1st November 2007 to 20th November 2008. I spent a total of 19 days at Mapara and approximately 150 days at Pukaha. This includes days on which I gained no recordings. Once the digital recorder was full the recordings were burnt onto CD and also placed onto an external hard drive so that they were fully backed up, then were deleted from the recorder.

Recordings were processed with Raven Lite version 1.0 (2008). Once in Raven Lite, element libraries were created: I listened to recordings while watching a real-time spectrogram and any elements heard and seen on the spectrogram were copied and

pasted into a new sound window. These were then saved and labelled with the date of the recording and the pair the recording was from.

2.4 Definitions

Element– One continuous trace on a spectrogram.

Element Type – A version of an element, e.g. A, B or C may be different element types.

Phrase/Phrase Type– Multiple elements which are in a predictable sequence.

Song Type – Multiple phrases which are in a predictable sequence.

Repertoire – All the different element types a bird sings.

Rhythmic Song – A song which recurs at predictable intervals.

Cultural Drift – The phenomenon of random cultural change with exposure to different cultures (Searcy et al. 1997).

Fundamental Frequency – The lowest frequency tone of a harmonic series.

Harmonics – An overtone that is an integral multiple of a fundamental frequency.

Tooks – A soft, short note which is commonly used in periods where song themes are not being sung, and pair members are close together (Molles et al. 2006).

Clicks – A short, sharp, single element.

Elements with Multiple Harmonics – An element with at least one harmonic above the fundamental frequency.

Pure Tonal Sounds – An element with no harmonics.

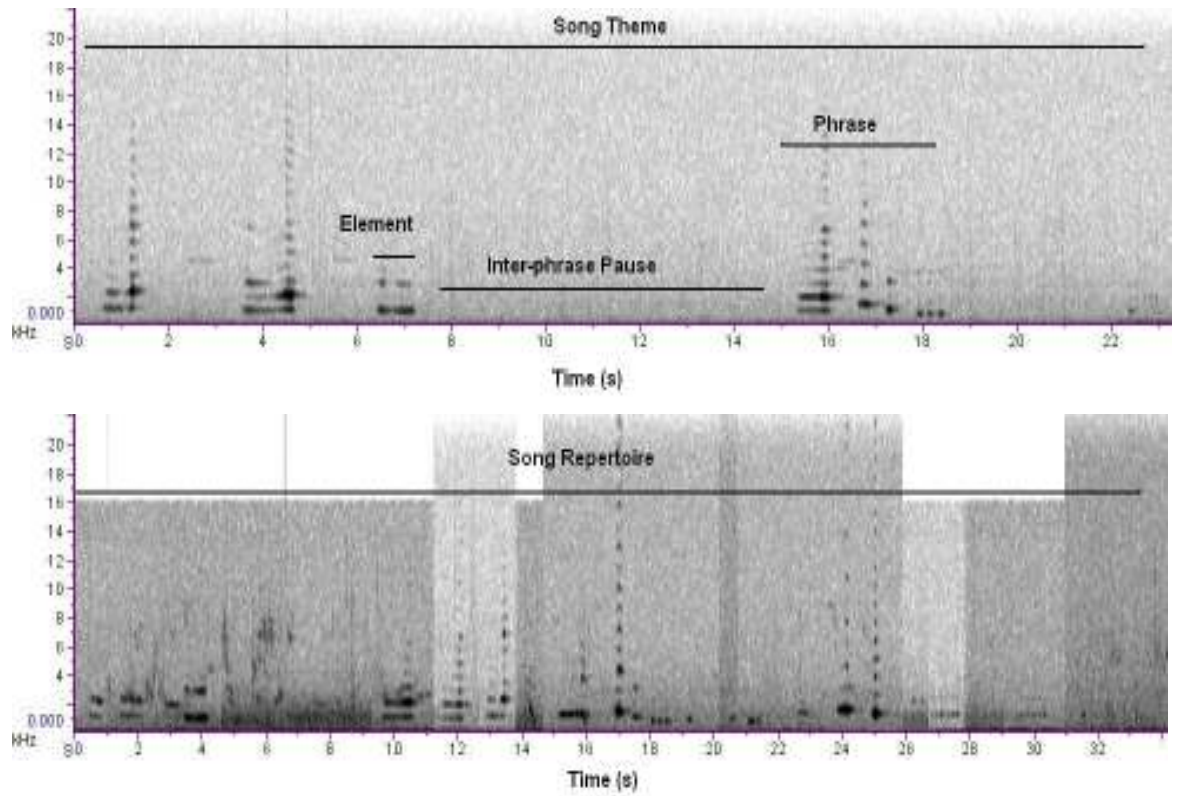


Figure 2.3: Spectrographic representation of an element, a phrase, a song theme, an inter-phrase pause and a song repertoire from Poutama. Frequency (kHz) on y axis.

2.5 References

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Chapter Three: Use of repertoire size to detect variation in kokako song.



Kokako preening on Tiritiri Matangi Island. Photo: Isabel Castro.

3.1 Introduction

In order to be able to compare and contrast the songs of birds, first one must find a way to quantify the songs. Repertoire size is the most commonly used method of quantifying bird song (Garamszegi et al. 2002; Botero et al. 2008). It can be judged in two ways; by looking at the number of song units, or elements, or by looking at the number of unique song types which are made up from those units (Kroodsma 1982). Whichever way one looks at repertoire size, it is often estimated from incomplete samples because of technological and time constraints (Garamszegi et al. 2002). It is also possible to miss rarely sung elements in species that have large repertoires, or misclassify them as ones already quantified (Garamszegi et al. 2002; Molles et al. 2006).

There are three main ways of estimating repertoire size: simple enumeration, curve fitting and the relatively new capture-recapture analysis method (Botero et al. 2008). Botero et al. (2008) describes simple enumeration as being a count of all element types present in a song sample (for definitions please refer to Chapter 2). As this is only feasible for birds with small repertoires, curve-fitting is often used for birds with larger repertoires. Curve-fitting involves creating a graph with the cumulative number of elements recorded on the x axis, and the cumulative number of new element types recorded on the y axis (Garamszegi et al. 2002; Molles et al. 2006). The graph shows when an asymptote is being reached and a researcher can assume that the majority of element types have been recorded (Garamszegi et al. 2002; Molles et al. 2006). The third method, capture-recapture, assumes that all element types have a different chance of being recorded, and that repertoire size is a fixed quantity (Botero et al. 2008). In this method song samples are divided up into '*trapping occasions*', in which groups of consecutive elements are placed. Elements in each *trapping occasion* are tracked, and the likelihood of a new element type being recorded in a new *trapping occasion* is calculated (Botero et al. 2008).

Repertoire sizes vary enormously among song-bird species. For example, the dark-eyed junco (*Junco hyemalis*) has an average song type repertoire size of 4.20 ± 0.17 (Mean \pm SE) out of a possible 70 song types, 15 of which are multi syllabic (Newman et al. 2008). Male bellbirds on Tiritiri Matangi Island have 10 song types and 3 calls, whilst

females may have up to 21 song types (Brunton and Li 2006). A call is defined as a single unit which is short and harsh sounding (Brunton and Li 2006). European starlings (*Sturnus vulgaris*) have a repertoire size ranging from 20 to 70 song types, with an average of 44.80 ± 13.50 (Mean \pm SD) (Eens et al. 1991). The willow warbler (*Phylloscopus trochilus*) has an average repertoire size of 29.69 ± 9.38 element types (Mean \pm SD) (Gil and Slater 2000).

Repertoire size can also vary within a single duetting species, males and females may have different repertoire sizes, and duet repertoires may differ from individuals' repertoire sizes. Single dominant white-crowned sparrow weaver males have an average repertoire size of 67.00 ± 4.00 syllable types (Mean \pm SD) (Voigt et al. 2006). The dominant pairs have an average duet repertoire size of 51.90 ± 2.10 syllables (Voigt et al. 2006). Male rufous-and-white wrens have an average solo song repertoire of 10.8 ± 0.7 song types, whilst females have an average of 8.50 ± 0.70 (Mean \pm SD) (Mennill and Vehrencamp 2005). When the male and female wrens duet they have an average duet repertoire size of 26.40 ± 3.70 song types per pair (Mennill and Vehrencamp 2005).

Kokako in Pongakawa Ecological Reserve have an average of 18.27 ± 0.59 phrases per pair, with a phrase consisting of, on average, three elements (Mean \pm SD) (Molles et al. 2006). Kokako in the Hunua ranges have a repertoire of approximately 9-10 element types (Miner-Williams 2007) and Mapara birds which have been translocated into the small Hunua population have been shown to have 10 unique element types, although these figures probably do not represent full repertoires (Miner-Williams 2007). This is because the Mapara birds had only just been translocated to the Hunua ranges, and had not settled into territories, thus the kokako were difficult to locate and get full recordings from (Miner-Williams 2007).

Looking at repertoires can tell us many things about an individual's social and biological status as well as potentially showing the population's or species' evolutionary history. For example, island species tend to have decreased repertoire sizes compared to their mainland counterparts, probably as a result of a small number of founders (Baker et al. 2003). Subsequent generations of island birds generally have fewer element types to learn as a result of cultural drift. For example bush warbler (*Cettia diphone*) males

who have colonised Haha-jima Island in Japan show reduced song complexity relative to their mainland conspecifics, with both the number and complexity of elements showing reductions (Hamao and Ueda 2000). A study on the singing honeyeater (*Meliphaga virscens*) found that, relative to a mainland population, two separate island populations are both depauperate in phrase types (Baker et al. 2001). There was also a larger amount of sharing between birds in the island populations, which could be explained by the birds on the island having fewer phrase types to choose from (Baker et al. 2001). However, there have been some studies which show an increase in repertoire size in island populations (Baker et al. 2003). An example is that of the Western gerygone (*Gerygone fusca*) in Western Australia (Baker et al. 2003). In this species a number of birds have colonised nearby Rottnest Island, and Baker et al. (2003) found that at least 37% of this new population sings a rhythmic song which is so different from the original one that it could be mistaken as being from a different species. The Western gerygone has only a single song type on the mainland; however 17% of the birds on Rottnest Island are singing both the new rhythmic song type and the original song type, effectively doubling their repertoire size (Baker et al. 2003). Baker et al. (2003) hypothesised that the development of the new song type and new repertoire may be the result of cultural innovation. Translocations also act as colonisation events, so there is potential for a translocation to affect the repertoire size, either increasing or decreasing it, or changing the composition.

Repertoire size can also be affected by social rearing conditions. In an experiment where blue tits and great tits were cross-fostered, the social environment in which the young were reared was shown to affect repertoire size (Johannessen et al. 2006). The average repertoire size of cross fostered males was found to be greater than those birds that were raised by their own species (Johannessen et al. 2006). The cross fostered males sang songs intermediate to both species, but also sang the songs of both their own species and the other species (Johannessen et al. 2006). This shows that young birds which may have templates of their own song can still learn that of another species. Consequently, if juveniles are raised in an area with multiple dialects it may be that they learn both dialects rather than one or the other.

In this chapter I will describe the element type repertoires of the four groups of kokako described in Chapter 2 - source, translocated, Pukaha-born and aviary – to determine

whether translocation has affected repertoire size in this new population. Generally in-depth kokako song studies carried out thus far examine phrase repertoires; however this thesis will look at a finer scale so these works are not directly comparable. I predict that the number of different element types will be greatest for the translocated and Pukaha-born groups, as these have the greatest chance of being able to learn new element types from multiple source dialects to add to their repertoires, even though the population has essentially been bottlenecked. If this is correct conservation managers will be able to determine if the population is changing its' song by comparing repertoire sizes between source and new populations. If there is a difference in repertoire sizes between populations more research could be carried out to determine if the repertoires are becoming more similar or different.

3.2 Methods

For study sites and recording methods please refer to Chapter Two.

For the purpose of this chapter the pair consisting of the Mapara female and unbanded male will be discussed in their own grouping, *mixed pair*, as well as the original grouping they fit into. This makes the groupings as follows:

- Source = M1, M2, M4, M5
- Translocated = A2, R18, Billy Goat (BG), mixed pair female
- Mixed Pair = Mapara female (Mixed pair female) & unbanded male (mixed pair male)
- Pukaha-born = Romeo, mixed pair male
- Aviary = Poutama

3.2.1 Determining Elements

The element libraries which were created were used to determine the number of different element types per pair or individual (Chapter 2). Element types were determined aurally and visually using a real-time spectrogram. Each element type was named with an alphabet letter, and tooks were denoted by a 't' and a number. A took is a soft, short note which is commonly used in periods where song themes are not being sung, and pair members are close together (Molles et al. 2006). All element types were

categorised based on sound and appearance, with frequencies being measured to distinguish similarly-shaped element types. Spectrograms of the complete repertoire for each pair or individual were then created. I determined repertoires for pairs, except in the case of the mixed pair where the repertoire of each individual was calculated separately. This was possible because I could see which bird was singing in all recordings, and the male and female fit into two different groups, translocated and Pukaha-born.

3.2.2 Determining Repertoire Size

In order to determine repertoire size I used the curve-fitting method as I was aware that kokako can have reasonably large element type repertoires (Laura Molles pers. comm.). A saturation curve was created for each pair or individual, this being a plot of the cumulative number of elements recorded versus the cumulative number of element types recorded. Based on the saturation curves for the three most intensively recorded pairs (Figure 3.1) I calculated that a minimum of 300 elements were necessary to obtain accurate data on repertoire size from each pair or individual. However, two pairs and one individual did not meet this criterion because they were difficult to find and record. The first of these was the Billy Goat pair, with only 115 elements. The second was the Mapara 5 pair with 208 elements recorded, and the third was the mixed pair male with 184 elements recorded.

As there were very few pairs available I decided to include these less-recorded birds in the analysis. I extrapolated the results for the birds with 300 or more elements to the birds with less to determine what may have happened to the number of element types had I continued recording to 300 elements. To do this I calculated the mean, standard error and range of the number of elements recorded at these three repertoire sizes for the pairs and individuals for whom I had over 300 elements. These were then used to estimate the repertoire size for the mixed pair male, Billy Goat and Mapara 5 birds. To do this I used the following equation:

$$\text{Number of element types} = \frac{\text{Number of elements recorded}}{\text{had I recorded to 300}} \times 100$$

average % of repertoire recorded
from other pairs at that point

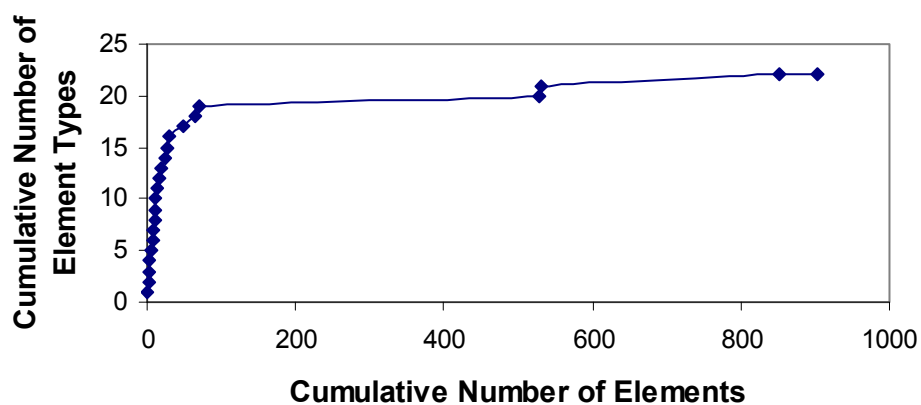
However, when these pairs are used in comparisons I will discuss what was actually recorded rather than the extrapolated repertoire sizes.

3.2.3 Comparison of Repertoires

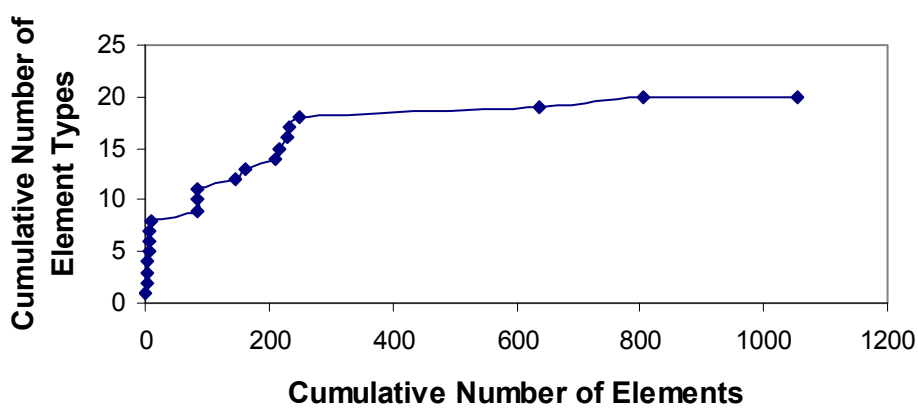
A basic comparison of the repertoire compositions was carried out. This included placing each element type into one of five categories; tooks, clicks, frequency sweeps, pure tonal sounds and elements with multiple harmonics (Figure 3.2). The frequency of use of each of these categories was then calculated and compared between pairs.

A Spearman rank correlation was carried out in R (Development Core Team 2009) to determine if the total number of elements recorded was correlated to the number of element types recorded. A Kruskal-Wallis analysis was done in Minitab (Ryan et al. 2007) to determine if the number of element types differed significantly between the five groups of birds. All averages are presented as mean \pm standard error.

a) A2 Pair



b) R18 Pair



c) Poutama

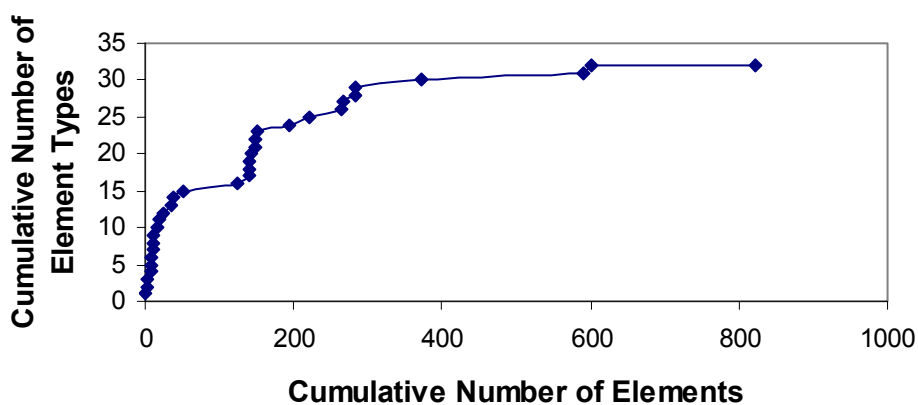


Figure 3.1: Saturation curves for the three most intensively recorded pairs showing the decreasing chance of recording new elements.

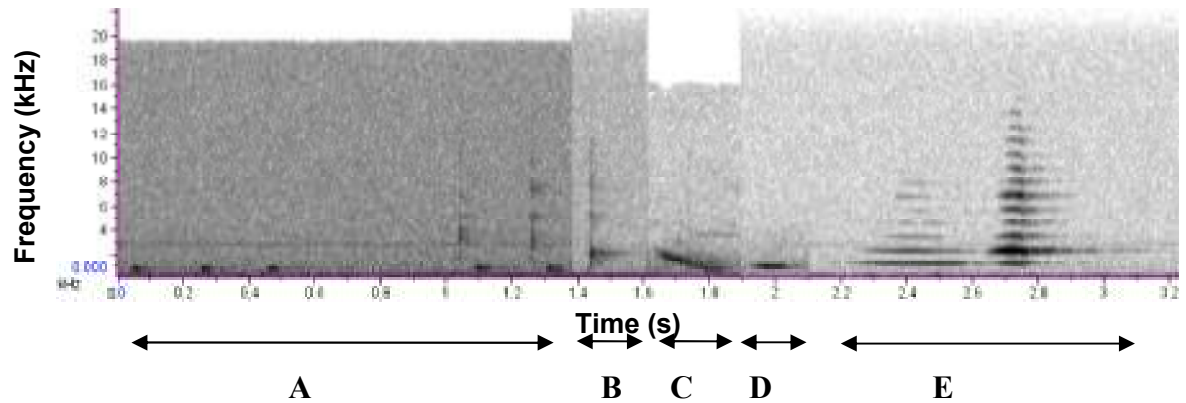


Figure 3.2: Spectrographic representation of the five different element categories A = Took, B = Click, C = Frequency Sweep, D = Pure Tonal Sound, E = Element with Multiple Harmonics.

3.3 Results

There was no relationship between the number of element types and the total number of elements recorded ($\rho = 0.082$, $N = 11$, $P = 0.81$). The range of element types and the total number of elements recorded was similar across groups (Table 3.1).

Table 3.1: The range of element types and the total number of elements recorded across groups.

	Range of Element Types Recorded	Average Number of Element Types Recorded	Range of Number of Elements Recorded	Average Number of Elements Recorded
All (Over 300)	13-32	22.38 ± 2.00	317-1053	629 ± 96.15
Source	19-26	23.25 ± 1.70	208-659	449.75 ± 92.54
Translocated[^]	13-27	20.50 ± 2.90	151-1053	605.75 ± 219.46
Mixed Pair	13-18	15.50 ± 2.50	184-317	250.5 ± 66.50
Pukaha-born*	18-21	19.50 ± 1.50	184-352	268 ± 84.00
Aviary	32	N/A	817	N/A

[^] Translocated includes mixed pair female. * Pukaha-born includes mixed pair male.

The number of different element types recorded was the same across groupings (Kruskal-Wallis test: $H = 5.75$, $DF = 4$, $P = 0.219$). Poutama, the aviary bird, had the largest number of different element types with 32 recorded (Table 3.2). The majority of element types were elements with multiple harmonics, followed by tooks. Frequency

sweeps represented the least number of elements in the repertoires, with only the Billy Goat pair, the mixed pair male and Poutama incorporating them into their repertoire (Table 3.2). For a complete list of element types please refer to Appendix Two.

Together, the mixed pair had 31 different element types. Although the mixed pair is considered separately because the male and female belong to different source groups they are a pair and do duet. So this pair has the second largest number of different element types.

Table 3.2: Number of element types present in kokako song recorded at Pukaha (Mt Bruce) during 2007-09 separated into categories.

Pair/individual	Total number of element types	Number of individual element types				
		Tooks	Clicks	Frequency Sweeps	Pure Tonal Sounds	Multiple Harmonics
Source						
Mapara 1	19	6	1	0	1	11
Mapara 2	26	11	1	0	1	13
Mapara 4	26	11	1	0	0	14
Mapara 5^	22/25.50	7	1	0	1	13
Translocated						
A2	22	6	1	0	1	14
R18	20	9	1	0	1	9
Billy Goat^	27/33.00	10	1	1	0	15
Mixed Pair						
Male^	18/21.00	1	1	1	1	14
Female	13	6	1	0	0	6
Mixed Pair	31	7	2	1	1	20
Pukaha-born						
Romeo	21	6	1	0	1	13
Aviary Bird						
Poutama	32	10	2	2	4	14

^ = denotes pairs/individuals with less than 300 elements recorded, number after / is extrapolation.

3.3.1 Comparison of Repertoires.

The most frequently used elements were the multiple harmonics, representing from 44 – 83% of elements in the repertoires (Figure 3.3). Clicks appeared to be used slightly more than pure tonal sounds in most instances, and the least used elements were frequency sweeps (Figure 3.3). There were very few pure tonal elements present in any repertoire, with the R18 pair having the most pure tonal sounds (Figure 3.3).

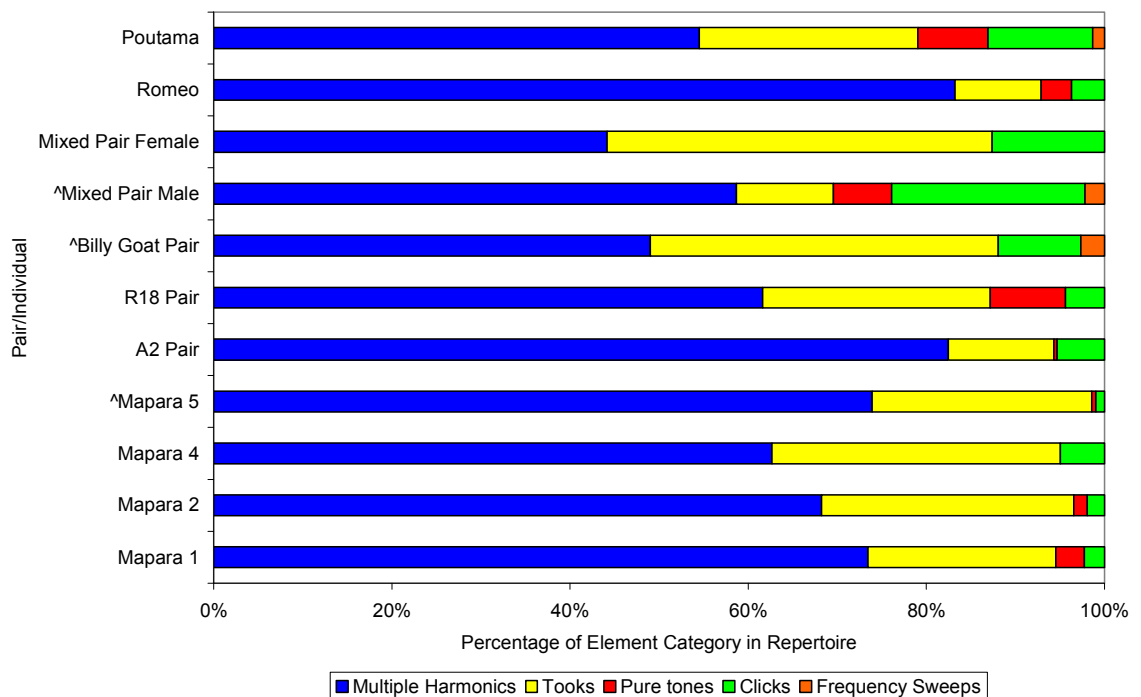


Figure 3.3: Proportion of different element types used in the repertoire by each pair or individual. ^ = denotes pairs/individuals that have fewer than 300 elements recorded.

3.4 Discussion

There was no relationship between the total number of elements recorded and the number of element types found. There was no difference in the number of element types found in each group. The most commonly used element type categories were the elements with multiple harmonics followed by the tooks. The least used element type categories were the pure tonal sounds and the frequency sweeps.

The curve fitting method of determining repertoire size was effective in this study as there were few new element types recorded after the cut-off of 300 elements was reached. Of the pairs or individuals that had over 300 elements recorded: two had no new element types recorded after 300, three only had one new element type recorded, one had two new types, and two had three new types. There was no relationship between the number of elements recorded and the number of element types found. This was unexpected, as all pairs or individuals that had greater than 300 song elements recorded did appear to be reaching an asymptote, so we can anticipate that few, if any, elements were missed. One of the drawbacks of the curve-fitting method is that it assumes that all element types have an equal chance of being sung, whereas this is often not the case (Botero et al. 2008). With kokako song the duet follows a predictable pattern, but elements will be added to or dropped from the song theme from rendition to rendition (Molles et al. 2006). Nevertheless there are element types that are very commonly sung as part of the duet and others that are not heard as often (Pers. obs.). So in the case of kokako we cannot assume that full repertoires have been recorded.

In contrast to the prediction made, the element repertoire sizes of source, translocated and Pukaha-born groups appear to be similar. Interestingly, it is the aviary born bird that has the greatest number of different element types. This may be a result of the multiple pairings this bird has enjoyed, or the fact that he is living in the presence of visitors who whistle and make noise by his aviary. Molles et al. (2006) suggested that kokako song functions to form pair bonds and carry out pair bond maintenance, so perhaps this aviary bird learnt a few element types from each of his partners, leading to an increased repertoire size. The other pair which has a large repertoire size is a somewhat unusual pairing, with a translocated Mapara female paired with a Pukaha-born bird. While this pair sings a large number of different element types it is interesting to note that the male and female do not share any element types. Because there is no sharing between these birds, I predict that in instances where mixed pairs have formed, there will be less sharing within the mixed pair than between pairs. The lack of sharing enables them to sing two different songs, and so defend their mate and territory against two dialects, perhaps making them a stronger pairing. However, the lack of sharing may make it more difficult to properly co-ordinate a duet. The pair members in this instance takes turns to sing; rather than alternating elements each will sing a block of several elements. This may indicate the mixed pair is unable to form a coherent duet with their two

repertoires. However, there are species which have sex-specific elements as well as shared elements, and the sex-specific elements are still able to be formed into a duet (Mennill and Vehrencamp 2005). Indeed there are phrase types sung by kokako that are more likely to be performed by either male or female kokako in the duet (Molles et al. 2006).

In this study I did not differentiate which elements were sung by individuals in a pair except for the pair consisting of a Mapara born female and an unbanded Pukaha-born bird of unknown sex. The reason for this is that I was only able to see which bird was singing during my recordings for this mixed pair and thus I could separate which elements were sung by which bird. The Mapara female had a very low number of element types, only 13, despite having over 300 elements recorded. Although at least some female kokako are able to sing full songs by themselves (Molles and Waas 2006) they do not often do so (Laura Molles, pers. comm.), so it is unlikely that I recorded a full repertoire in this case. Compared to the other translocated birds this is an exceptionally low number of different element types, even compared to the Billy Goat pair who only had 151 elements recorded. The unbanded male is also particularly interesting. He had only 184 elements recorded, yet he had 18 different element types, only three less than the other Pukaha-born bird, Romeo, who had over twice as many elements recorded. However, my extrapolation showed that had I continued recording to 300 elements, he would still only have the same number of elements as Romeo. It may be that male and female kokako contribute different element types to their shared repertoires. Had I looked at males and females separately for all pairs I may have found that there are some element types only sung by males or females, and some that are shared by both, indicating that kokako have two different repertoires. As mentioned earlier, male and female rufous-and-white wrens have solo repertoires which they combine to make a larger duet repertoire (Mennill and Vehrencamp 2005). This may be the same with kokako.

Aside from the mixed pair male, there were two pairs that did not have greater than 300 elements recorded; Mapara 5 and the Billy Goat pair. Estimation of their true repertoire size showed that Mapara 5 could have had another four or five element types unrecorded, with another six for the Billy Goat pair. For the Mapara 5 pair the estimate puts them on a par with two of the other source pairs, each of which had 26 element

types. However, with the Billy Goat pair this estimated total would give them the largest repertoire out of all the sampled birds, with 33 element types. Even with only 151 elements recorded the Billy Goat pair has more element types recorded than the other translocated pairs. Their large pair repertoire may be due to the location of their territory. The Billy Goat pair is on top of a ridge which is part of the highest point of the reserve and is occupied by all the known Mangatutu-born birds (Please refer to Chapter One for a history of translocations at Mount Bruce). In comparison the other two translocated pairs are located down the bottom of the reserve, near the visitor centre, with no neighbouring Mangatutu territories. It is highly unlikely that summit birds can hear the birds lower down in the reserve because of the distance and weather conditions at Pukaha. The Billy Goat pair's relatively large repertoire size may be due to the fact that they are learning new elements from the Mangatutu dialect which surrounds them (Chapter 4).

The Billy Goat pair gives us an indication of how repertoire change may happen in translocated birds. Perhaps kokako do not lose elements when translocated between populations, but may depend on frequent interaction with new neighbours to be able to alter their repertoires. In this case, the density of the new population, rather than the translocation itself, will have a greater influence on repertoire size. Within the wren genus *Cistothorus* there is a positive correlation between repertoire size and density (Kroodsmma et al. 2001). The increase in repertoire size may be useful for territory defence, where birds share components of their repertoire with each other, so that in areas with a high density of neighbours individuals need to have a larger repertoire or higher sharing levels in order to successfully defend their territories (Hughes et al. 2007). If this was the case with kokako we would expect a high degree of sharing between Romeo, Poutama, A2 pair and R18 pair (all located lower down in the reserve), and between the mixed pair and the Billy Goat pair near the summit (I will look at sharing levels in Chapter 4).

Colonisations or translocations act as bottleneck events, where a small subset of a population inhabits a new area, and this can modify song in one of two ways. First, it can lead to a decrease in repertoire size, complexity or song structure. This may be because of changes in habitat structure, or it may just be because the colonisers have a smaller subset of elements from the source population. For example chaffinches

(*Fringilla coelebs*) show a decrease in phrase and song type diversity after colonising the Chatham Islands (Baker et al. 2006). Male bush warblers show an increase in song types, but a decrease in complexity after colonising a nearby island (Hamao and Ueda 2000). The kokako translocated to Pukaha effectively went through a bottleneck, which could decrease their repertoire size relative to the source population. Alternatively, it could lead to an increase in repertoire size, complexity or song structure. One explanation for this change could be the environment. Western gerygone showed an increase in repertoire size following island colonisation (Baker et al. 2003). The rufous-collared sparrow (*Zonotrichia capensis*) showed a difference in temporal structure, with shorter trill intervals in closed habitat than open habitat (Lijtmaer and Tubaro 2007). The song theme also showed lower minimum and maximum frequencies in closed habitat (Lijtmaer and Tubaro 2007). The research suggested that these changes occurred after the habitat was converted from closed to open habitat, and so the changes may be explained by habitat (Lijtmaer and Tubaro 2007). It is possible that these changes can be seen at Mapara, depending on where the kokako sing. There are many wide open tracks throughout Mapara North, and if the birds sing on the edges of these tracks it may change their frequency. A second explanation for song changes following translocation could be the mixing of source dialects. The kokako translocated to Pukaha were brought into an area where two dialects were artificially mixed, which could increase their repertoire sizes. Neither effect seems to have occurred, with the actual number of different element types recorded being similar to repertoire sizes in the source population. Instead of changes in repertoire size the changes may be in the syntax of any shared elements between the source, translocated and Pukaha-born birds (Chapter 5).

In conclusion, repertoire size does not differ between groups. The largest repertoire was that of Poutama, the aviary bird, who has 32 element types. I believe this is a result of the multiple pairings he has enjoyed. Being in an aviary he has had frequent contact with other kokako, and may have learnt new element types from each partner. This seemingly large repertoire size could be used as an indicator to conservation managers that variation in song is occurring, and that this mechanism for change may be active in wild kokako populations. Kokako may depend on frequent interactions with their neighbours in order to alter their repertoire; the density of the new population rather than the translocation itself may affect the repertoire. If this is the case we expect to see

a high level of sharing between Pukaha kokako whose territories are on the front face, and a high level of sharing between the pairs whose territories are around the summit. If there is a change in repertoires it may be at a different scale, we may see changes in the syntax of phrases. These ideas will be discussed in Chapters Four and Five respectively.

3.5 References

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Chapter Four: Decreased repertoire sharing and evidence of new element types in translocated kokako.



Kokako and nest at Pukaha. Photo: Tony Silbery.

4.1 Introduction

The benefits of having a large song repertoire, such as the potential for more matings and successful territorial defence (Hughes et al. 2007; Nicholson et al. 2007), will only be realised if listeners can detect the different element types composing the song (Kroodsma 1982). To send an effective message, individuals should have greater within-repertoire variation than the variation that occurs between repertoires in a population (Kroodsma 1982). If individuals use shared elements in competition for territories, resources and mates and mate attraction (Read and Weary 1992) it may be necessary to have sufficient element types shared to compete successfully. However there are some instances where the more element types an individual has the fitter they are thought to be (Kroodsma 1982). So a balance is needed between sharing and individuality in song repertoires.

The sharing of element types may be particularly important for duetting species. If a species uses its duet for territory defence, we would expect pairs to share element types with their neighbours, although they may not necessarily share their song or duet types (Marshall-Ball and Slater 2008). For instance male and female plain wrens (*Thryothorus modestus zeledoni*) match phrase types to playback when defending their territory, but not duet types (Marshall-Ball and Slater 2004). If a species uses its duet for pair-bond formation and maintenance it may be important for pair members to share element types and be able to successfully combine them. Male and female rufous-and-white wrens are able to successfully share and combine their repertoires (Mennill and Vehrencamp 2005). Duets are initiated by either partner, and these duets are pair-specific (Mennill and Vehrencamp 2005). The wrens also share multiple song-types with their neighbours, and the amount of sharing lessens with greater distance between the pairs, indicating the duet may also be used for territorial defence (Mennill and Vehrencamp 2005).

Differences in repertoire composition within and between populations can often be explained by geographic variation. Microgeographic variation refers to differences between neighbouring populations, where interbreeding is possible, whereas macrogeographic variation refers to differences between populations where a barrier,

such as distance, discourages interbreeding (Mundinger 1982). The chowchilla (*Orthonyx spaldingii*) exhibits a form of microgeographic variation, where groups sing predominantly matching song, and levels of dialectic similarity fall away at 1km distances (Koetz et al. 2007). There are no barriers separating the populations, all can interbreed, yet there are pronounced differences in song. Blue tits show macrogeographic variation by the presence or absence of a trill: on the European mainland all recorded blue tits have a trill, whereas in North Africa and the Canary Islands trills have never been reported (Doutrelant and Lambrechts 2001).

In species where individuals learn their vocalisations, geographic variation in song may arise rapidly following colonisation of new areas. There are five proposed mechanisms for this variation (Newman et al. 2008). The first of these suggests that song evolves in response to different habitat types (Baker 2006). For example house finches (*Carpodacus mexicanus*) show a change in song structure between urban and desert sites (Badyaev et al. 2008). The sites examined were adjacent to each other, and house finches are highly mobile, yet they still exhibit a change between sites (Badyaev et al. 2008). The two different habitat types provide two different food types, small or large seeds, which lead to a change in bill morphology (Badyaev et al. 2008). These changes in bill morphology led to a change in song (Badyaev et al. 2008). The second proposed mechanism suggests that the song evolves because of a loss of phrase or element types at the time of colonisation as the colonisers only have a subset of the phrase or element types present in the source population (Baker and Jenkins 1987). For example, the chaffinch lost its elaborate end phrase after colonising the Chatham Islands from New Zealand (Baker and Jenkins 1987). The third hypothesis proposes that it is through new cultural mutations that novel song evolves (Baker et al. 2003). This phenomenon is demonstrated by the Western Gerygone: 37% of the Rottneest Island population has added a unique rhythmic song to their repertoire which is not heard on the mainland (Baker et al. 2003). This new song may be a cultural innovation arising on the island. The fourth hypothesis suggests that new song may be a result of colonising adults and juveniles becoming separated, and thus the juveniles fail to learn the song from the adults (Thielcke 1973). Juvenile short-toed treecreepers (*Certhia brachydactyla*) colonised Africa from Europe, and did so before they had learnt the song from the adult birds (Thielcke 1973). The African birds now exhibit their own characteristic song, completely different than that of the European birds (Thielcke 1973). The last

hypothesis proposes that song changes in response to some aspect of sexual selection such as: the agent (for example female choice), target (for example song or plumage), or the intensity of sexual selection (Badyaev et al. 2002). In the case of the finches, Aves subfamily *Carduelinae*, there is a strong negative correlation between song complexity and elaborate plumage (Badyaev et al. 2002). This may be because both are very costly to produce, so there may be a trade-off between song and plumage complexity.

Kokako are known to exhibit both macrogeographic and microgeographic variation in song (Rowe and Bell 2007). Each kokako population has its own dialect and there is no dispersal between kokako populations without human intervention, as kokako are poor flyers and populations are separated by large tracts of unsuitable habitat (Sibson 1982; Rowe and Bell 2007). There can also be multiple dialects within one population, for example the Mapara population has three dialects, North, Central and South (Rowe and Bell 2007). Kokako are a duetting species, and it is hypothesised that their duet functions for territorial defence and pair-bond formation and maintenance, so one would expect element type sharing among neighbours (Molles et al. 2006). Kokako are also able to match or anticipate phrase types in response to song (Molles and Waas 2006).

In this chapter I will compare and contrast the element type repertoires of the four groups of kokako described in Chapter 2: source, translocated, aviary and Pukaha-born. The translocation of kokako to Pukaha was essentially a colonisation event, and if the song of the translocated birds has altered, I expect to find evidence of both macrogeographic variation and microgeographic variation and high levels of sharing among neighbours.

- Macrogeographic variation between the source birds and the three groups of birds now at Pukaha (translocated, Pukaha-born and aviary). I expect the source group to have higher within-group sharing levels than the other three groups. I also expect them to have lower numbers of unique element types than the other three groups because they are not exposed to multiple dialects, nor have they been through a bottleneck/colonisation event (for the purpose of this study). Unique element types are those which are not shared with any other pair, in any group.
- Microgeographic variation between translocated birds and Pukaha-born/aviary bird: I predict that the sharing between the translocated birds and

source birds is greater than the sharing between the Pukaha-born/aviary birds and source birds. I also expect the Pukaha-born and aviary birds will have a greater number of unique element types than the translocated birds because they were born in the presence of multiple dialects and so have a greater chance of being able to learn more element types.

- Microgeographic variation between two territorial groupings (front face and summit) of birds at Pukaha, with sharing within the two territorial groupings being greater than sharing between the two groupings. I also expect the summit birds to have more unique element types than front face birds because of their proximity to the second dialect.
- Macrogeographic variation between the two territorial groupings with the source birds sharing less with the summit birds than they do with the front face birds.

By looking at the geographic variation in song I am providing a tool with which managers can use to determine the status of their kokako population. Looking at different levels of element type sharing will show how close the songs are becoming, which may indicate a higher potential for interbreeding. If the levels of element type sharing are low managers will know that those kokako are not as likely to interbreed.

4.2 Methods

For the purpose of this chapter the members of the mixed pair will be discussed as individuals, with the female (MPF) being grouped with the translocated birds and the male (MPM) grouped with the Pukaha-born birds.

For recording methods and study areas please refer to Chapter 2. For methods on how element types and repertoires were described please refer to Chapter 3.

4.2.1 Element Type Renaming

Previously, each pair or individual had different names for what may be the same element type, so renaming was necessary for ease of comparison. As mentioned in Chapter 3, spectrograms of the complete repertoire for each pair or individual were

created using Raven Lite 1.0 software (2008a). Using real-time spectrograms and the element type descriptions I renamed all the elements, ensuring that those elements which I decided were the same had the same name.

4.2.2 Comparison of Similar Element Types Using PCA

Some elements were difficult to classify, so Principal Component Analyses (PCA) were carried out to determine whether to lump or split a subset of elements. The majority of elements could be easily classified by visual and aural comparisons, the PCA analysis allowed me to make decisions about a few difficult to classify elements and potentially uncover examples of element types that may be beginning to change due to drift. To do this first I chose six element types for comparison using PCA. To get a baseline comparison of what a plot of several individuals' versions of a matching element type looks like I chose element A, an element type I was sure was the same between all the pairs. Likewise I chose an element type that was unique to each individual or pair, and thus produced a plot for elements that were definitely different (from here this is termed "different" element). I then chose the four element types, elements D, F, P and Y, that I thought could be the same, although I had heard slight differences between each individual or pair's rendition when renaming them. These four element types were not necessarily shared by all four groups, but each was shared by at least two groups.

Once I had chosen the six element types for analysis I aimed to take a maximum of ten instances of each element type from each pair that used it. However, I did not have ten recordings of each element type for all pairs, so used as many examples as were available (Table 4.1). I tried to take the elements from multiple recording bouts for each pair, so that I could determine whether elements differed between recording sessions. Each instance of each element type was saved to its own separate file so they could be standardised. Standardisation was carried out in Audacity (Mazzoni and Dannenberg 2000). First the elements were filtered, with a high pass filter of 300Hz and a low pass filter of 12,000Hz. This means that any sounds with frequencies of less than 300Hz or greater than 12,000Hz were taken out of the element, to reduce background noise. Then the elements were normalised, which removed any DC offset and shifted the maximum amplitude to -3dB. This ensured that all the elements were at the same volume for the measurements to be taken.

Once the standardisation had been carried out four different measurements were taken from each element. The first was a measurement of the length of the element. This was measured using Raven Pro 1.3 (2008b) to calculate the delta time, as Raven Lite does not have this function. The other three measurements, the fundamental frequency, the change in frequency and the entropy were carried out in Raven Lite (2008a). The fundamental frequency was calculated by measuring the frequency in the middle of the trace of the fundamental. The change in frequency was measured by taking the frequency at the bottom of the fundamental at each end and subtracting to get the change in frequency from the start to the end of the element. The entropy was measured by counting how many harmonics had a power of at least 50% of the power of the fundamental. This provided an index of harmonic richness for the element.

Table 4.1: Instances of elements in PCA from each pair

	A	Different	D	F	P	Y	Total Number of Songs Recorded
M1	10	0	10	10	0	0	8
M2	10	4	7	10	0	0	4
M4	10	6	0	10	0	0	3
M5	1	10	1	2	0	0	3
A2	10	3	10	10	10	0	10
R18	10	10	10	0	10	0	11
Billy Goat	10	10	0	2	0	2	1
Mixed Pair Female	10	0	0	10	10	0	9
Mixed Pair Male	0	6	0	0	0	8	9
Romeo	10	10	0	2	10	10	7
Poutama	10	10	0	0	10	0	8

These measurements were subjected to a PCA using Minitab15 (Ryan et al. 2007). A number of scatterplots were created using the scores from the top two principal components (PC's), and statistical tests were carried out to determine whether there was a significant difference between groups. Kruskal-Wallis tests were used for non-parametric data, and one-way ANOVA tests were used for data which followed a normal distribution. If these results were significant post-hoc tests were carried out: Mann-Witney tests for non-parametric data and 2-sample t-tests for data following a normal distribution. Where multiple comparisons were made I adjusted the critical p-

value to 0.025 to reflect the decreased strength of the test. For post-hoc comparisons the D, F and Y elements were separated into groups, Mapara (M1, M2, M4, M5) versus non-Mapara (A2, R18, BG, MPF, MPM, Romeo, Poutama). Element P was separated into translocated (A2, MPF, R18) versus non-translocated (Poutama, Romeo) as this element was not shared by the source (Mapara) pairs. First I plotted all the elements together, to determine if they separated out visually. Post-hoc Mann-Whitney tests were carried out to determine whether the elements differed statistically. I then plotted individual scatterplots for each of the elements.

4.2.3 Comparison Within and Between Groups

Once I had determined which elements were the same and which were different the proportions of shared element types between pairs were calculated. This was done using the following formula

$$\frac{2 * (\text{shared})}{(\text{Repertoire 1}) + (\text{Repertoire 2})} \quad \begin{array}{l} \text{(Where } \textit{Repertoire} \text{ is the repertoire size} \\ \text{from each pair and } \textit{shared} \text{ is the number of} \\ \text{shared element types)} \end{array}$$

For some analyses the birds at Pukaha were also grouped into one of two territory clusters; birds down on the front face, and birds up by the summit. The front face group consisted of the A2 pair, the R18 pair, Romeo and Poutama. The summit group consisted of the mixed pair male, the mixed pair female and the Billy Goat pair.

Mann-Whitney tests in Minitab (Ryan et al. 2007) were used to compare:

- the sharing levels within and between Mapara source and translocated/Pukaha-born/aviary birds
- the sharing levels between Mapara source birds and translocated birds to sharing levels between Mapara source birds and Pukaha-born/aviary birds
- levels of sharing within and between the two territory groups, and to compare the proportion of element types each group shared with the Mapara source birds
- number of unique element types between original groups and between territory groups

4.2.4 Frequency of Use of Shared Element Types

Once I had concluded which element types were shared I compared how frequently shared element types were used by each group. As there were many different element types that were shared I only chose five element types for comparison (A, B1, F, T1, and TC1). These five element types were shared between the majority of the pairs or individuals, and represented the three most-used element type categories, elements with multiple harmonics, toots and clicks (Chapter 3). I carried out Kruskal-Wallis tests to determine if there were significant differences in the frequency of use of any of these element types.

4.3 Results

In total, 96 different elements types were recorded. 47 of these were elements with multiple harmonics, 7 were pure tone elements, 3 were frequency sweeps, 3 were clicks and 36 were toots (Appendix Two; Figure 3.2).

4.3.1 Principal Component Analysis

In this study the chosen element types visually separated out in the PCA, although there were areas where the element types overlapped (Figure 4.1). In particular, element Y was scattered in the middle of the graph (Figure 4.1). A possible explanation for the overlap is the large amount of individual variation in the element type, which is discussed below. There were significant differences between some of the element types (Kruskal-Wallis test: PC1 $H = 180.90$, $DF = 5$, $P = <0.01$; PC2 $H = 205.57$, $DF = 5$, $P = <0.01$). Element A differed in the change in frequency (Table 4.2), which did not weight on PC1 or PC2, but weighed very heavily on PC3, and so could not be seen in the statistical analyses or on the scatterplot, explaining why it was found to be similar to other elements (post-hoc Mann-Whitney test: A vs. F PC1 $W = 7032.0$, $N = 89, 56$, $P = 0.03$; A vs. P PC1 $W = 5981.0$, $N = 89, 50$, $P = 0.2754$; A vs. Diff PC2 $W = 6974.0$, $N = 89, 69$, $P = 0.7233$).

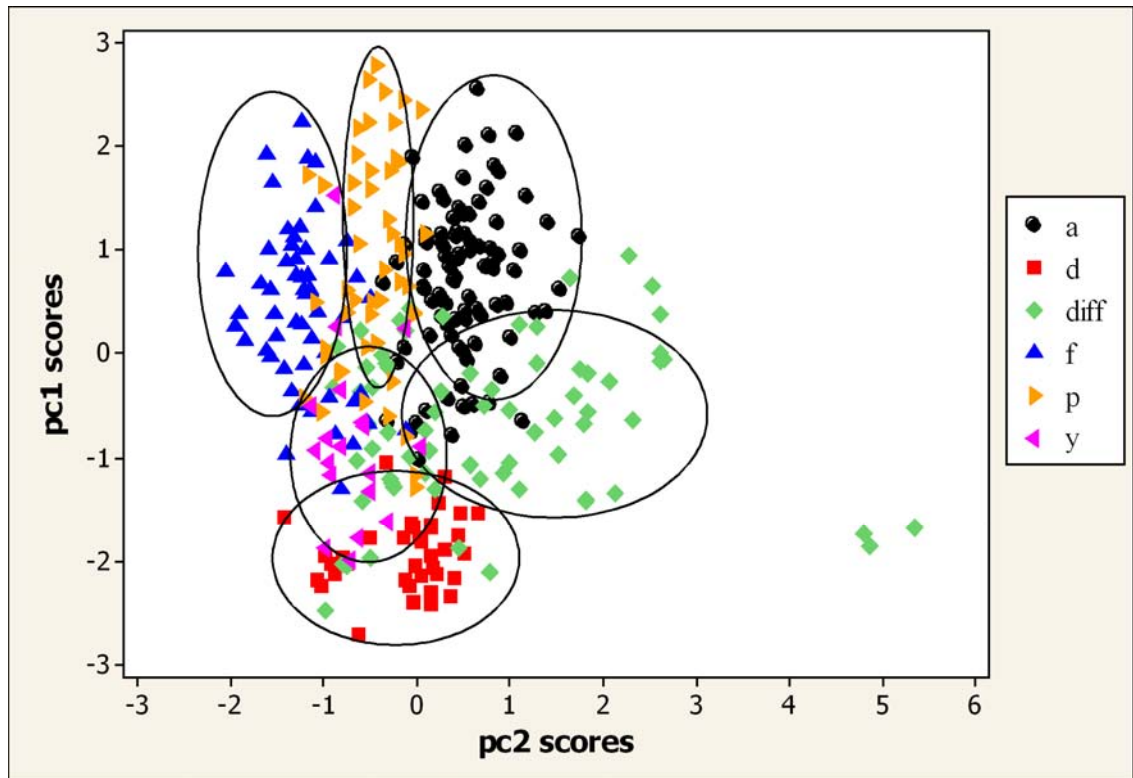


Figure 4.1: Scatterplot of PCA scores (Table 4.2) for all elements. Circles drawn by hand to indicate grouping of elements.

The PCA for element A showed considerable overlap between pairs and individuals, as one would expect for an element type which is the “same” between pairs (Figure 4.2 a). However, there was a significant difference between at least two of the pairs (Kruskal-Wallis test: PC1 $H = 48.97$, $DF = 7$, $P = <0.01$; PC2 $H = 47.43$, $DF = 7$, $P = <0.01$). The difference was between the Mapara and non-Mapara birds (Post-hoc Mann-Whitney test: PC1 $W = 1843.0$, $N = 31, 59$, $P = <0.01$; PC2 $W = 1934.0$, $N = 31, 59$, $P <0.01$), and could be because element A may be starting to drift in the new population. Element A separated out well in the PCA of all the element types (Figure 4.1) so I do not believe it should be split into multiple different element types at this point; however, in the future it may become a distinctly different element.

The “different” element separated out visually in the scatterplot (Figure 4.2 b). There was significant variation between pairs for the “different” element (Kruskal-Wallis test: PC1 $H = 52.99$, $DF = 8$, $P = <0.01$; PC2 $H = 52.68$, $DF = 8$, $P = <0.01$). There appears to be some overlap in the “different” element for R18 and Romeo (Figure 4.2 b). However while they may have similar measurements they are very obviously audibly different: the Romeo “different” element is sung three times in quick succession,

whereas the R18 element is sung once only. There was no difference between the “different” element for Mapara and non-Mapara singers (post-hoc Mann-Whitney test: PC1 $W = 832.0$, $N = 20, 49$, $P = 0.0820$; PC2 $W = 847.0$, $N = 20, 49$, $P = 0.0527$), so the differences are likely related to individual variation rather than group variation.

These baseline comparisons of how a “same” and “different” element type act in PCA and statistical analyses can now help to determine the status of the four “similar” element types (D, F, P, Y). A “similar” element type which splits into “different” element types will separate visually and statistically in a PCA. A “similar” element which is found to be the “same” element type may separate visually or statistically, but not both. Ideally a “same” element type does not do either.

Table 4.2: PCA eigenvalues, cumulative values and co-efficients for PC1 and PC2.

Variables PC1	A	Different	D[^]	F	P	Y	All
Eigenvalue	1.3150	1.2680	1.7683	1.3846	1.5905	1.6628	1.5393
Cumulative % Variance	0.329	0.317	0.589	0.346	0.398	0.416	0.385
Element Length	-0.560	-0.607	0.705	0.720	0.590	0.573	0.606
Fundamental Frequency	0.741	0.661	-0.679	0.162	0.154	-0.240	0.099
Entropy	0.007	0.082	N/A*	0.622	0.532	0.706	0.655
Change in Frequency	0.370	0.434	0.206	0.261	0.587	0.340	0.440
<u>Variables PC2</u>							
Eigenvalue	1.0795	1.1471	0.9911	1.0738	0.9860	1.1017	1.1696
Cumulative % Variance	0.599	0.604	0.920	0.615	0.644	0.691	0.677
Element Length	0.607	0.368	0.019	0.078	0.066	-0.540	-0.413
Fundamental Frequency	0.099	0.408	-0.273	0.784	-0.988	-0.562	0.800
Entropy	-0.309	-0.834	N/A*	-0.037	0.094	-0.053	-0.030
Change in Frequency	0.726	0.051	-0.962	-0.614	0.107	0.624	0.434

[^] denotes missing values, * the co-efficient for entropy is missing for this element as it is a pure tone element, with no harmonics.

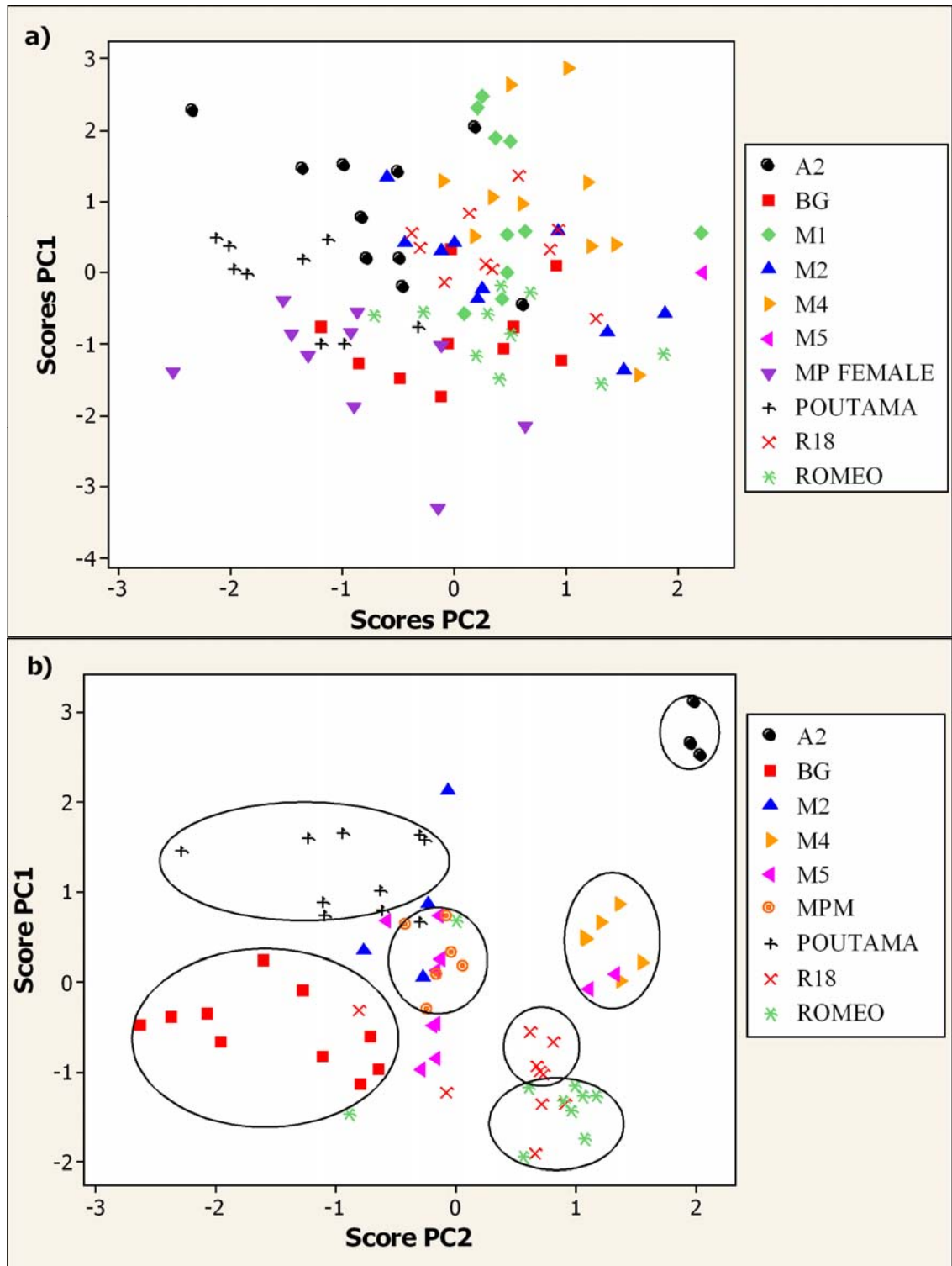


Figure 4.2: Scatterplots of PCA scores (Table 4.2) for 'same' and 'different' elements. a) Shows element A. b) shows the different element, with the circles drawn to indicate groupings of the different elements.

Element D visually separated into three different element types (Figure 4.3 a). There was a difference (Kruskal-Wallis test: PC1 $H = 32.14$, $DF = 4$, $P = <0.01$; PC2 = 13.16,

DF = 4, $P = 0.011$) between Mapara and non-Mapara in PC1 (post-hoc Mann-Whitney tests: PC1 $W = 174.0$, $N = 18, 20$, $P = <0.01$; PC2 $W = 354.0$, $N = 18, 20$, $P = 0.9417$). This means that element D is at least two different element types, which are changing between the source Mapara population and the translocated birds. Looking at the attributes weighting on the PC scores (Table 4.2) the translocated birds have a longer element with a lower fundamental frequency than the source birds. The A2 pair and R18 pair have clear groupings, suggesting that these pairs have their own individual version of this element type.

Element F shows no clear visual groupings (Figure 4.3 b). However there was a significant difference between pairs (1-way ANOVA test: PC1 $F = 2.92$, $DF = 7$, $P = 0.013$; PC2 $F = 5.09$, $DF = 7$, $P = <0.01$) indicating that there are differences between elements which could not be seen on the scatterplot (Figure 4.3 b). These differences are not between Mapara and non-Mapara (post-hoc 2-sample t-tests: PC1 $t = -0.64$, $DF = 46$, $P = 0.527$; PC2 $t = -0.54$, $DF = 46$, $P = 0.592$), instead differences may be due to individual variation. Looking at the attributes weighting on the PC scores (Table 4.2) the Billy Goat and M4 elements are similar, with both having a lower fundamental frequency and a greater change in frequency than the other pairs. It also appears that A2 and M1 have longer elements that have greater entropy (Table 4.2). There is a large amount of variation in the scatterplot (Figure 4.3 b) and it is possible that the element type is typically very variable. There may be differences between males and females singing the element type, or it may be that the low sample size of the Billy Goat pair (Table 4.1) is affecting the test. So element F does not separate visually but does statistically, and thus it is likely that element F is a single element type which is typically variable.

Element P shows two visual separations, with the mixed pair female's elements clustering on the right hand side of the graph, and the A2 pair and Poutama clustering around the top of the graph (Figure 4.3 c). There was a significant difference between at least two of the pairs/individuals (Kruskal-Wallis tests: PC1 $H = 15.03$, $DF = 4$, $P = <0.01$; PC2 $H = 23.70$, $DF = 4$, $P = <0.01$), however the difference is not between translocated and non-translocated birds, as there are no Mapara source birds which have this element type (post-hoc Mann-Whitney tests: PC1 $W = 658.0$, $N = 30, 20$, $P = 0.0349$; PC2 $W = 719.0$, $N = 30, 20$, $P = 0.3676$). Looking at the attributes weighting on

the PC scores the element length and change in frequency contributed to PC1, while fundamental frequency contributed to PC2 (Table 4.2). I believe that the significant difference is due to the mixed pair female having a lower fundamental frequency than the other birds. So this element separates visually and there is statistically significant variation, showing that the element P is at least two different element types.

Element Y separates visually into three groups, one for each pair or individual that uses the element; the Billy Goat pair, the mixed pair male and Romeo (Figure 4.3 d). However, there is no significant difference between elements (Kruskal-Wallis tests: PC1 $H = 4.38$, $DF = 2$, $P = 0.112$; PC2 $H = 4.83$, $DF = 2$, $P = 0.090$). This element type may be sung very variably, or the small sample size may be affecting the results and had I recorded more instances of this element from the Billy Goat pair and the mixed pair male they may have clustered more tightly with Romeo. Whatever the reason, this element is a single type.

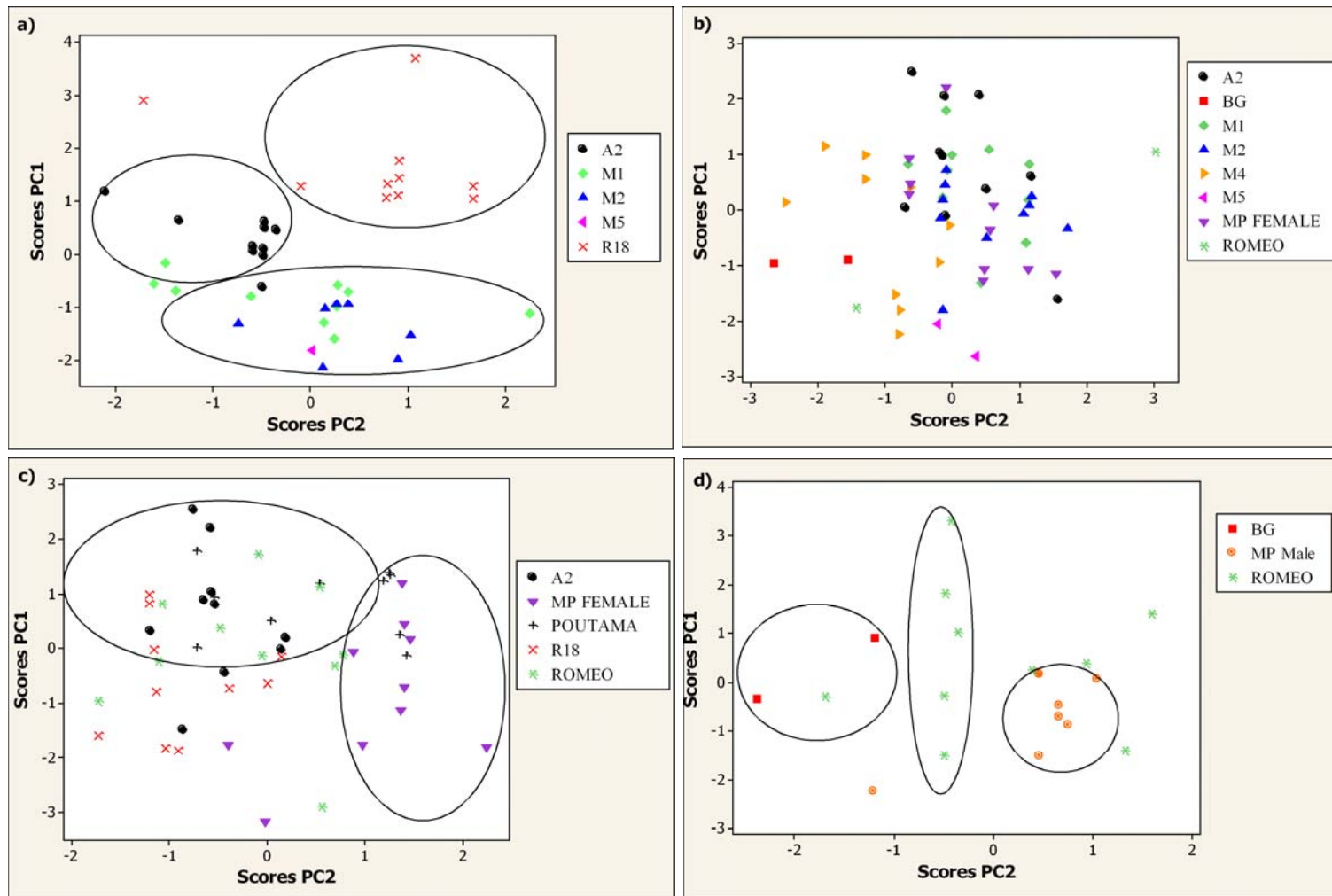


Figure 4.3: Scatterplots of PCA scores (Table 4.2) for similar elements. Circles drawn by hand to indicate groupings of potentially different elements when appropriate. a) Element D. b) Element F. c) Element P. d) Element Y.

4.3.2 Comparison of Element Types within and between Groups

I found macrogeographic variation with the source pairs having higher levels of within-group sharing than the translocated and Pukaha-born groups (Mann-Whitney test: $W = 630$, $N = 6, 7$, $p = 0.0034$). The source pairs share over 80% of their repertoires with each other whilst the translocated and Pukaha-born groups only share 30% and 5% respectively (Figure 4.4a; Table 4.3). When the birds present at Pukaha are split into their territory groupings we can see that the front face birds do not have a higher level of within-group sharing than the summit birds (Mann-Whitney test: $W = 37.0$, $N = 6, 3$, $p = 0.0933$; Figure 4.4 b). The level of sharing within the original groupings is higher than the level of sharing between groupings (Mann-Whitney test: $W = 470.0$, $N = 13, 42$, $p = 0.0366$). The level of sharing within the source group is higher than the sharing between the source and translocated groups (Mann-Whitney test: $W = 117.0$, $N = 6, 16$, $p = <0.001$) however the level of sharing within the translocated group is the same as the level of sharing between the source and translocated groups (Mann-Whitney test: $W = 54.0$, $N = 6, 16$, $p = 0.2851$). The reason for this is that there is a low amount of sharing within the translocated group and this matches with the low amount of sharing between source and translocated groups (Table 4.3). The within-group sharing levels for the summit and front face groups are no different to the between-group sharing levels (Mann-Whitney test: $W = 114.0$, $N = 9, 12$, $p = 0.3028$).

Table 4.3: Proportion of repertoire shared within and between groups. Values on the diagonal represent within-group sharing.

	Source	Translocated	Pukaha-born	Aviary
Source	0.844	0.43	0.28	0.28
Translocated		0.315	0.26	0.25
Pukaha-born			0.051	0.16
Aviary				1

The source pairs do not share more of their repertoire with the translocated birds than they do with the Pukaha-born/aviary birds (Mann-Whitney test: $W = 267.5$, $N = 16, 12$, $p =$

0.1042). The Pukaha-born birds share approximately the same amount of their repertoire with the source birds as they do with the translocated (Mann-Whitney test: $W = 71.0$, $N = 8$, $p = 0.7929$; Table 4.3). The aviary bird shares only 16% of his repertoire with the Pukaha-born birds. The amount shared between the different territory groups is 26%, which is approximately the amount of sharing shown between the other groups. The source group shares more of its repertoire with the front face birds than it does with the summit birds (Mann-Whitney test: $W = 285.5$, $N = 16$, $p = 0.0139$).

There are fewer unique elements in the source group than there are in the translocated, Pukaha-born and aviary groups (Mann-Whitney test: $W = 10.0$, $N = 4$, $p = 0.0107$; Figure 4.5 a). However, there is no difference in the number of unique elements found in the translocated, Pukaha-born and aviary groups (Mann-Whitney test: $W = 14.0$, $N = 4$, $p = 0.5959$). There is also no difference in the number of unique elements found in the territory groupings (Mann-Whitney test: $W = 13.0$, $N = 3$, $p = 0.8597$). The two groups appear to have the same proportion of unique elements in their repertoires (Figure 4.5 b).

It is possible that the level of element sharing found in this study is related to the amount of recording available for analysis. (Table 4.4). However, the source group still has a high level of within-group sharing despite not being as well recorded as the translocated group. The Pukaha-born group may be affected by the smaller amount of recording available, and may have had a higher level of within group sharing had there been more recordings available.

Table 4.4 Summary of level of sharing and the amount of recording available for analysis.

Group	Sample Size	Level of Sharing Within Group	Total Number of Elements Recorded	Total Number of Days Recorded
Source	4	0.844	1799	18
Translocated	4	0.315	2423	31
Pukaha-Born	2	0.051	536	16
Aviary	1	1	821	8

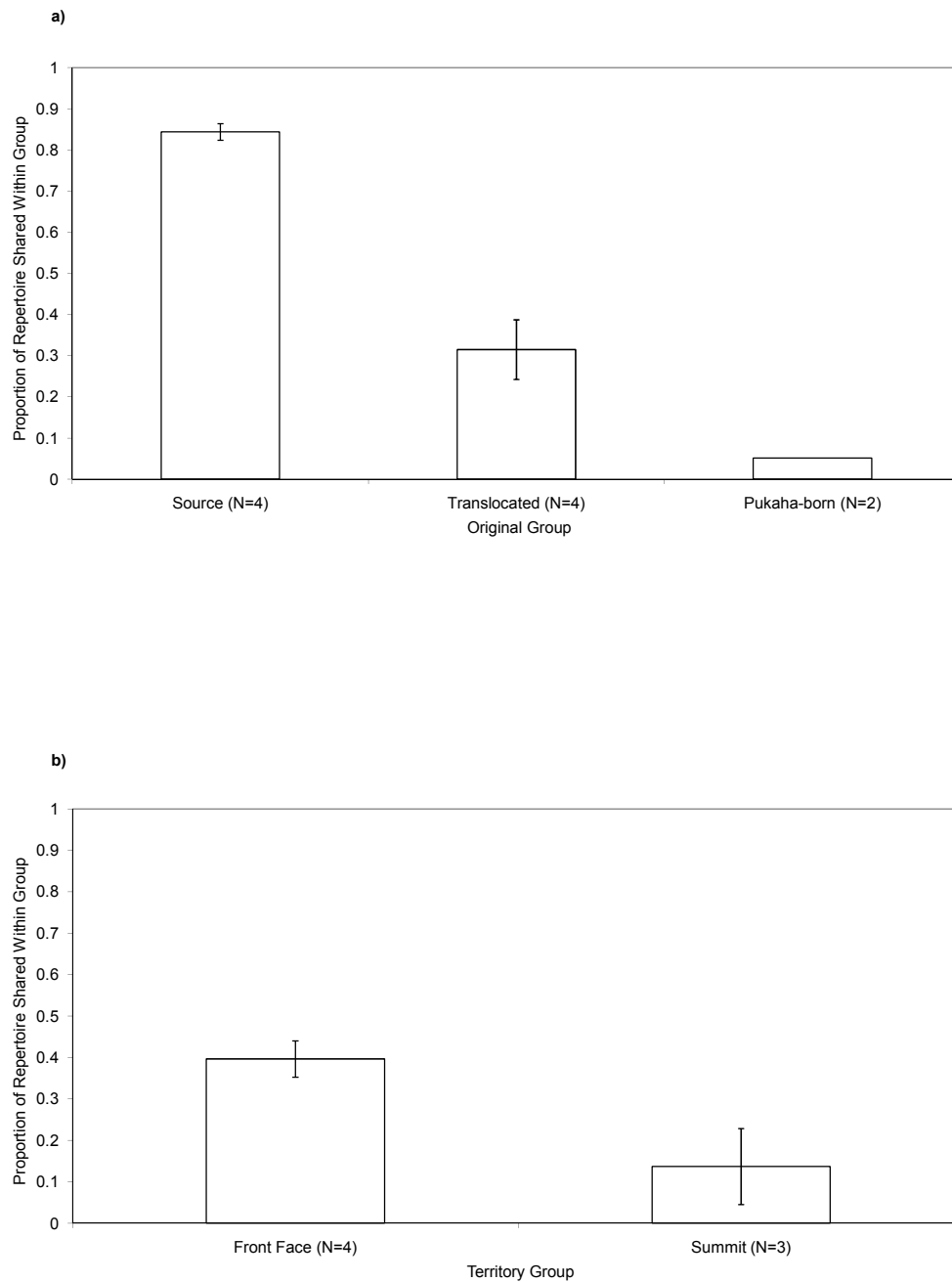


Figure 4.4: Proportions of Shared Elements within Groups – with pairs split into two different groups, a) where the birds have come from (Original groups) and b) where the birds at Pukaha have their territories (Territory group). Bars show standard error.

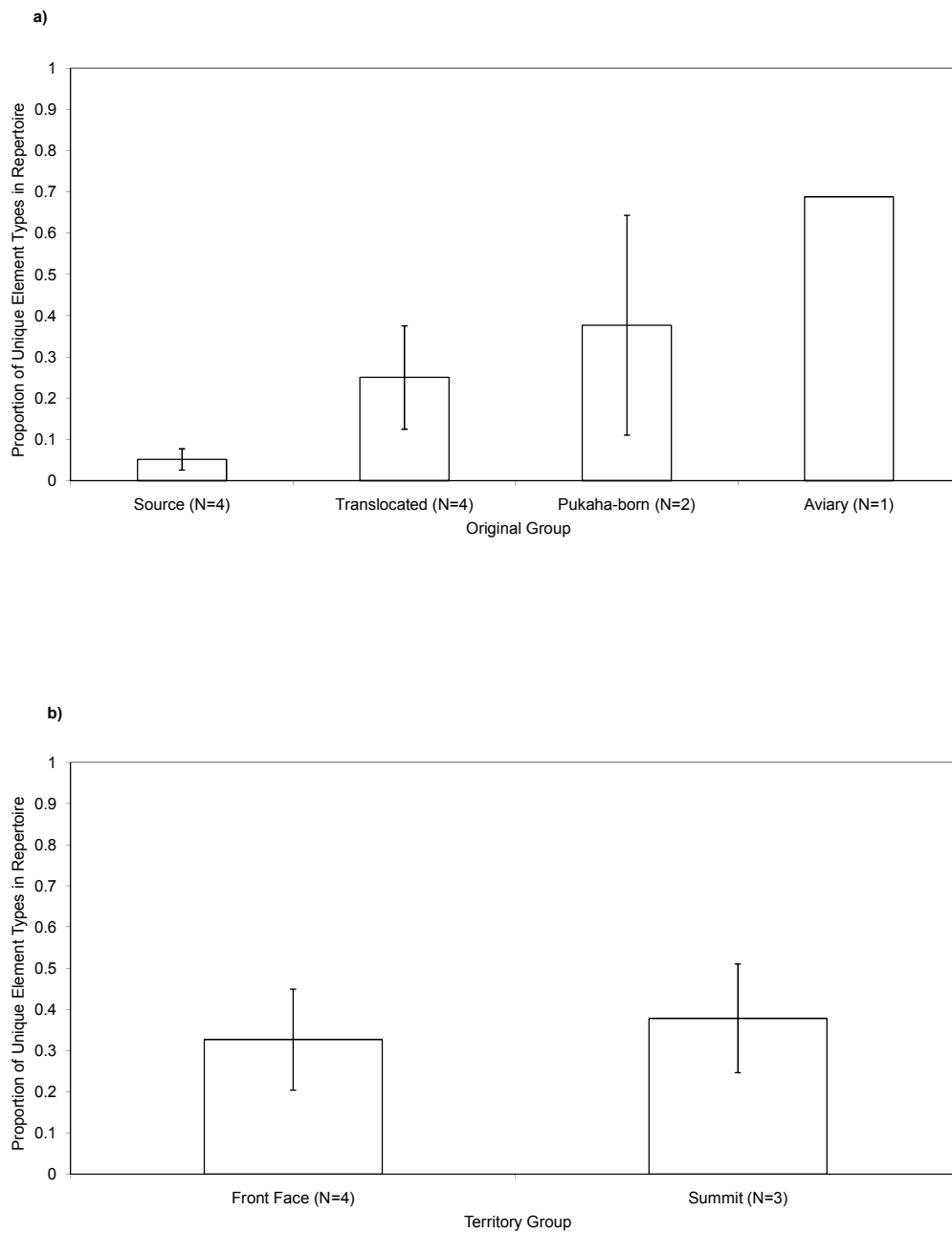


Figure 4.5: Proportions of Unique Elements in Repertoires - with pairs split into two different groups, a) where the birds have come from (Original groups) and b) where the birds at Pukaha have their territories (Territory group). Bars represent standard errors.

4.3.3 Frequency of Use of Shared Element Types

Elements A and F are used in decreasing frequency from the source to translocated to Pukaha-born to aviary birds (Figure 4.6). Element F is not used at all by the aviary bird. Element B1 also shows this trend, excluding the aviary bird (Figure 4.6). Elements T1 and TC1 however show an increased use by the translocated and aviary birds, but a decreased use by the Pukaha-born birds relative to the source pair (Figure 4.6). Both of these trends are very interesting, as none of the elements are used in the same frequency at Pukaha as they were at Mapara, they all show either an increase or decrease in frequency of use. It is also interesting to note that the Pukaha-born birds use all five of these elements less frequently than the source birds. However none of these trends were significant (Kruskal-Wallis tests: element A $H = 2.05$, $DF = 3$, $P = 0.563$; element B1 $H = 2.59$, $DF = 3$, $P = 0.459$; element F $H = 3.79$, $DF = 3$, $P = 0.285$; element T1 $H = 2.59$, $DF = 3$, $P = 0.459$; element TC1 $H = 2.59$, $DF = 3$, $P = 0.459$).

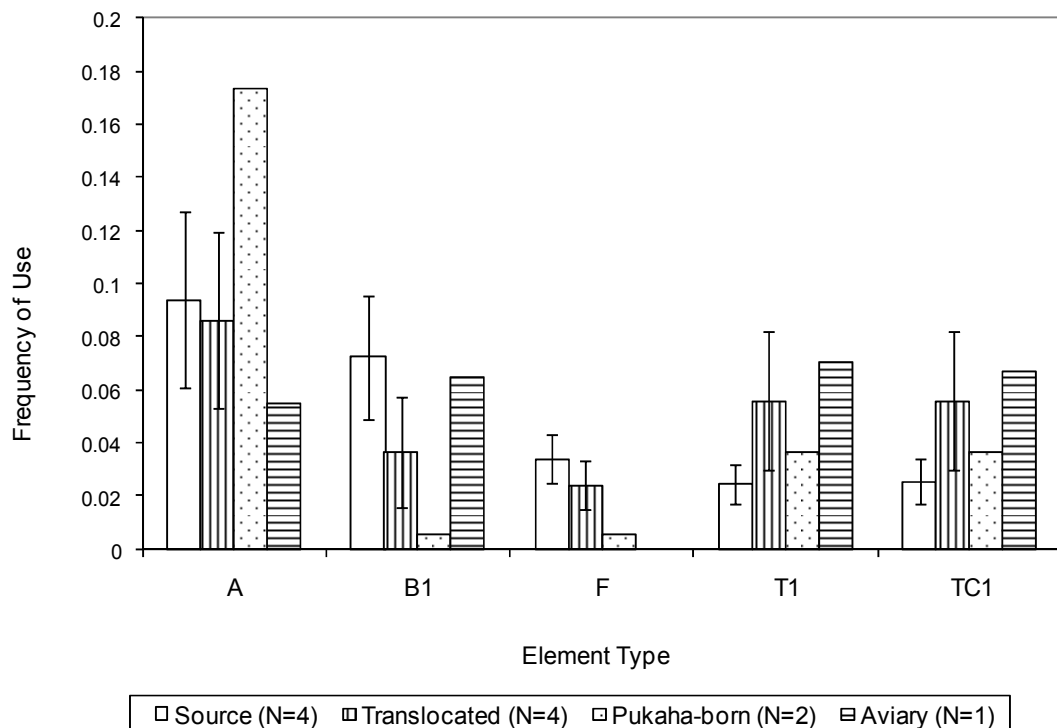


Figure 4.6: Frequency of Use of Shared Elements – with error bars showing standard error.

4.4 Discussion

Of the four element types I suspected might be changing in the new population, two separated visually and statistically, meaning that they are more than one element type. Element D separates into at least two element types, with a difference between Mapara and non-Mapara birds, but may be three different element types with a further difference between A2 and R18. Element P separates into at least two element types and the difference appears to be in the mixed pair female. The change in both of these element types involves a lowering of the fundamental frequency. The drop in frequency may be due to chance, or may come about because there may be vegetation differences between Mapara and Pukaha and low frequencies transmit better through dense vegetation (Slabbekoorn et al. 2007). The change in frequency may also be due to random genetic changes in syrinx mass, which determines the minimum vocal frequencies a bird can produce (Podos et al. 2004).

As predicted, the sharing within the source group is greater than that within any other group. However, unexpectedly, the front face birds at Pukaha do not share more element types within their group than the summit birds do. One explanation for this may be that it is a form of macrogeographic variation and cultural drift, where the song at Pukaha is becoming less alike among the Pukaha birds as they disperse. Song is known to be important for establishing territories and attracting mates (Hughes et al. 2007; Stewart and MacDougall-Shackleton 2008). We expect to see a high amount of sharing in birds that settle in the same area, as they compete for territories and mates. Kokako often participate in counter-singing bouts where they match or anticipate the song of another pair, so we anticipate they share song with their neighbours in order to allow them to counter-sing (Molles and Waas 2006). At Mapara there is a high density of birds, with many territories sharing boundaries; this may be the reason the Mapara North birds studied exhibited a high amount of sharing among each other. However, there are other factors which may be affecting the level of sharing, one of which is the small sample size and low number of recordings for the summit group. Had there been more recordings we may have seen a difference in sharing levels within the front face and summit groups at Pukaha. The low level of sharing within the Pukaha-born group may be sex-biased, as this group is formed

of two unpaired males. Had there been females included in this grouping we may have seen a higher level of sharing.

The source group shares more with each other than they do with the translocated birds, but the translocated group shares the same amount with the source birds as they do with each other. This is caused by low levels of sharing both within the translocated group and between source and translocated birds rather than being as a result of high levels of sharing between the two groups. The establishment of the translocated birds at Pukaha may have lead to rapid song modifications by each pair, which may be explained by a bottleneck effect in the translocated birds. The original translocated birds may have shared a low number of element types with the rest of the source population at Mapara by chance, leading to the seeming alteration of the song in the birds translocated to Pukaha. Another explanation is that the translocated birds have learnt new element types from the Mangatutu dialect that is also present at Pukaha. While it is widely thought that many songbirds are age-limited learners who cannot learn more element types after crystallisation, experiments have shown that novel auditory feedback can lead to changes in song (Leonardo and Konishi 1999; White and Mooney 1999). So it is possible that the translocated birds are learning song from the other birds present at Pukaha, and that territory placement is influencing which element types are learnt, leading to low levels of sharing between translocated birds.

The sharing within territory groups is no different to the sharing between them, and is a result of a low amount of sharing both within and between the two groups. The front face group shares more element types with the source pairs than the summit group does. This may be a form of microgeographic variation at Pukaha, where the two territory groups are diverging from each other. The chances of the birds on the front face being able to hear the summit birds are very slim, and the birds would only be able to hear each other on a very still day, with no wind, traffic or background noise. This may explain why they share more with the source birds than the summit birds do. The summit birds are constantly exposed to Mangatutu dialect, and are able to hear each other even on a windy day.

There are more unique element types found in the repertoires of the translocated and Pukaha-born birds than the source birds. There are just as many unique element types found in the front face group as in the summit group which is surrounded by Mangatutu birds. In a study on white-crowned sparrow new song types emerged as a result of mixes of the existing song types (Slabbekoorn et al. 2003). Slabbekoorn et al. (2003) also found that within a single population the components which make up the song types are not shared, even though the song types themselves are shared between the neighbouring populations. This suggests that different song components may transmit throughout populations differently (Slabbekoorn et al. 2003). The unique element types that have arisen in the birds at Pukaha may not be unique but may be element types from the Mangatutu dialect which the birds have learnt. Another explanation may be that the unique element types found are ones which the translocated birds did not share with the source population but have been brought with them to Pukaha. Likewise they may have been shared within the source population but were lost from the source population when the translocated birds left.

There is also no difference in how frequently element types are used, but there are trends that are appearing. Of the five shared element types whose frequency of use was analysed, three were used less frequently and two were used more frequently by the translocated birds. It may be due to chance that they are used differently, particularly as there is not a single increasing or decreasing trend, which is what may be expected. However, the differences in frequency of use may be a mechanism for matching their song to their Mangatutu neighbours in order to successfully defend their territories. Mature birds do not tend to learn new element types, they rely on learning the correct song for their area when they are young (Leonardo and Konishi 1999). If this is the case, and we assume that kokako do use their song for territory defence, then in order to successfully defend their territory the kokako must change something about their song as they may not be able to learn new element types. Perhaps they adjust the frequency of use of different element types so that ones which are similar to the Mangatutu dialect are sung more frequently, and ones that do not match it are sung rarely. A study on eastern male song sparrows where mates do not share the necessary song types to match each other showed that while partial-matching does not indicate a threat, it may indicate that the birds are paying attention (Anderson et al.

2008). So while the translocated kokako may not be able to learn the element types of the other dialect they may be able to use relatively similar element types to show the Mangatutu birds that they are attentive.

The aviary bird, Poutama, represents an interesting case in this study. He was born in the aviaries at Pukaha to a Taranaki father, has been shifted to Otorohanga and back again, and has had numerous partners of differing dialects. He has a large repertoire size, 32 elements, and nearly 70% of his repertoire is unique. He shares nearly twice as many element types with the source and translocated birds than he does with the Pukaha-born birds, which is surprising considering he was born at Pukaha and Romeo often spends time around his aviary. We would perhaps expect this bird to have a large, varied repertoire that is representative of the partners he has had. If, as suspected, kokako song functions in both territorial defence and pair-bond formation and maintenance, then Poutama would need to know multiple dialects because of the multiple partners he has had (Campbell 2004; Molles et al. 2006). He may share more with the source and translocated birds for two reasons. Firstly, his last partner was the female of the mixed pair – a Mapara born bird. Secondly, two of the translocated pairs, A2 and R18 (Mapara born), have been known to visit the aviaries. If they sing when visiting Poutama he may learn some of their dialect.

In a short period, only three years, we are already seeing changes in kokako song at Pukaha. The level of sharing between birds is decreasing at Pukaha, which may have implications for territory defence and mate attraction. A number of new element types that are unique to pairs are appearing, but these element types may be from the Mangatutu dialect. There may be microgeographic variation appearing at Pukaha, which may lead to two new dialects emerging, one in the summit birds and one in the front face birds. By using levels of sharing seen within their kokako population, managers could determine whether there is likely to be interbreeding between their kokako and could manage their populations accordingly. If the levels of sharing are low more birds could be translocated to increase density and potentially speed up the process. If the sharing levels are high then one could perhaps expect interbreeding between the birds from different areas, or at least breeding between their offspring.

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Chapter Five: Phrase syntactical and temporal variation in translocated kokako and its possible implications for territory defence.



An aviary kokako at Pukaha. Photo by: Emily Platt

5.1 Introduction

After colonisation events we often expect bird song to change, usually as a result of a bottleneck, selection or drift (Newman et al. 2008). Generally we look at additions or deletions of element types, phrases or song types from repertoires, however there are other ways that song can change. Whilst individuals may share the elements that make up the song type, they may place them in different sequences to create different phrases or song types. In the United States, house finches on the East Coast have a highly stereotyped song, where the phrase types are repeated exactly by individuals within a population, and the different song types are repeated precisely by all individuals that share that particular song type (Pytte 1997). In Wisconsin however, house finches rarely sing the same song type more than once; variations are seen in the repetition of phrases, their sequencing and the types of phrases that comprise a song type (Pytte 1997). In white-crowned sparrows inter-song variation consists of syntactical variants such as the presence or absence of a second phrase and songs with the same structure but using different element types (Slabbekoorn et al. 2003). A comparison of two closely related wren species (*Hippolais polyglotta* and *Hippolais icterina*) showed that allopatric populations have pronounced temporal and syntactical differences, with *H. icterina* singing at a slower pace with more repetitions than *H. polyglotta* (Secondi et al. 2003). However when these two species appear together in a contact zone, the two song characteristics that vary the most between the allopatric populations, temporal and syntax characteristics, are those that converge the most; this leads to both species producing similar songs. Hybridisation is possible and viable offspring are produced (Secondi et al. 2003). This demonstrates how having two dialects in one area can lead to song convergence.

Whilst individuals may share phrases and song themes, the timing with which they sing them can differ. Chaffinches all have different song types, but these song types all have one similar syntax, songs consist of a trill (two-five phrases of repeated elements) followed by a flourish (shorter sequence of non-repeated elements), and individuals are able to change the timing of these (Leitao et al. 2004). The trill and flourish lengths vary both within and between song types as well as between birds, however the lengths are much more varied

between song types than within song types, and flourish length is more variable than trill length (Leitao et al. 2004). Female chaffinches prefer longer flourishes while males do not respond as strongly to them (Leitao et al. 2004). This shows that timing characteristics, in this case the duration of a flourish or trill, can affect the reaction to a song. In spotted antbirds (*Hylophylax naevioides*) males and females sing their songs with different speeds, with male antbirds singing their song slower than females (Bard et al. 2002). It is hypothesised that these differences play a role in territorial defence, that they may allow individuals to recognise the sex of an intruder and identify if the intruder could be a potential mate (Bard et al. 2002). Canaries change the duration of their song seasonally, with song being significantly longer during breeding season (Voigt and Leitner 2008). These examples show us that temporal differences in song arise for many reasons, in many different ways.

However, in many species we still expect to find enough sharing and similarity within groups so that the functions of the song are not jeopardised. If a species' song is used for territory defence, we expect individuals to share enough of their song with their neighbours to be able to communicate effectively. For instance male and female plain wrens match phrase types to playback when defending their territory, but not duet types (Marshall-Ball and Slater 2004). If a species duets in order to form and maintain pair-bonds it is important that individuals' songs are similar enough to do so. Australian magpie-larks (*Grallina cyanoleuca*) are antiphonal duetters whose duet functions in territory defence, pair-bond formation and maintenance, and mate-guarding (Hall 2006). Both males and females benefit from singing co-operatively and extra-pair paternity and divorce rates are low. The repertoires of the magpie-larks are very similar, with males and females having similar repertoire sizes and sharing similar proportions of their song within and between sexes (Hall 2006).

Kokako in Pongakawa Ecological Reserve have an average phrase length of 0.58 to 4.81s (mean 1.96 ± 0.24) and phrases consist of 1-3 elements (Molles et al. 2006). They have an average repertoire size of 18 phrases and there is a high degree of sharing among pairs, with $86\% \pm 1\%$ of the phrase repertoire shared between pairs (Molles et al. 2006). Duets in

this species are well known for their long inter-phrase pauses, often thought to allow the kokako to listen for neighbours or intruders and respond accordingly (Molles et al. 2006). To my knowledge the work carried out on kokako song thus far looks at phrases at the larger scale and how they are made into themes, and no work has been carried out looking at the finer scale of elements and element timing within phrases.

This chapter will examine changes in the syntax and temporal characteristics of kokako song. The aim is to compare and contrast the phrase repertoires of groups of kokako which were described earlier (Chapter 2): source, translocated, Pukaha-born and aviary. I will look at the: number of phrase types, number of elements per phrase, timing within phrases and degree of phrase type sharing. These measurements will allow me to tell if and how the phrases and phrase repertoires are changing. My aim is to determine if phrase repertoires differ within and between groups. I predict that:

- The source birds will have the lowest number of different phrase types. This is because the source birds are not exposed to multiple dialects, so there are not as many phrase types for them to learn or match with their neighbours. The Pukaha-born birds will have the highest number of phrase types because they learnt their song at Pukaha in the presence of multiple dialects and thus had more opportunity to learn.
- The translocated birds will share fewer phrase types with each other than the source birds do because different translocated birds are exposed to the alternative dialect to different degrees, and are under less pressure to learn new phrases to match with their neighbours because of their dispersed territories. Pukaha-born birds will have the lowest levels of sharing for similar reasons; in addition they will be the birds most likely to have learned a great variety of different phrase types because they have been in a multi-dialect environment from birth.
- Translocated birds will show more variation in the number of elements which constitute a phrase than do source birds, for the same reasons they are expected to have lower levels of within-group sharing.
- The timing within phrases and the phrase syntax will change from the source

Mapara population to the Pukaha population as phrases begin to vary.

Looking at phrase syntax and timing is another way in which the song of mixed dialect populations can be used as a monitoring tool. By looking at the phrase repertoire we can see if shared element types are being used in the same way, or if they are placed in phrases differently. Song matching occurs commonly in kokako, and it may be that element types are the same, but are being used in different ways; which may lead to the kokako being unable to match songs in counter-singing bouts. The timing, and any change that may occur, can also potentially tell us if the meaning of the song is changing.

5.2 Methods

For recording methods and study areas please refer to Chapter 2. For methods on how elements and repertoires were described and compared please refer to Chapters 3 and 4.

For the purpose of this chapter the mixed pair will be discussed both as a pair and as individuals. The groupings will be as follows:

- Source = M1, M2, M4, M5
- Translocated = A2, R18, Billy Goat (BG) and Mixed Pair Female (MPF)
- Pukaha-born = Mixed Pair Male (MPM) and Romeo
- Aviary = Poutama
- Mixed Pair = mixed pair female and mixed pair male (MPF and MPM)

Element type comparisons were carried out previously (Chapter 4) so this chapter is focused on the element types which are used to create phrases and the timing between elements.

5.2.1 Phrase Identification and Comparison

I define a phrase in this instance as a sequence of two to six elements which occur in a predictable pattern. It is possible to identify phrases in the field, however often they have elements added or taken away, so a more impartial approach was needed to properly identify phrase types. In order to objectively identify the phrase types for each pair or individual I used lag sequential analysis, carried out in GSEQ, which allowed me to detect non-random sequences of events (Bakeman and Quera 1995). An event of interest, in this case an element type, is chosen as a starting point and for each occurrence of the event a count is made of the number of times all other behaviours, in this case other element types, occur immediately after (lag + 1) the starting event (Bakeman and Quera 1995). Observed and expected frequencies for sequences of events are calculated, as are p-values, so one is able to determine if each particular element type does follow the element type of interest more or less often than would be expected by chance (Bakeman and Quera 1995).

All recordings were used in this analysis, and it was carried out so that each element type in the repertoire was selected as the element type of interest, with a lag of +1. If sequences of element types occurred more than seven times in the recordings, and if the sequence had a p-value of 0.000+ they were linked together as a chain. With the newly made chains as the events of interest the analysis was repeated, adding element types to the end of chains, until no more new chains could be made that met the p-value and occurrence requirements. These chains were accepted as phrases.

Pearson correlation analyses were carried out in Minitab15 (Ryan et al. 2007) in order to determine if there was a relationship between the number of phrase types found and the total number of elements recorded or the number of element types found. This was important as it could have affected how the findings of this chapter are interpreted.

Kruskal-Wallis tests were carried out to determine if the groups differ in: the number of phrase types, the number of elements that make up a phrase and phrase type sharing within groups. Between-group phrase type sharing could not be calculated because of the nature of

the phrase types that were found. Many phrase types were partially-shared between groups but exhibited additions or deletions of elements. These are discussed in terms of how the different phrase types are changing between groups.

5.2.2 Analysis of Phrase Temporal Characteristics

Seven shared phrase types were chosen for the temporal analysis (k-t1-tc1, g1-g1-g1, d-e, t5-f, g2-g2-g2, a-p, and y-z). To do this I looked at the original recordings for instances of the phrase type which occur in sensible timing, i.e. elements were less than ten seconds apart. This was because in some instances the elements which make up the phrase were not sung together as a phrase, but were separated by gaps up to a minute long. I measured the length of time between elements in the phrase in Raven Lite (2008). I measured at least five instances, but up to ten.

Once I had measured the timing between the elements I carried out Kruskal-Wallis analyses in Minitab and post-hoc Mann-Whitney tests to determine if there were timing differences between Mapara (M1, M2, M4, M5) and non-Mapara (A2, R18, BG, MPF, MPM, Romeo, Poutama) birds. However, three of the phrase types whose timing characteristics I looked at were recorded from only two pairs, so for these I only carried out Kruskal-Wallis tests to determine if there was a difference between the two pairs.

5.3 Results

5.3.1 Phrase Identification and Comparison

Using the lag sequential analysis I was able to determine a number of different phrase types for each pair except for the Billy Goat pair, which had no phrase types found (Table 5.1). For a complete list of phrase types found please refer to Appendix Three. The average number of phrase types found between all pairs was 5.75 ± 0.72 . There was no relationship between the number of phrase types found and the total number of elements recorded (Pearson correlation = 0.579, $P = 0.062$) or the number of element types found (Pearson

correlation = 0.068, $P = 0.842$). So although the Billy Goat pair had the least number of elements recorded (151) that cannot explain the fact that there were no phrase types found for this pair. However, the small sample size may be affecting this result. The number of phrase types found did not differ between groups (Kruskal Wallis test: $H = 3.73$, $DF = 3$, $P = 0.292$). There was also no difference between groups in the number of elements that make up these phrase types (Kruskal-Wallis test: $H = 1.78$, $DF = 3$, $P = 0.620$).

In the lag sequential analysis I looked at the mixed pair together and as individuals to determine if they formed phrase types together (Table 5.1). The analysis of their combined contributions detected no phrase types with contributions from both birds. Instead, there was evidence that in some cases they may have “interrupted” one another’s phrases. For example, the female had six phrase types in the analysis of her alone, but only five of these phrase types were detected in the analysis of the pair as a whole. This was the same with the male, who had four phrase types in his individual analysis, but only three were detected in the pair analysis.

Table 5.1: Phrase type repertoire of pairs/individuals. Showing number and average length of phrase types (\pm SE)

Group	Pair	Number of Phrase Types	Average Length of Phrase Type (Elements)
Source	Mapara 1	8	2.625 ± 0.263
	Mapara 2	8	2.5 ± 0.189
	Mapara 4	7	2.857 ± 0.261
	Mapara 5	3	2 ± 0
Translocated	A2	7	2.714 ± 0.36
	R18	5	3.2 ± 0.49
	Billy Goat	0	0
	Mixed Pair Female	6	2.167 ± 0.167
Mixed Pair	Mixed Pair	8	2.375 ± 0.263
Pukaha-born	Mixed Pair Male	4	2.5 ± 0.5
	Romeo	5	2.2 ± 0.2
Aviary	Poutama	8	3 ± 0.5

Within-group phrase type sharing levels did not differ between groups (Kruskal-Wallis test: $H = 1.86$, $DF = 2$, $P = 0.394$). Only one phrase type, k-t1-tc1, was shared between all four groups (source, translocated, Pukaha-born, aviary). Of the remaining phrase types two were shared between two groups: b1-b1 shared between source and aviary, and t5-f shared between source and translocated. There were many phrase types which changed through addition or deletion of elements (Table 5.2). Four phrase types showed changes between groups, and two showed changes within groups (Table 5.2). The two phrase types which change within a group both belong to the source birds.

Of the changes, two were deletions of a single element, and twelve were additions of one to two elements (Table 5.2). Within the source group changes to phrase types were in the form of additions. The only deletions were found in the translocated and Pukaha-born groups.

Table 5.2: Phrase types showing changes within and between groups.

Core of Phrase type	Source	Translocated	Pukaha-Born	Aviary
i1-h[^]	h-i1-h-t5 i1-h h-i1-h			
g1-g1-g1	g1-g1-g1	g1-g1-g1- p	g1-g1_	
d*-e	d1*-e	d2*-e p-d3*-e		
t4-c[^]	a-t4-c t4-c t4-c- t7-a			
g2-g2-g2	g2-g2-g2	o-g2-g2_-p g1-g1-g2-g2-g2		
a-p		a-p		a-p-c

[^] denotes within-group changes. * denotes an element which is changing between groups. Additions to the phrase type are in **bold**, deletions are indicated by _.

5.3.2 Temporal Characteristics of Phrases

Six of the seven phrase types that were analysed showed differences in timing between groups or pairs. The one phrase type which did not show any difference, y-z, was only shared by the mixed pair male and Romeo, both of whom are Pukaha-born (Kruskal-Wallis test: $H = 1.31$, $DF = 1$, $P = 0.253$). The phrase k-t1-tc1, looked at in two parts to represent the timing between each of the elements, showed differences between groups (Kruskal-Wallis test: k-t1 $H = 18.78$, $DF = 7$, $P = 0.009$; t1-tc1 $H = 22.81$, $DF = 7$, $P = 0.002$) but the difference was only between Mapara and non-Mapara birds for the second half of the phrase, t-tc1 (post-hoc Mann-Whitney: k-t1: $W = 1052.5$, $N = 28, 50$, $P = 0.5809$; t-tc1: $W = 1372.0$, $N = 28, 50$, $P = 0.0057$). The difference in timing in k-t1 may be caused by M1 and M2 having slightly longer gaps (Figure 5.1 a). The difference in t1-tc1 was due to the A2 pair having a longer gap (Figure 5.1 b)

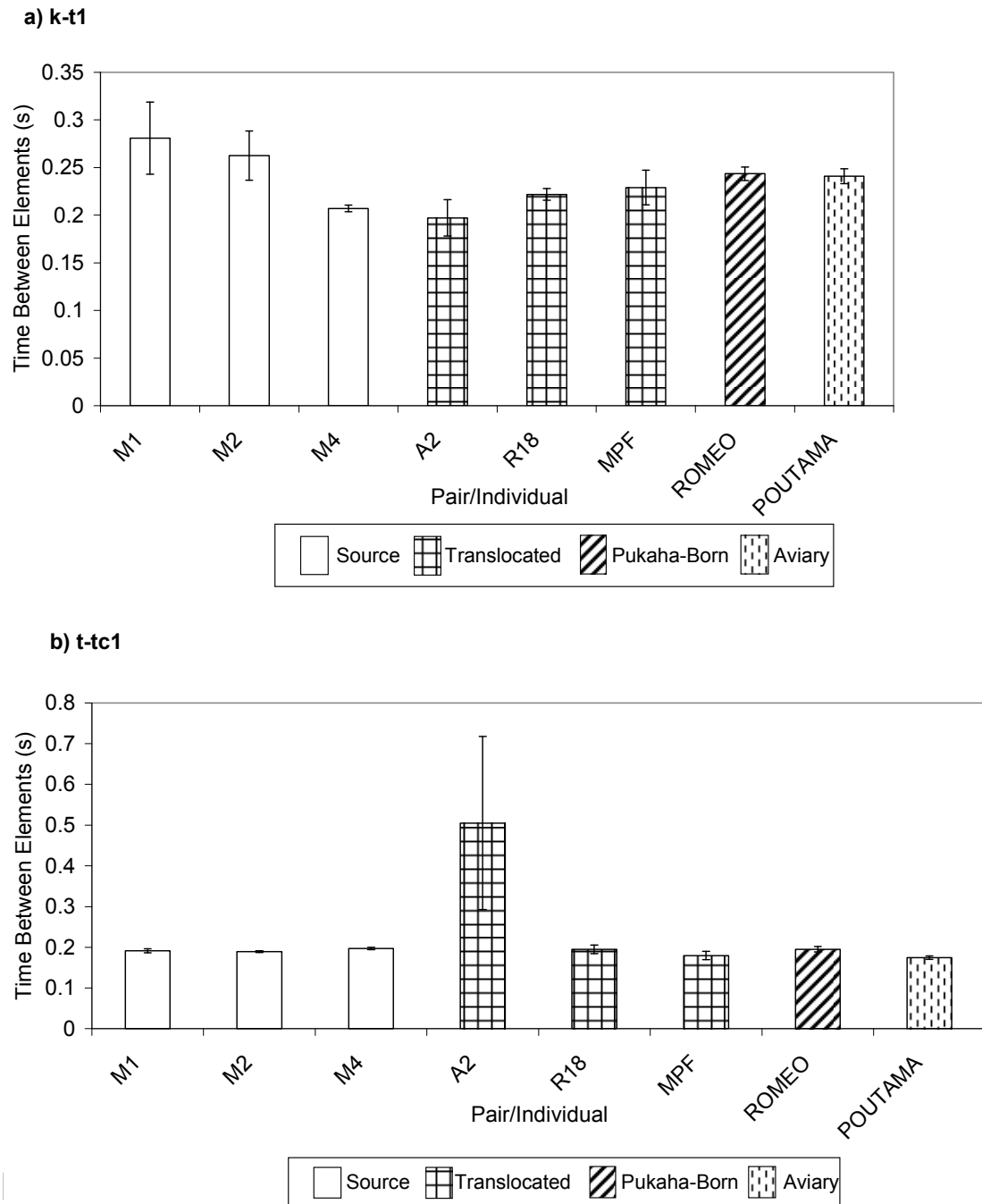


Figure 5.1: Length of Time between Elements – for phrase k-t1-tc1. A = k-t1, B = t1-tc1. Bars are SE.

The remaining five phrase types all showed statistically significant differences in timing. g1-g1-g1 shows a difference between some of the pairs (Kruskal-Wallis test: $H = 30.89$, DF

= 5, $P = <0.001$), with the source pairs exhibiting a longer gap between elements than the translocated and Pukaha-born pairs (post-hoc Mann-Whitney: $W = 964.5$, $N = 26, 28$, $P = <0.001$). d – e is only shared by three pairs; M1, A2 and R18. As mentioned in Chapter 4, element D is changing and there are three versions; a Mapara version, an A2 version and an R18 version. Although I determined it is an element which is changing, it still forms the basis of a shared phrase type. The timing characteristics of this phrase type are changing between the pairs (Kruskal-Wallis test: $H = 18.05$, $DF = 2$, $P = <0.001$) with M1 having a shorter gap between elements than A2/R18 (post-hoc Mann-Whitney: $W = 925.0$, $DF = 10, 20$, $P = 0.0064$) (Figure 5.2).

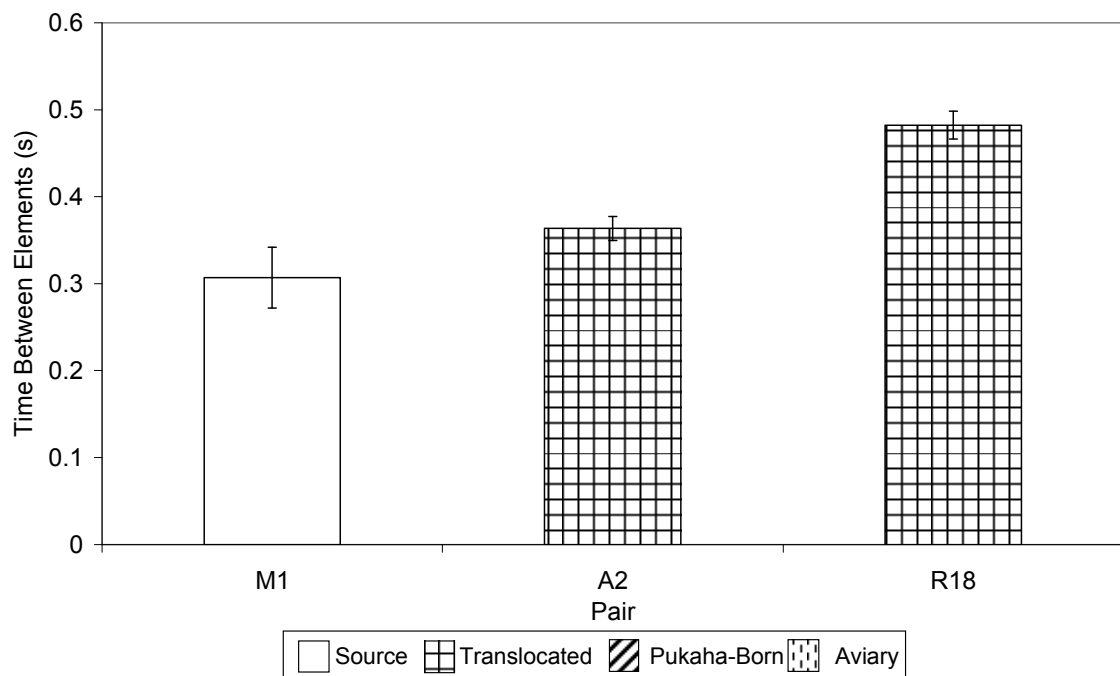


Figure 5.2: Length of Time between Elements – for phrase d-e. Bars are SE

t5 – f, which is shared by M1, M2 and A2, showed a difference in timing (Kruskal-Wallis test: $H = 6.30$, $DF = 2$, $P = 0.043$) which is not between the two Mapara pairs and A2 (post-hoc Mann-Whitney: $W = 200.0$, $N = 15, 8$, $P = 0.2081$). We can see from the graph that perhaps the difference is between M2 and M1/A2 (Figure 5.3).

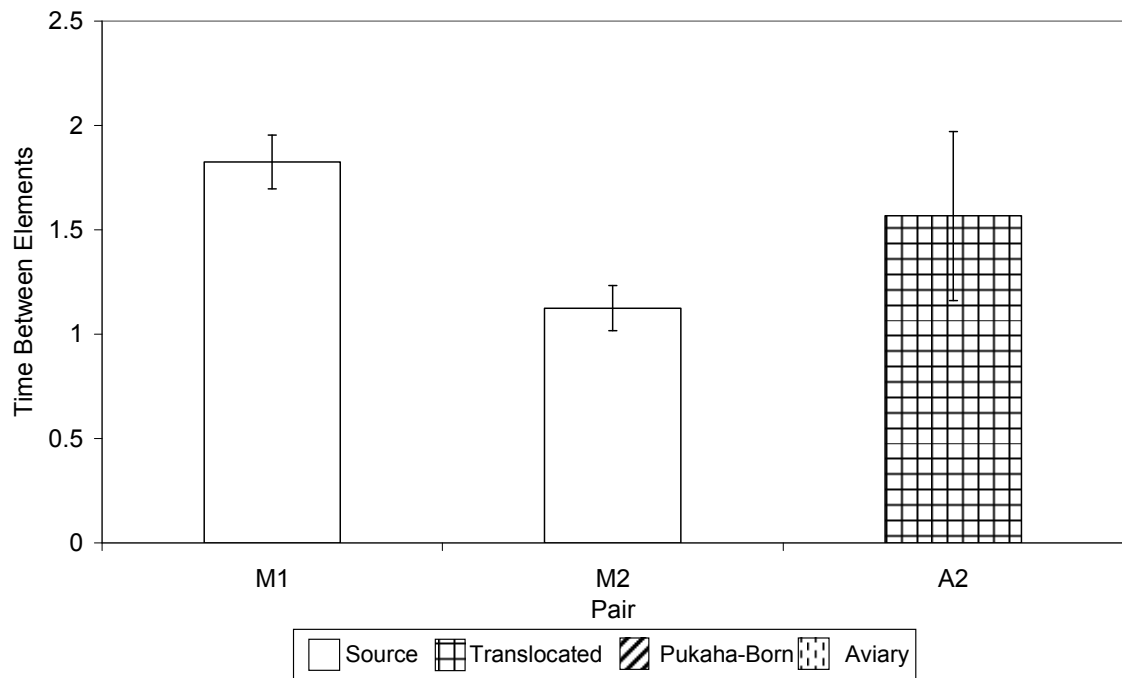


Figure 5.3: Length of Time between Elements – for phrase t5-f. Bars are SE.

The remaining two phrase types, g2-g2-g2 and a-p both showed significant differences between pairs. g2-g2-g2 is shared by A2 and R18, and A2 has a longer gap between elements than R18 (Kruskal-Wallis test: $H = 14.29$, $DF = 1$, $P = <0.001$). Phrase a-p is shared by the mixed pair female and Poutama, and Poutama has a longer gap between elements (Kruskal-Wallis test: $H = 10.59$, $DF = 1$, $P = 0.001$).

5.4 Discussion

There was no difference in the number of phrase types, or the number of elements which constitute a phrase, between groups. However, there were obvious changes in phrase syntax, with additions and deletions of elements detected both within and between groups. Only one phrase type was clearly shared between all three groups, and two were shared by two different groups. There were also differences in phrase timing, with six out of seven analysed phrase types showing temporal differences.

Birds with larger repertoires do not have more phrase types. I thought there might be a difference shown by the three pairs who had less than 300 elements recorded; the Billy Goat pair, the M5 pair and the mixed pair male. These three pairs/individuals had 0 phrase types, 3 phrase types and 4 phrase types respectively. I had thought that perhaps I did not have enough instances of each element recorded to detect phrase types in these pairs/individuals; however there was no significant difference in the total number of elements recorded and the number of phrase types found. The number of elements used to make a phrase did not differ between groups, with 2-3 elements generally being used. The reason for the lack of variation between groups, and the lack of correlation between the number of phrase types and repertoire size or number of elements recorded may be the small sample size. However, there may truly be no difference. This was found in zebra finches (*Taeniopygia guttata castanotis*), which, when domesticated, showed changes in element morphology and singing rate but not in the number of elements per phrase (Zann 1993).

The number of shared phrase types within groups did not differ between groups. As the song evolves at Pukaha phrase type sharing levels did not decrease, suggesting that any changes are common to all pairs. The mixed pair members did not share any phrase types with each other, there are no phrase types formed by a mixture of the male and female elements. This was not unexpected, as in the field they appeared to sing separately, taking turns. Kokako sing antiphonally by alternating phrases, so the fact that this pair does not share phrase types does not necessarily mean they are not duetting (Molles et al. 2006). However the lack of sharing within this pairing may be due to the fact that they are a relatively new pairing, with the female being released at the beginning of this study. They may begin to share more as the pairing continues. There is only a single phrase type which was shared between all of groups. We would expect the level of phrase type sharing between groups to be higher, particularly between the groups at Pukaha. Kokako pairs participate in counter-singing bouts where they are able to match or anticipate the songs of their neighbours (Molles and Waas 2006). If these birds only share a single phrase type then they may not be able to effectively participate in these counter-singing bouts. The lack of sharing at Pukaha may be because of the dispersal of territories. It is possible that the

front face birds are spread out enough that they do not hear each other, or the summit birds, reducing their need to counter-sing. The Mapara-sourced and Pukaha-born pairs around the summit, which is more densely populated, may be sharing phrase types with the Mangatutu birds, rather than each other. If this was the case we would expect sharing levels to increase in the years to come as the area becomes more populated.

Evidence of changes in syntax comes from phrase types that could have been shared between the groups but that are changing through the addition or deletion of elements. This phenomenon is one commonly observed in kokako, with basic phrase types often exhibiting variation from song bout to song bout (Laura Molles, pers. comm.). However I have found what may be permanent directional changes, showing that phrase syntax has changed post-translocation. This change is primarily in the form of additions of elements to the phrases. The domestic Bengalese finch (*Lonchura striata* var. *domestica*) has altered in syntax from their wild ancestors, with the ancestor singing very simple, stereotypical song types, while the domesticated finches now sing extremely complex striking song types (Okanoya 2002). It is possible that the kokako syntactical variations will eventually become entrenched in the Pukaha population.

The temporal characteristics of the shared phrase types are exhibiting the largest change out of all the phrase measurements analysed. All but one of the seven phrase types analysed showed a change in timing between elements. Experiments carried out on zebra finches and budgerigars demonstrated their ability to discriminate fine-scale temporal changes in song (Lohr et al. 2006). This leads me to believe that the changes in timing found here may be significant in showing that the song is changing, and that while the differences may not be obvious to the human ear they may be to kokako. The types of information that can be found in song timing include male quality, aggressive intent or social status (Poesel and Dabelsteen 2005; Brumm and Slater 2007; Amy et al. 2008). Overlapping song can indicate a more aggressive intruder, and can in turn trigger a lower song rate by the resident bird (Poesel and Dabelsteen 2005). In some species, overlapping of song indicates a male's willingness to escalate a verbal confrontation (Amy et al. 2008). It is interesting to note

that, of the phrase types whose temporal characteristics are changing, the Pukaha kokako whose territories are around the summit have shorter gaps between elements than the birds on the front face. This may be due to the higher density of birds around the summit, and the shorter timing between elements may indicate an aggressive response to the Mangatutu birds. The shorter time between elements may also indicate the strength of a pair's bond. Well coordinated duets often signal pair stability and commitment (Brumm and Slater 2007). It is also possible that the changes in timing characteristics are being caused by changes in habitat structure (Badyaev and Leaf 1997). However, it may just be due to individual differences between kokako, and had my sample size been larger the apparent effect of changes in song timing may be different.

This analysis has shown examples of shared phrase types diverging and of a low amount of phrase type sharing between groups. Phrase syntax is diverging slightly, but timing changes are more obvious. This raises an interesting issue of which is more important to kokako: the ability to match phrase types or phrase and song timing. Kokako have long inter-phrase pauses in their singing bouts, and are able to both match and anticipate the song of other birds during counter-singing bouts (Molles et al. 2006). This suggests that, for kokako generally, timing and syntax are both important. However, perhaps at Pukaha it is the timing rather than syntax which is important because of the presence of multiple dialects. Having more than one dialect means the kokako at Pukaha are not going to be able to sing the same phrase types, so in territorial counter-singing interactions they may not be able to match or anticipate the song of their neighbours. So in this instance perhaps the changes in timing of the phrases at Pukaha may provide information to the birds' neighbours which would usually be found in the syntax. If the kokako at Pukaha were reacting to the timing of the playback song then perhaps this affected the timing of their songs. In order to test reaction to song timing the length of time between elements or phrases within the playback song could be both lengthened and shortened and then reaction to the altered song gauged. By using this information conservation managers can establish if their kokako are able to ignore the fact that they do not share element types and are using song timing to communicate or vice versa.

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Chapter Six: Conclusions and Recommendations



Kokako chicks. Photo: Tony Silbery

6.1 Conclusions

This thesis came about because of a very unique problem exhibited by kokako. Kokako only exist in small remnant populations separated by large tracts of unsuitable land. Kokako are also very poor flyers, only able to fly for approximately 100 metres at a time. So in order to prevent inbreeding and a loss of genetic diversity in the remaining kokako populations, managers are carrying out translocations to establish new populations, maintain gene flow and prevent inbreeding. However, these translocations have the potential to be unsuccessful because kokako exhibit macrogeographic variation in their dialects, and tend not to breed with individuals from different dialect areas. If the purpose of the translocation is to enhance genetic diversity by having kokako from different areas breed then song is an important factor that must be dealt with.

Song is extremely important to kokako for a number of reasons. Chiefly, it is hypothesised that song is their primary means of territory defence. A kokako gains all its resources from its territory, so it is imperative that they successfully defend it. Their duet song functions in territory defence, but also acts to form and maintain pair bonds. In order to try and address the potential issue that song could cause in translocations I studied if and how song evolves in multiple dialect areas.

This study shows that translocation into multiple dialect areas can affect kokako song. It does not affect the size of the kokako repertoires, as it does in other bird species (Hamao and Ueda 2000; Baker et al. 2003; Johannessen et al. 2006). However, kokako may depend on frequent interactions with their neighbours in order to alter their repertoire; the density of the new population rather than the translocation itself may affect the repertoire. At Pukaha we are seeing changes in repertoire composition and sharing in just a short amount of time, only three years. The level of element type sharing between the birds at Pukaha has decreased from the levels of sharing seen in the source population. This could have implications for territory defence and mate-attraction. If the kokako do not share many element types it is unlikely they will be able to participate in the counter-singing bouts which are thought to be used in territory defence.

A number of new element types that are unique to pairs are emerging; however it may be that these new element types can be found in the Mangatutu dialect, which is also present at Pukaha. If this is the case translocated Mapara birds and Pukaha-born birds may be sharing more of their repertoires with the Mangatutu birds than each other, which would explain the low sharing levels found. Another explanation is that these element types were seen in the source population but have ceased to be used once the translocated birds were removed. The birds on the front face share more element types with the source Mapara population than with the summit birds do; which may mean that the summit birds are sharing more of their repertoire with the translocated Mangatutu birds who surround them. This, combined with the low density of birds at Pukaha, could lead to the emergence of two new dialects at Pukaha, one on the front face and one around the summit.

These changes in repertoire composition have, in turn, affected the phrases which are sung. This study only found one phrase type truly shared between all groups of birds. Phrases which were shared within the source Mapara population have been shown to diverge slightly in syntax in the translocated birds; however this divergence is more obvious in the temporal characteristics of the phrases. This raises an interesting issue of which is more important to kokako: the ability to match song phrase types or song timing. At Pukaha it may be that the timing rather than syntax is important because of the presence of multiple dialects. The changing of timing characteristics may be providing information that otherwise would be found in syntax. The types of information that may be communicated include male quality, aggressive intent or social status (Poesel and Dabelsteen 2005; Brumm and Slater 2007; Amy et al. 2008).

So in conclusion, the kokako at Pukaha appear to have the same size repertoires as the source population, but seem to share fewer element types and have more unique element types. There is variation at Pukaha depending on where territories are situated, with those birds situated closer to the summit, and thus the Mangatutu dialect, sharing fewer element types with the source Mapara population than the kokako on the front face. And finally, the way in which elements are formed into phrases shows slight changes in syntax, but large temporal differences. These results have repercussions for future kokako translocations. A

low amount of phrase and element type sharing combined with changes of intra-phrase timing could lead to the Pukaha kokako's inability to successfully defend their territories. This study has shown that by looking at whether the song and its components are becoming similar between dialects or if they are remaining different we can assess the possibility of kokako in mixed dialect populations interbreeding.

6.2 Recommendations

6.2.1 Translocations

In order to ensure translocations are a success the density of birds in the new population should be taken into consideration. It is likely that the more kokako there are in an area the faster they will form mixed dialect pairings. If the goal of the translocation is to promote gene flow then there should be as many birds translocated as possible to give this the best chance of occurring. A good example to follow is that of the Hunua Ranges, where there is a managed area of 1,000ha and approximately 45 regularly-seen kokako. At Pukaha there is an area of 945ha and fewer than 20 regularly-seen kokako.

It may also be sensible to translocate young birds, 1-2 years old, and employ sound anchoring techniques. This is because kokako set up territories and begin to breed when they are approximately 2 years old. If young birds are translocated and sound anchoring using multiple dialects is carried out then the translocated kokako may still be young enough to learn multiple dialects easily.

Another option if forming a new population from multiple dialects is to translocate kokako whose dialects are similar to each other. It is likely that some kokako populations sound more alike than others, and if this is the case it may be easier for individuals to mix.

6.2.2 Research

This study only concentrated on looking at how a single dialect changed at Pukaha, but research needs to be carried out on whether the same thing is happening with the other dialect. It may be that the dialects are altering at different rates or in different ways, and so similar research could also be carried out on other populations which have been started by translocations from more than one dialect area. This thesis was carried out over one year, but if more research was undertaken in subsequent years we may get a better picture of how the alteration of the song continues. Additional data may clarify patterns of change, particularly for those pairs that had fewer than 300 elements recorded. In regard to the additions and deletions from the core phrases this may be a normal process, as it is in the Bengalese finch where ancestors sing a simple song which has changed into a complex song sung by their descendants (Okanoya 2002). In order to determine if this is the case in kokako the phrase syntax needs to be studied in subsequent years.

The issue of timing in kokako song is of particular interest considering the results found in this study. All but one of the seven phrases analysed show a change in timing between elements, and of these changes the birds around the summit are showing decreases in timing between elements. The shorter timing can mean one of several things, including aggressive intent and social status (Brumm and Slater 2007; Amy et al. 2008). Kokako are well-known for their inter-phrase pauses (Molles et al. 2006) and this suggests that timing is important to kokako song and its functions. It would be interesting to use playback experiments to test if intra-phrase timing is also significant. To do this one could take a kokako phrase and cut the inter-element timing to make it longer and shorter, and then play back the recording to see if the kokako react more aggressively to the different timing than they do to the normal phrase timing.

6.3 References

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Appendix 1

Appendix One: Census Information for Pukaha Kokako.

Bird	Bands	Territory	Sex	Parents	Year Born/Released	Paired With	Located 03/04	Located 04/05	Located 05/06	Located 06/07	Located 07/08
Turk	L-M	Summit	♂	?	R 2003	Gale	Yes	Yes	Yes	Yes	Yes
Gale	M-Y	Summit	♀	?	R 2003	Turk	Yes	Yes	Yes	Yes	Yes
Whakatere	0-M	Summit	♂	?	R 2003	Was Rain, now?	Yes	Yes	Yes	Yes	Yes
Rain	M-R		♀	?	R 2003	Was Whakatere	Yes	Yes	Yes	No	
Pumpkin	M-W		♀	?	R 2003		Yes	No	No	No	No
Petal	M-G		♀	?	R 2003		Died Dec 03				
GM-Y	GM-Y		♂	Turk & Gale	B 2003/2004		Yes	No	No	No	No
Son of Turk	GM-R	Summit	♂	Turk & Gale	B 2003/2004	Was Mihitai	Yes	No	Yes	Yes	Yes
Zara	Y-OM	Summit	♀	?	R 2004	Mystery?		No	No	Yes	No
Papa	G-OM		♀	?	R 2004			No	No	No	No
Basil	O-OM		♂	?	R 2004			No	No	No	No
Zack	Has a bung /hazy eye		♂	?	R 2004			No	Yes	Yes	No
Morehu	R-BM	Summit	♂	?	R 2004	Mihitai		No	No	Yes	Yes
Y-BM	Y-BM		♀	?	R 2004			Died Oct 04			
M1	B-MB		♂	?	R 2005				Died Sept 05		

Bird	Bands	Territory	Sex	Parents	Year Born/Released	Paired With	Located 03/04	Located 04/05	Located 05/06	Located 06/07	Located 07/08
M2	G-MB	Summit	♂	?	R 2005	M3			Yes	Yes	Yes
M3	B-ML	Summit	♀	?	R 2005	M2			Yes	Yes	Yes
M4	Y-ML	Front Face	♂	?	R 2005	M5			Yes	Yes	Yes
M5	Y-MW	Front Face	♀	?	R 2005	M4			Yes	Yes	Yes
M6	O-MR	Front Face	♀	?	R 2005	M7			Yes	Yes	Yes
M7	G-MR	Front Face	♂	?	R 2005	M6			Yes	Yes	Yes
Unbanded 1			?	M6 & M7	B 2005/2006				Yes	?	?
Unbanded 2			?	M6 & M7	B 2005/2006				Yes	?	?
B-RM	B-RM		♂	M6 & M7	B 2005/2006				Yes	No	No
W-RM	W-RM		♂	Turk & Gale	B 2005/2006				Yes	No	No
M-B	M-B		♂	M4 & M5	B 2005/2006				Yes	No	No
Romeo	M-WR	Front Face	♂	M4 & M5	B 2005/2006				Yes	Yes	Yes
Mihitai	R-OM	Summit	♀	?	R 2006	Son of Turk, Morehu				Yes	Yes
BM-OG	BM-OG		♂	M2 & M3	B 2006/2007					Yes	No
BM-OW	BM-OW		♂	M2 & M3	B 2006/2007					Yes	No
Unbanded 3			?	Turk & Gale	B 2006/2007					Yes	?
Unbanded 4			?	M4 & M5	B 2006/2007					Yes	?
Unbanded 5			?	M4 & M5	B 2006/2007					Yes	?

Bird	Bands	Territory	Sex	Parents	Year Born/Released	Paired With	Located 03/04	Located 04/05	Located 05/06	Located 06/07	Located 07/08
Unbanded 6			?	Son of Turk & Mihitai	B 2006/2007					Yes	?
Mapara	W-GM	Summit	♀	?	R 2007	Unbanded					Yes
Unbanded 7			?	M4 & M5	B 2007/2008						Yes
Unbanded 8			?	M4 & M5	B 2007/2008						Yes
Unbanded 9			?	Turk & Gale	B 2007/2008						Yes
Unbanded 10			?	Turk & Gale	B 2007/2008						Yes
Unbanded 11			?	M2 & M3	B 2007/2008						Yes
Unbanded 12			?	M2 & M3	B 2007/2008						Yes
Unbanded 13			?	?	B 2007/2008						Yes

Appendix 2

Appendix Two: All Element Types Found, their Categories and Use by Pairs. Yes = indicates if this pair uses the element type.

Element Type	M1	M2	M4	M5	A2	R18	BG	MPF	MPM	Romeo	Poutama
A	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes		Yes	Yes
B1	Yes	Yes	Yes	Yes	Yes	Yes	Yes			Yes	Yes
B2			Yes		Yes	Yes		Yes		Yes	Yes
C	Yes	Yes	Yes	Yes	Yes			Yes		Yes	Yes
D	Yes	Yes		Yes	Yes	Yes					
E	Yes	Yes	Yes	Yes	Yes	Yes					
F	Yes	Yes	Yes	Yes	Yes		Yes	Yes		Yes	
G1	Yes	Yes	Yes	Yes	Yes	Yes				Yes	
G2		Yes			Yes						
G3						Yes	Yes			Yes	
H	Yes	Yes	Yes	Yes	Yes		Yes				
I1	Yes	Yes	Yes	Yes	Yes					Yes	
I2				Yes							
J	Yes	Yes	Yes	Yes							
K	Yes	Yes	Yes	Yes	Yes	Yes		Yes		Yes	Yes
L	Yes	Yes	Yes	Yes							
M		Yes	Yes	Yes							
N			Yes								
O					Yes	Yes					
P					Yes	Yes		Yes		Yes	Yes
P2											Yes
Q					Yes						
S							Yes		Yes		
U							Yes				
V							Yes				
W							Yes				
X							Yes		Yes		
Y							Yes		Yes	Yes	
Z							Yes		Yes	Yes	
AA							Yes				
BB							Yes		Yes		
CC							Yes		Yes		
DD							Yes				
EE									Yes		
FF									Yes		
GG									Yes		
HH									Yes		
II									Yes		
JJ									Yes		

Element Type	M1	M2	M4	M5	A2	R18	BG	MPF	MPM	Romeo	Poutama
KK									Yes		
LL									Yes		
MM									Yes		
OO											Yes
PP											Yes
QQ											Yes
RR											Yes
SS											Yes
TT											Yes
UU											Yes
VV											Yes
WW											Yes
XX											Yes
YY											Yes
ZZ											Yes
AAA									Yes		
BBB										Yes	
CCC											Yes
T1	Yes	Yes	Yes	Yes	Yes	Yes		Yes		Yes	Yes
T2	Yes	Yes	Yes	Yes		Yes		Yes		Yes	
T3	Yes	Yes	Yes	Yes	Yes			Yes			
T4	Yes	Yes	Yes	Yes						Yes	
T5	Yes	Yes	Yes	Yes	Yes						
T6	Yes	Yes	Yes					Yes		Yes	
T7		Yes	Yes	Yes							
T8		Yes	Yes								
T9		Yes	Yes								Yes
T10		Yes	Yes								
T11		Yes	Yes			Yes					
T12				Yes			Yes				
T13					Yes						
T14					Yes						
T15					Yes						
T16						Yes	Yes				
T17						Yes	Yes				
T18						Yes					
T19						Yes					
T20						Yes					
T21						Yes					
T22							Yes		Yes		
T23							Yes				
T24							Yes				
T25							Yes				
T26							Yes				

Element Type	M1	M2	M4	M5	A2	R18	BG	MPF	MPM	Romeo	Poutama
<i>T27</i>								Yes			
<i>T28</i>								Yes			
<i>T29</i>											Yes
<i>T30</i>											Yes
<i>T31</i>											Yes
<i>T32</i>											Yes
<i>T33</i>											Yes
<i>T34</i>											Yes
<i>T35</i>											Yes
<i>T36</i>										Yes	
<u>TC1</u>	Yes	Yes	Yes	Yes	Yes	Yes		Yes		Yes	Yes
<u>TC2</u>							Yes		Yes		
<u>TC3</u>											Yes

Plain = Elements with multiple harmonics, **Bold** = Pure Tones, ***Bold Italics*** = Frequency Sweeps, *Italics* = Took, Underlined = Clicks

Appendix 3

Appendix 3: All Phrases Identified in Lag Sequential Analysis – Element - element

M1	M2	M4	M5	A2	R18	BG	MPF	MPM	ROMEO	POUTAMA
K-T1-TC1	K-T1-TC1	K-T1-TC1		K-T1-TC1	K-T1-TC1		K-T1-TC1		K-T1-TC1	K-T1-TC1
H-I1-H-T5	I1-H	H-I1-H								
G1-G1-G1	G1-G1-G1	G1-G1-G1		G1-G1-G1-P					G1-G1	
D-E	D-E			D-E	P-D-E					
A-T4-C	T4-C	T4-C-T7-A	T4-C							
B1-T2		B1-T2								
T5-F	T5-F-T7			T5-F						
J-I1	J-I1									
	G2-G2-G2			O-G2-G2-P	G1-G1-G2-G2-G2					
		A-E-F								
		I1-I1								
			T3-B1							
			B1-B1							B1-B1
				I1-A						
				B2-C						
					T17-O					
					B2-T16-A					
							F-A			
							T6-T6			
							T28-T28			
							A-A			
							A-P			A-P-C

M1	M2	M4	M5	A2	R18	BG	MPF	MPM	ROMEO	POUTAMA
								Y-Z	Y-Z	
								GG-HH		
								T22- TC2- TC2-S		
								II-II		
									BBB-T36	
									P-C	
										W-WW
										UU-T34
										T9-T9
										P2-QQ-RR- CCC-CCC- CCC
										SS-TC3- TC3-TT