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Song and Territorial Behaviour of Male-Male and Male-Female Pairs of the North Island Kokako (*Callaeas cinerea wilsoni*)

A thesis
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by

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Abstract

Male-male pairing has been previously described for captive individuals of two duetting passerines. The sexually monomorphic North Island kokako (Callaeas cinerea wilsoni) is an endangered forest bird which is declining on the mainland of New Zealand, and is the only duetting species for which male-male pairing is known to be common in wild populations. This thesis determined whether male-male kokako pairs can be distinguished from male-female pairs on the basis of song and territorial behaviour. The first study began with a detailed analysis of the contributions that male-female pair members make to duets (n=11 pairs), with a focus on their use of fundamental frequencies and the proportion of the duet that was sung by each sex. Whole male-female songs were also examined in terms of the combined fundamental frequencies used by the pair as a unit (n=16 pairs). Females typically sang less in the duet than males (8 of 11 pairs) and they had a higher song pitch than males (5 of 5 dialects examined). However, some females sang much more than others and they sang at male-typical song pitches. The duet analysis led me to predict that male-male pairs divide the duet more equally and sing less at female-dominated song pitches than male-females pairs. The predictions were then tested on confirmed (n=3) and suspected (n=6) male-male pairs. One confirmed male-male pair only met the first prediction, while one confirmed and four suspected male-male pairs only met the second prediction. One suspected male-male pair met both, and the remaining two male-male pairs (one confirmed, one suspected) met neither of the predictions. These results are discussed in terms of being able to identify male-male pairs, and in terms of the adaptive significance of male-male pairing. Male-male pairs may be identified using the predictions, however some male-female pairs might also meet the predictions in some dialects which could limit the reliability of this as a sexing technique. The second study examined the territorial responses of male-male pairs (n=6) and male-female pairs (n=7) to determine whether kokako pairs can 'range' song and to identify other ways of distinguishing between these pair types. Pairs were presented with their own songs in an undegraded and a degraded form, and data were recorded on intra-pair spacing, song matching, song output, and the pair's movements in relation to the speaker. Kokako showed no differences in their response to the two treatments, nor did male-male pairs respond differently to male-female pairs. These results were attributed to an insufficient sample size, and the fact that the birds were able to have close-range experience with the speaker during playback which could have provided all pairs with obvious cues to locating the source of the sound. From the outcome of the first study, I recommended that the use of the predictions be confined to non-breeding kokako pairs because of the risk of encountering females that sing male-dominated song, and that the stability of kokako song features be assessed to determine whether patterns which currently distinguish male-male from male-female pairs in a population can be applied in the long term. From the outcome of the second study, I recommended that kokako song studies should first focus on obtaining an understanding of the structure of song and of the use of individual song elements, before further playback experiments are attempted. Recommendations with regard to the use of playback in population surveying were also given, with particular regard to ensuring that the source song is coherent to the birds.

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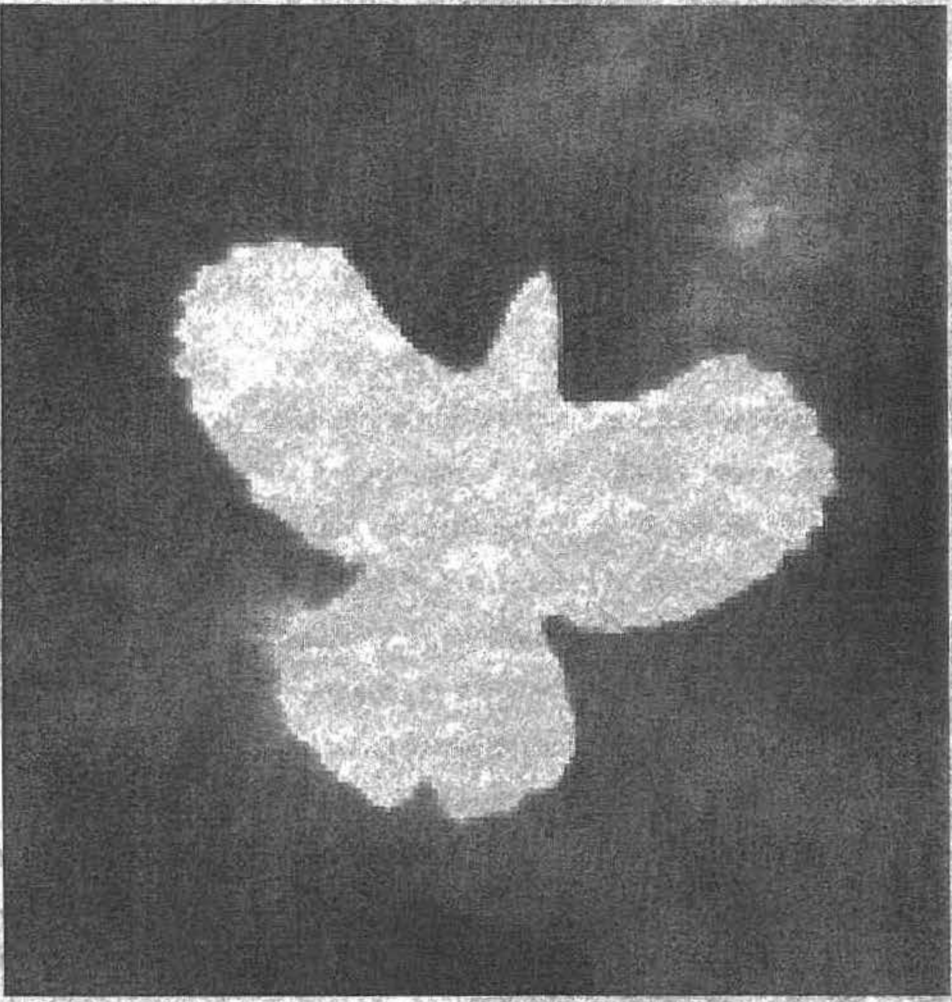
CHAPTER ONE



INTRODUCTION

Chapter 1

Introduction

1.1 Song theory

1.1.1 Definition and proposed functions of bird song

Birds produce a wide variety of sounds that can be divided into calls and song (Catchpole 1986). By definition, songs are 'long complex vocalisations produced by males in the breeding season', while calls are 'shorter and simpler and are produced by both sexes throughout the year' (Catchpole 1986; Catchpole & Slater 1995). Song is produced by a wide range of avian groups occupying many different latitudes, and it occurs in a variety of habitats. In fact, as I will discuss later, not all songbirds comply with the definition prescribed above. Nonetheless, one of the most prominent features of singing behaviour, that is common to a majority of species, is its high delectability. Because of this, song is thought to pose a high cost to singers both in terms of energy consumption and in the obvious risk of attracting predators (e.g. great tits *Parus major*(Kacelnik 1992)).

The most common targets of passerine song are thought to be territorial competitors and current or prospective mates (Kroodsma & Byers 1991; Lampe & Espmark 1994). In American wood warblers (Parulinae), different song subsets within an individual's repertoire are directed toward different targets (Spector 1991; Catchpole & Leisler 1996). Male grace's warblers *Dendroica graciae* preferentially use two distinct types of singing behaviour, one with a strong intersexual component (used before pairing and whenever males interact with females) and the other being strongly intrasexual (used mainly by paired males during interactions with neighbouring males) (Staicer *et al.* 1996). In other species, males may possess many songtypes in their repertoire. Some species may use some songtypes more often in certain contexts (e.g. plain titmice *Parus inornatus* (Johnson 1987)), while other species appear to use their songtypes more generally (e.g. great tits, pied flycatchers *Ficedula hypoleuca*, and swamp sparrows *Melospiza georgiana* (Searcy *et al.* 1982; Lambrechts & Dhondt 1986; Lampe & Espmark 1994)). In pied flycatchers and great tits, male success in both territorial occupancy and mate attraction is positively related to the size of the repertoire (Lambrechts & Dhondt 1986; Lampe & Espmark 1994), and this has also been shown in red-winged blackbirds *Agelaius phoeniceus*, (Searcy 1990; Searcy & Yasukawa 1990), western meadowlarks *Sturnella neglecta* (Aweida 1995) and northern mockingbirds *Mimus polyglottos* (Logan & Hyatt 1991). Whether the evolution of large repertoires is the direct result of intersexual selection or intrasexual selection is not well understood. This may be because of the difficulties of trying to determine the influence of male quality on female choice, without including territory quality (Lampe & Espmark 1994).

Three theories have been proposed that may account for the effectiveness of large song repertoires in territorial defence (Aweida 1995). The first of these is called the versatility-continuity relationship or 'monotony threshold hypothesis', and it implies that the singing of highly variable songs decreases the chance that a potential rival will habituate to and eventually ignore the singer (Hartshorne 1956). The second idea is that a large number of songtypes may create the illusion of more than one singer, and that this deters any new birds seeking to establish a territory in the vicinity (Krebs 1977). This idea, called the Beau Geste hypothesis, offers a functional explanation for the monotony threshold hypothesis in that newcomers may attempt to estimate the density of a population by the rate at which they habituate to the songs there (Krebs 1977). The third explanation is that large repertoires enable territory holders to engage in song matching, whereby they respond to a potential intruder by singing the same songtype (Falls *et al.* 1982). As a result, non-neighbours which do not possess the full repertoire of the resident bird will find it more difficult to match song and will therefore provide a cue that can trigger rapid escalation to a fight (Craig & Jenkins 1982).

It is thought that strangers are more threatening to a territorial occupant than its neighbours, because they do not have a territory and could challenge the resident bird for its own (Searcy *et al.* 1982). Neighbour-stranger discrimination has been demonstrated in white-throated sparrows *Zonotrichia albicollis* (Falls & Brooks 1975), swamp sparrows (Searcy *et al.* 1981), great tits (Falls *et al.* 1982), black-headed grosbeaks *Pheucticus melanocephalus* (Ritchison 1983), song sparrows *Melospiza melodia* (Stoddard *et al.* 1991), American redstarts *Setophaga ruticill* and yellow warblers *Dendroica petechia* (Weary *et al.* 1992). The ability to discriminate neighbours from strangers is shown by a highly aggressive response toward stranger song compared with a much lower response toward neighbour song (Falls *et al.* 1982; Weary *et al.* 1992), but if the neighbour's song is played from the opposite side of the resident bird's territory from where it is normally heard, the two responses become very similar (Falls & Brooks 1975; Stoddard *et al.* 1991).

Song matching, or matched countersinging, not only represents the transfer of information on 'local knowledge' to enable strangers to be detected before they become established, but it also provides cues between familiar birds as to each other's exact locations. This ability for the bird to pinpoint the distance of a singing conspecific is called 'ranging' (Morton 1986).

1.1.2 Ranging and dialects

As a song travels through its environment it is altered in two ways. The first is an overall decrease in sound energy, an effect known as spherical divergence, and this accounts for a drop of 6 decibels in perceived amplitude for every doubling of distance from the source. The second way in which sound is altered is known as habitat induced degradation, whereby certain attributes of the song are lost or altered by the environment through reverberation and absorption (Morton 1975). Degradation is thought to be the main cue used by songbirds to estimate the distance of singing conspecifics (Simpson 1985; McGregor *et al.* 1983; Richards & Wiley 1980).

Accurate ranging by birds is thought to be achieved by comparison of the perceived song with an undegraded version stored in the perceiver's long-term memory, often referred to as a 'standard' (Morton & Page 1992). Standards are derived from songs learnt from the bird's parents, and from its territorial neighbours (Morton *et al.* 1986). Great tits show an ability to range when the perceived songtype is present in the bird's own repertoire (McGregor *et al.* 1983) but this effect is much reduced when birds are presented with unused songtypes. Conversely, western meadowlarks are able to range songs which are sung by their neighbours but are absent in their own repertoires (McGregor & Falls 1984). The need to range the songs of neighbours is thought to be one reason why males of many bird species learn more songs than they actually sing (McGregor *et al.* 1983; McGregor & Falls 1984).

Neighbouring populations of the same bird species may have subtle differences in habitat or climate which may select for different sound properties (Catchpole & Slater 1995). If the movement of birds from one population to the other was hindered or restricted, then over a period of generations those sounds that were less distinctly heard between neighbouring birds within each population will tend to disappear from the song repertoire (Mundinger 1982). The cultural transmission of song elements best suited to the local habitat is thought to result in the songs of one population sharing certain structural characteristics that are different from the songs of the other population. This results in the formation of song neighbourhoods, or 'dialects' (Nottebohm 1985; Catchpole 1986). Dialects are a taxonomically widespread phenomenon and are known to occur in non-passerine families as well as in passerines (Mundinger 1982). Although dialects are most obvious in songbird species with small repertoires (e.g. white crowned sparrows *Zonotrichia leucophrys oriantha*, which have just one songtype (Baptista & Morton 1982)), they also occur in species with larger repertoires. For example, Catchpole & Rowell (1993) identified two dialects within the same population of European wrens *Troglodytes troglodytes*. This population had 15 songtypes, 12 of which were exclusive to either dialect. An interesting feature of this study was that the two dialects were separated by a lake which was just 200 metres wide. A minor boundary such as this may not affect dispersal between two adjacent areas, but it may be sufficient to socially isolate the groups by preventing them from interacting on a regular basis. An experiment incorporating song playback with sex hormone implants showed that wild female brown-headed cowbirds *Molothrus ater* conducted the strongest solicitation displays toward songs of males from their own dialect area (O'Loghlen & Rothstein 1995). Also, first-year male indigo buntings can increase their mating success by matching the song of an adult on a neighbouring territory (Payne 1982). Hence a learned female preference for the predominant local songtypes may be a major factor governing the stability of dialects, since this makes it advantageous for males to conform to the local song (O'Loghlen & Rothstein 1995). There is, however, evidence which appears to contradict this idea, one point in particular being that females often select mates in areas outside of their natal dialect (Baptista & Morton 1982; Payne & Westneat 1988; O'Loghlen & Rothstein 1995).

1.1.3 Duetting

The song features described so far are for temperate songbird species, whereby only the male sings and defends a territory during the breeding season. However, these features also apply to the tropics, where for many songbird species both sexes participate in territoriality and song (Morton 1996). The joint participation of males and females in singing behaviour is called duetting.

Duetting is a highly co-ordinated display which incorporates both vocal and visual elements (Todt *et al.* 1981; Todt *et al.* 1982; Hultsch & Todt 1984). Duetting species are not confined to the tropics, although it is there that they occur at the highest abundance (Farabaugh 1982; Morton 1996). Apart from song, the most common characteristics of duetters that distinguish them from temperate species are year-round territoriality and prolonged monogamous pair bonds, and these are also thought to be the two main factors responsible for the evolution of duetting (Farabaugh 1982). Also, duetters are often sexually monomorphic, but there are a number of exceptions (such as Cuban grassquits (*Tiaris canora*) (Baptista 1978) and dusky antbirds (*Cercomacra tyrannina*)(Morton & Derrickson 1996)). This suggests that sexual monomorphism is more likely to be an artefact of year-round territoriality and prolonged monogamous pair bonds, rather than an explanation for duetting in itself (Farabaugh 1982).

Permanent territorial occupation (and year-round defence) by duetting species is attributed to a lack of seasonality in the abundance of food resources, enabling birds to remain in the same area instead of having to migrate (Farabaugh 1982). Constraints on food availability in some years may, however, place limits on the number of individuals that can reside on any one territory. Subsequently, participation by females in territorial defence is favoured when the potential loss in reproductive fitness that is associated with allowing other females to share the territory resources is higher than the cost of defence against other females (Farabaugh 1982; Levin 1996b). Having more than one female to a territorial male may benefit the male in terms of potentially doubling his lifetime reproductive success, but there is no such benefit to the female (Farabaugh 1982). Furthermore, co-ordination with the male is thought to be advantageous in territorial disputes because it allows each bird to monitor the activities of its mate, thereby preventing extra-pair fertilisations from taking place, and it also allows each bird to direct their attacks only toward members of the rival pair (Farabaugh 1982; Levin 1996b; Morton & Derrickson 1996).

The role of the pair bond in the evolution of the duet is not clear, perhaps because there is considerable variation among species. One of the earliest theories was that duetting evolved to enable pair members to keep in contact with one another in dense habitats (Hooker & Hooker 1969). This occurs in species which live in auxiliary groups comprising of the principal pair and its close relatives (e.g. stripe backed wrens *Campylorhynchus nuchalis* (Wiley & Wiley 1977) and common crows *Corvus brachyrhynchos* (Brown & Farabaugh 1996)), but it has little relevance in the majority of species whereby duetting takes place with both birds in close visual contact with each other (Farabaugh 1982). Another theory suggests that duetting in tropical environments stimulates and synchronises reproductive condition, because other cues (seasonality, daylength and so on) are not as pronounced or are less predictable (Kunkel 1972). Again, a few species do appear to comply with this idea (e.g. the bou-bou shrike *Laniarius* *ferrugineus* which shows a peak in duetting just prior to the breeding season (Harcus 1977)), but such evidence is sparse. The final theory, called the Coyness model, implies that the learning of a pair-specific duet represents a non-transferrable investment on the part of the learner, in that the song must be perfected before the pair bond is established and mating can take place (Wickler 1980). In many species, however, either pair bonds appear to be relatively transient (e.g. robin chats *Cossypha heuglini* ; Hartlaub (Todt 1975) and golden whistlers *Pachycephala pectoralis* (Brown *et al.* 1994)) or the duet does not seem to require a significant learning period (Farabaugh 1982). The duets of newly paired bay wrens *Thryothorus nigricapillus*, for example, are equally as precise as other pairs' duets, and the birds show no evidence of changing their song to accommodate a new mate (Levin 1996a).

1.2 The North Island kokako

1.2.1 Classification

Kokako belong to the endemic New Zealand wattlebird family, the Callaeidae. This is a far removed family group which includes only two other members, the hiua (*Heteralocha acutirostris*, now extinct) and the saddleback or tieke (*Philesturnus carunulatus*, now only found on predator-free islands) (Turbott 1990). There are two allopatric subspecies of kokako, the North Island kokako *Callaeas cinerea wilsoni*, and the South Island kokako *C. c. cinerea*. The North Island kokako is regarded as endangered, while the South Island subspecies is now presumed to be extremely rare, if not extinct (Turbott 1990).

1.2.2 Distribution and habitat

Once widespread over much of the North Island of New Zealand, North Island kokako (henceforth kokako) are now absent from most forest tracts; there are now thought to be less than 1500 kokako left (Best & Bellingham 1990). Currently there are three regions of the North Island where significant populations of kokako still exist (Heather & Robertson 1994). These include parts of the Bay of Plenty (upper central North Island; including the Mamaku, Horohoro, Kaharoa and Rotoehu forests), the King Country (central North Island; Pureora forest and Mapara Reserve) and the East Cape (northern Te Urewera ranges). Populations derived from mainland stock have also been established on Little Barrier Island (Hauraki Gulf, near Auckland) and on Kapiti Island (near Wellington), and a recent transfer of birds was made from Mapara to Tiritiri Matangi (also in the Hauraki Gulf). Kokako are only able to fly for short distances, and as a result their dispersal between distant populations without human assistance is extremely unlikely (Lavers 1978). Figure 1-1 shows the current range of kokako.

A few fragmented mainland kokako populations occur in Northland and Auckland (e.g. Puketi, Raetea, and Waiopoua/Mataraua forests in Northland, and the Hunua Ranges near Auckland), as well as in southern Waitomo (central North Island) and in northern Taranaki (western central North Island) (Heather & Robertson 1994). However, many of these populations may be near collapse and may not survive for more than a few years into the next century (Rasch 1992).

1.2.3 Description of morphology, locomotion and vocalisations

Adult kokako weigh approximately 230 grams and are around 38 centimetres (bill to tail) in size (Heather & Robertson 1994). Both sexes are identical in appearance and have a slatey-grey body, with a distinctive black mask over the eyes and a pair of fleshy wattles which originate from the edges of the gape and extend to under the base of the bill. The wattles are small and lilac in colour in the juvenile bird, but they increase in size and change to a deep ultramarine as the bird matures (Figure 1-2). Due to their short wings, kokako cannot sustain level flight for more than around 20 metres. Flight is mainly limited to flapping and gliding between trees, and diving down steep slopes or from the tops of tall emergent trees (Hay 1980). The tail is slightly downcurved and can be fanned to slow the bird during landing. Kokako may spend a significant proportion of their time in the forest understorey as well as in the canopy, and so must traverse frequently between the different forest levels.

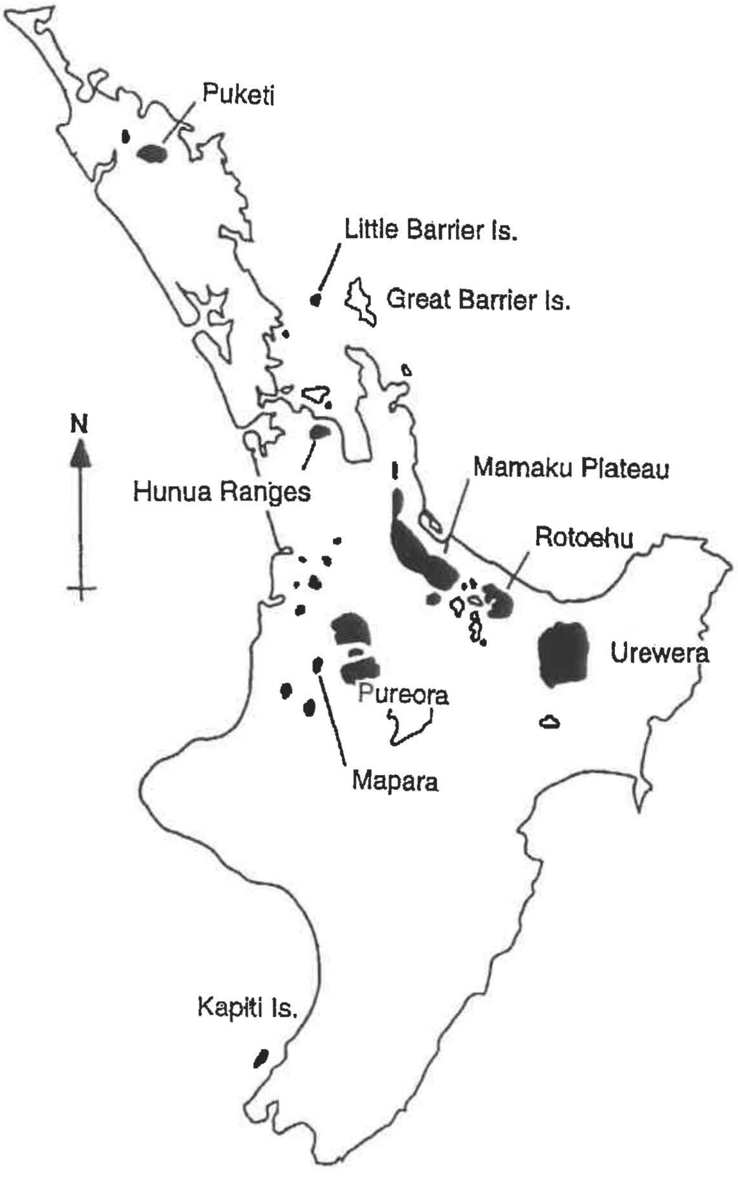
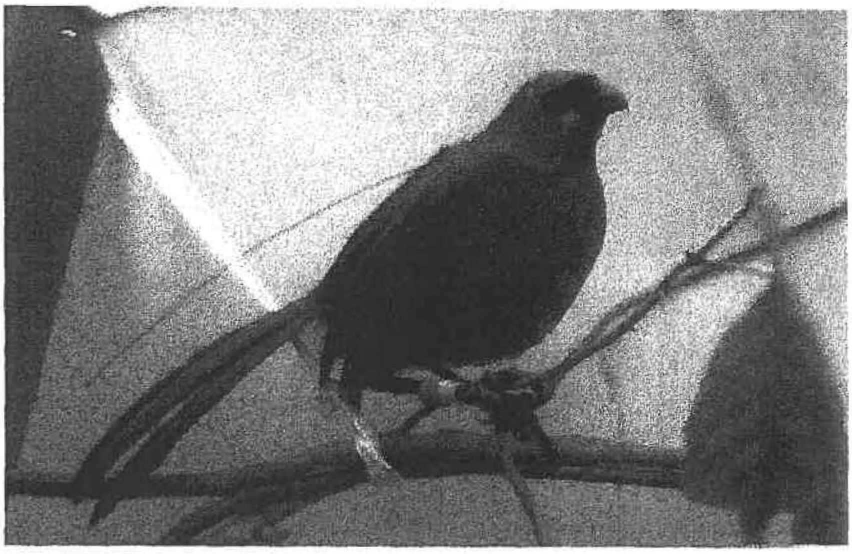


Figure 1-1 Current distribution of kokako (marked in black)

To move vertically and horizontally through their habitat, which is often very dense, kokako rely mostly on their ability to climb along branches and vines.

Two types of locomotion have been named for kokako, these being 'laddering' (rapid upward leaping through the branches) and 'squirreling' (running through the canopy). The wings are used for balance, while kokako also have powerful legs and long, sharp talons which are well suited for this type of locomotion. The feet are also used to hold food during feeding activities, in much the same way that parrots use theirs (Hay 1980).

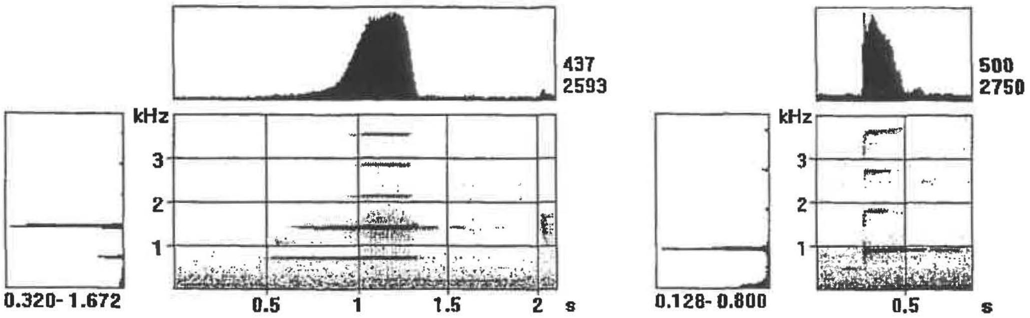


(photo: J. McLeod)

Figure 1-2 Female kokako *(Callaeas cinerea wilsoni)* from the Mapara Reserve. The photograph is of 'Cloudsley Shovel', captured and held in a tent prior to transfer to another population. The object attached to the bird's back just above the wing is a 'weak link' radio transmitter, which will enable the bird to be located and tracked in its new habitat. Such transmitters are designed to detach if the bird becomes ensnared.

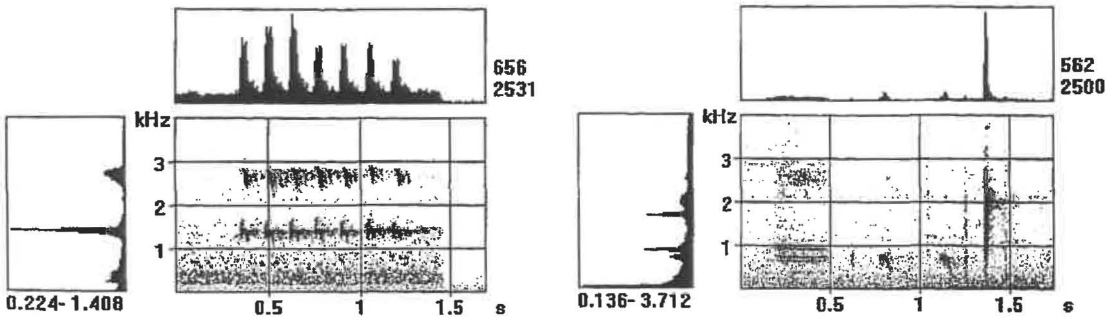
Singing activities tend to occur near places frequented by the birds for feeding, and in most cases kokako sing to other neighbouring birds from the closest tall trees available to them (Best & Bellingham 1990). Song is most frequent in spring, summer and autumn and generally occurs during the first and last quarters of the day (Best & Bellingham 1990).

Kokako song is characterised by its high volume, marked amplitude modulation and an unmistakably sonorous timbre. There is generally very little frequency modulation (Hughes 1981). The song is presented in an ordered sequence of chimes and long, high-intensity pure tone notes. These are combined with rapid 'chitter' elements, low-intensity low-frequency 'tooks' and occasional clicks and 'whurs'. Kokako song elements are represented as sonagraphs in Appendix 1, and examples of each note type are shown in figure 1-3.



a) Example of a pure-tone note (mn2d)

b) example of a chime (r2d)



c) Example of a chitter (mnCall7)

d) Example of a song element combining a whur, two tooks and a click (mn1a)

Figure 1-3 Examples of four kokako song elements (see beginning of Appendix 1 for interpretation of sonagram windows and an explanation of song element notation)

A general feature of kokako song and calls is that there is dissimilarity between regions, yet within a region there may be very little variation in the structure or the sequencing of the song (Hughes 1981; pers. obs.). That is, kokako have obvious dialects. Furthermore, there may be more than one dialect within the same interbreeding population, an example being the Mapara Reserve. Although this population covers little more than ten kilometres from one side to another, it has at least two distinct dialects without any elements occurring in common to both. Birds within each of these dialects sing almost identical songs. I have named the dialects 'Mapara North' and 'Mapara South', each of which has (in addition to their distinct songs) their own accompaniment of calls. There may also be a third dialect at Mapara, which I have tentatively named 'Mapara Central' based on my sample of two pairs from this area. This song combines elements from both north and south with several new elements, all of which occur in a sequence that is not heard in either of the other dialects. Mapara Central also has a number of unique calls. A map of the Mapara Reserve is presented in figure 1-4.

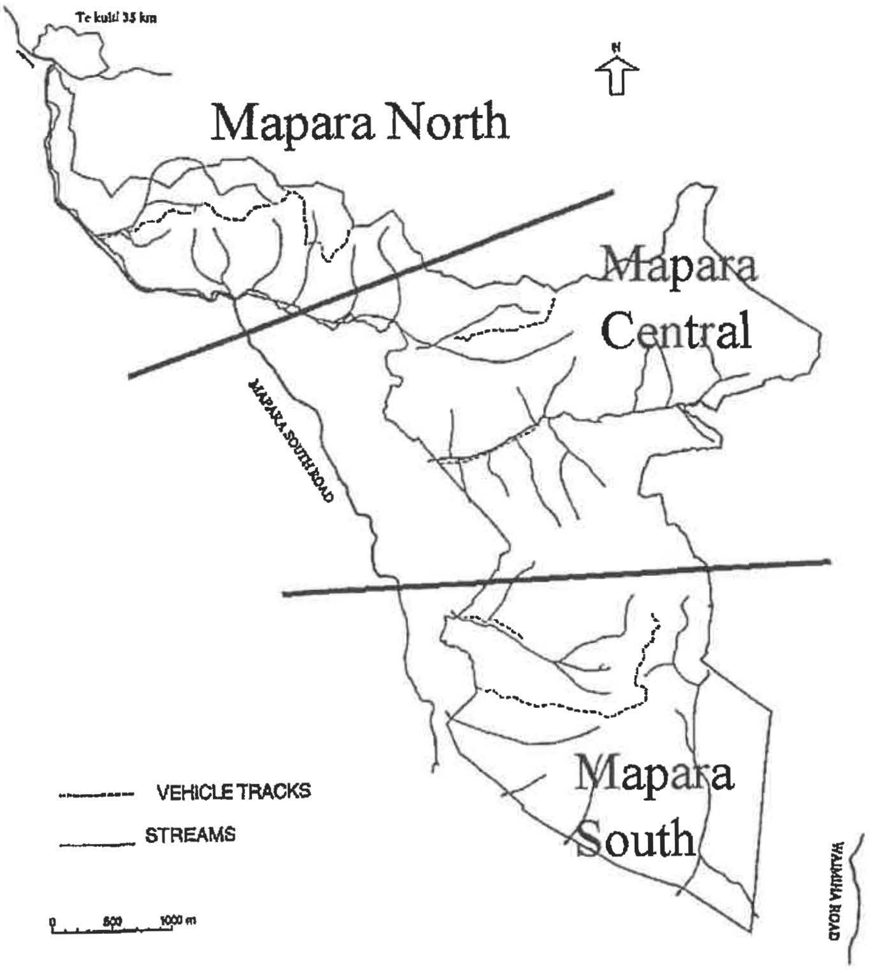


Figure 1-4 Map of the Mapara Reserve showing divisions into forest tracts (adapted from Hughes (1981)). (see Appendix 3 for locations of pairs within each block)

Kokako songbouts are highly variable in length and are composed of several song cycles. I have called each song cycle of a particular dialect's song a 'rendition'. Renditions are divided into verses, which are usually separated in time by at least the equivalent duration of a verse. Each song verse is divided into song phrases, and then into song syllables. A song phrase was defined as a group of syllables, whereby the timing between each syllable did not change from one rendition to the next. Some phrases may be comprised of a single syllable if they are not produced with other song elements in a temporally consistent fashion. A song syllable is the smallest song unit, and for the purpose of this thesis is described as a continuous trace on the sonagraph which does not undergo a major shift in fundamental frequency (that is, a shift of more than approximately 500 hertz within the space of 0.5 seconds). Hence syllables are often discrete units, although some pure tone notes may be composed of more than one syllable (see figure 1-5). Dividing notes in this way allowed me to take measures of their fundamental frequency, which is the basis for the song study in chapter 2. For any one pair, the timing between phrases is generally much shorter and less variable than the timing between verses, while the timing between syllables is the least variable of all song intervals. An explanation of the

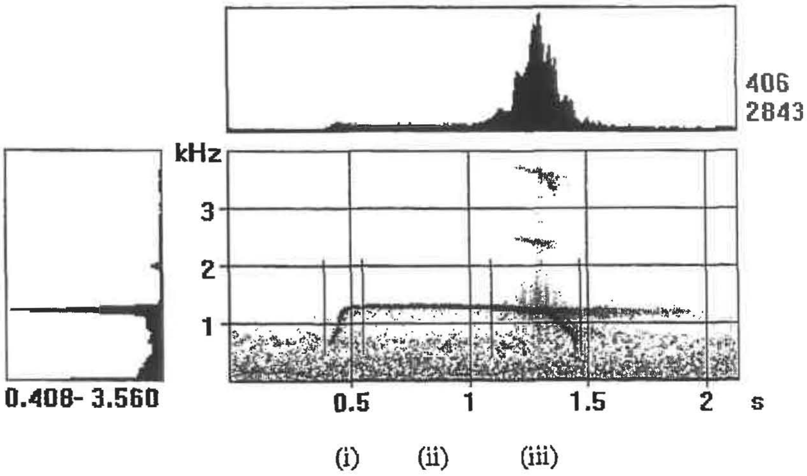


Figure 1-5 Sonagram of the Urewera 'woo' (phrase u4b(i-iii)), showing division into syllables (see beginning of Appendix 1 for interpretation of sonagram windows and an explanation of song element notation)

notation I have used to classify song elements is provided at the beginning of Appendix 1.

Many of the high amplitude components of kokako song, in particular the pure tone notes and chimes, are accompanied by multiple harmonics (Hughes 1981). Subsequently, some pure tone phrases can undergo a gradual shift of fundamental frequency from one harmonic to the next (e.g. phrase 'ms4f' and phrase 'h4a' in Appendix 1-A and 1-F, respectively), while other phrases can shift more abruptly (e.g. phrase 'r2a' in Appendix 1C).

Any calls that occur throughout the song can be classified in a similar manner to phrases. Specific calls may be given just before full song begins (e.g. call 'msCall1' in Appendix 1-A), while these and other calls may be given during inter-song intervals and when the songbout is winding down (Hughes 1981; pers. obs.). Some calls which are heard outside the song context may also be given in a stereotypical manner within the song, which suggests they have been incorporated as song syllables by some pairs (e.g. call 'mnCall1' in Appendix 1-B may be given in place of phrase 'mn4b' in some cases).

Kokako duet so that song elements are usually divided between the birds (pers. obs.). However, simultaneous production of particular syllables will occur quite often within the songs of some pairs (pers. obs. ; J. Hudson pers. comm.). The song is usually produced with both pair members in the same tree, or in adjacent trees, at mid- to upper-canopy level (pers. obs.). While males generally deliver song from a prominent perch in the direction of singing neighbours, females do not appear to sing from particularly prominent positions, nor do they appear to face in any preferred direction during song (Hughes 1981; pers. obs.). Almost all song elements and calls are accompanied by bow-wingflap displays, expansions of the chest cavity, and head, bill and neck movements (Hughes 1981; pers. obs.).

1.2.4 Habitat, territoriality and diet

Kokako reside on year-round territories in two types of forest: mature hardwood forest dominated by tawa *Beilschmiedia tawa*, such as Mapara and Hunua; and podocarp-dominated forest with tall tawa such as Te Urewera (Lavers 1978). Although products from podocarp trees such as rimu do not make up a large component of kokako diet, podocarps are favoured by the birds as song posts (Hay 1980). The altitude of kokako habitats ranges from 195-285m above sea level for Rotoehu, to 300-560m for the Mapara Reserve, and around 400-690m for the Hunua Ranges and Te Urewera (Hay 1980). Many kokako territories can be found close to canopy gaps or forest margins, such as alongside landslips and roads (Lavers 1978).

Territories are of variable size, generally around 10 hectares but in some cases up to 30 hectares, and are held by single and paired kokako throughout the year (Hay 1980; Innes *et al.* 1996). Kokako generally concentrate their activities on upper ridge crests and flanks, although different areas of the territory are used at different times of the year depending on nesting and on the seasonal abundance of particular food species. As a result, kokako are active over most of their home range during late winter and early spring, while only relatively compact areas are used over summer and autumn (Best & Bellingham 1990; Hay 1980). Single territory holders are usually male, while single females are usually transient (Hay 1980). However, females in established pairs have been known to attain a new male mate within the same territory. This has occurred for cases where the original male has never been resighted and also in situations where the previous mate has resurfaced elsewhere (I. Flux, in. litt.). Both sexes may traverse over large distances well outside of the natal dialect in order to establish a territory or to find a mate (J. Hudson, pers. comm.; P.Bradfield, pers. comm.).

Kokako diet is known to consist of more than 85 plant and invertebrate species. Composition of diet varies seasonally, depending on which species are most abundant, however kokako can also be very selective towards relatively rare food species. Much of the diet consists of fruit and leaves, with leaves constituting a significant portion of the diet over the winter and spring when fruit is unavailable. Kokako diet is also supplemented by flowers, moss, invertebrates (mainly 6-penny scale insects *Ctenochiton viridis* and bag moths *Liothula omnivorus*) and bark. Feeding activity per hour is highest over winter (up to 48 percent of all activities) and lowest over summer (up to 21 percent), probably due to the smaller range of foods available over the colder months (Hay 1980). The need to spend proportionally more time feeding is also reflected in a decrease in singing during the winter (Hay 1980; Best & Bellingham 1990).

1.2.5 Breeding and conservation

Kokako lay their first clutch during October to December, usually in November. In the weeks prior to nesting, kokako pairs become very difficult to follow, and this makes observations of kokako courtship behaviour and nest-building activities relatively scarce (Innes & Hay 1995). Males have been seen to perform a courtship display called the 'Archangel display', whereby the bird fans its wings and tail for several seconds whilst giving a 'chirr' call (Innes & Hay 1995). Observations of actual matings are rare for kokako, although a detailed account was given for a pair in the Hunua Ranges. When presented with playback, this pair did not approach the sound, but instead circled the area several times. The male then proceeded to mount the female with vigorous wing flapping and calling (the latter being described as a 'bubbling' sound). Afterwards, the pair faced each other on the same branch and bowed to each other several times in rapid succession (Lovegrove 1974).

In the weeks leading up to nest building, kokako pairs (particularly the females) concentrate their activities within a small subsection of the territory, and it is here that the nest is built (Innes & Hay 1995; J. Taylor, pers. com.). The female takes sole responsibility for building the nest, as well as incubating the eggs and brooding the young, although the male feeds the female at or near the nest throughout. Kokako have a long nesting period which may last for up to seven weeks. Clutches usually comprise of three eggs, which are grey with brown spots (Innes & Hay 1995).

A kokako pair may produce as many as three broods in the same season, and this has been shown to be directly related to the abundance of plant species in fruit during that particular year (Innes *et al.* 1996). Heavy fruiting of several food species (including *Coprosma spp.*, kotukutuku *Fuchsia excorticata*, nikau *Rhopalostylis sapida*, kiekie *Freycinetia baueriana*, bush lawyer *Rubus cissoides*, tawa, pigeonwood *Hedycarya arborea* and podocarps) occurred over the 1994/1995 nesting season throughout much of the North Island, and this resulted in a highly productive kokako breeding season for both the Mapara and Hunua populations (Bradfield & Flux 1996; DOC, unpub. report 1996).

Even during breeding seasons with only mediocre food availability, kokako pairs which are known to be capable of producing young very seldom make no attempt to breed. Yet within a population, certain kokako pairs may never attempt to breed even in phenologically good years. These non-breeding pairs differ neither in weight nor diet to breeding pairs, hence the cause cannot be attributed to lack of condition. Instead, it is now understood that such pairs are in fact likely to be male-male (Innes *et al.* 1996).

Male-male kokako pairs are thought to occur because of an excess of male birds in the population. Evidence of their existence is supported primarily by breeding records (either from the length of time a pair has failed to make any attempt to breed, or from the outcome of re-pairings whereby each of the birds of previously unknown gender were able to father a clutch) and from comparing leg measurements with birds that are known to be males (Innes *et al.* 1996).

An excess of males, or more precisely a loss of females, is thought to arise from a high risk of nest predation. Females, to their own detriment, are extremely protective of older chicks, and are thought to be particularly susceptible to nest predators (Innes *et al.* 1996). Also, the kokako nesting period coincides with seasonal increases in several mammalian predators, including ship rats *Rattus rattus*, feral cats *Felis catus* and stoats *Mustela erminea* (Innes & Hay 1995). The main predators of kokako nestlings and eggs are now known to be the Australian brush-tailed possum *Trichosurus vulpecula*, ship rats, and the Australasian harrier hawk or kahu *Circus approximans*. Possums and rats are thought to be one of the most significant nest predators because they are ubiquitous in all kokako habitats on the mainland (Innes *et al.* 1996). Kahu may only be a problem in populations that have a fragmented canopy since this means that kokako nests are generally more exposed (H. Downham, pers. comm.). Another predator which may occasionally attack kokako nests is the stoat, although evidence of this occurring is not substantial (Innes *et al.* 1996).

Widespread habitat destruction by logging has had a major impact on dissecting the kokako range and lowering the quality of kokako habitat (Lavers 1978; Rasch 1992). Presently, however, degradation of kokako habitat is almost entirely attributed to introduced mammals. Kokako populations which have received intensive pest management have considerably greater plant diversity, and this may be reflected by a smaller mean kokako territory size in comparison to less replete areas (Bradfield & Flux 1996; Innes *et al.* 1996). As well as being the most significant nest predators of kokako, possums prefer many of the same plant food species that kokako eat, such as five-finger *Pseudopanax arborea*, hangehange *Geniostoma rupestre*, kohekohe *Dysoxyhim spectabile*, mahoe *melicytus ramiflorus*, pigeonwood, raukawa *Raukaua edgerleyi*, raurekau, rewarewa *Knightia excelsa* and supplejack *Ripogonum scandens*. Possums also defoliate a large number of canopy species causing a reduction in cover, and they browse heavily on northern rata *Metrosideros robusta*, which is a favoured song post for kokako (Best & Bellingham 1990). Goats *Capra hircus* are another major competitor for many kokako food species (DOC, unpub. report 1995).

1.3 Aims and format of thesis

This thesis investigates differences in song and territorial behaviour between male-male and male-female kokako pairs. To date, only two other songbird species have been known to demonstrate male-male pairing, neither of which occurred under wild conditions or with such apparent regularity as kokako male-male pairs. Consequently, this is the only known species in which male-male pairing can be closely studied without using captive animals, or having to resort to an extremely small sample size. Conservation management of kokako has reached the stage where steps can be taken to restore declining populations, however there is currently no way to determine the sex ratios of unmanaged populations without having to capture the birds. This presents a major obstacle to the restoration of regionally diverse kokako populations on the mainland, since it is hard to know whether a population needs urgent help from outside to recruit female numbers. Hence the main objective of this thesis was to provide a reliable means of distinguishing male-male pairs from male-female pairs, solely on the basis of differences in their respective behaviours.

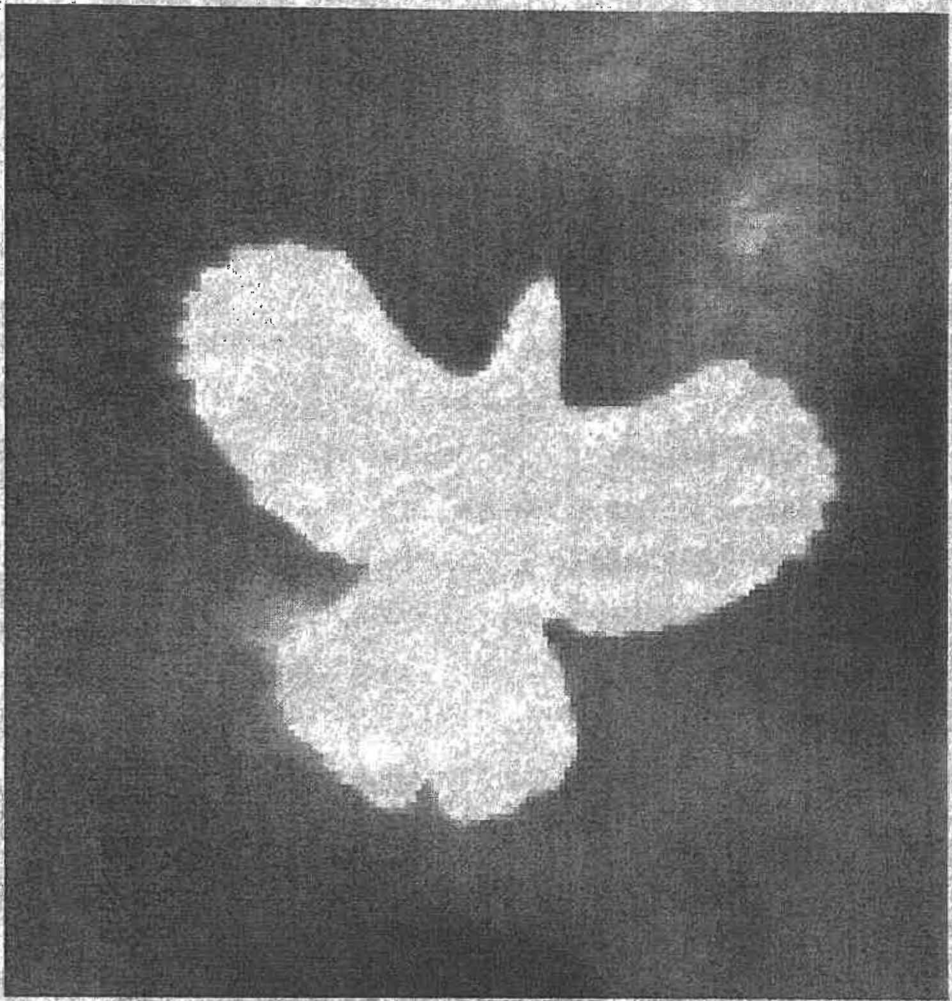
Chapter two is an observational study of kokako duets which seeks to determine song patterns that distinguish male-male pairs from male-female pairs. The approach involved making extensive recordings of the songbouts of the few known available male-male pairs, and their confirmed male-female neighbours. Time-frequency data were then extracted using a sonagraphic analysis program. I compared the songs of male-male and male-female pairs and pair members for trends in their use of the fundamental frequency, particular song components, and in the amount of time spent singing by pair members. Each male-male pair was treated separately, due to the small sample size, while data from male-female pairs were pooled to examine overall patterns.

In chapter three, I conducted a playback experiment which compared the response of male-male and male-female kokako pairs to their own songs in an undegraded form, to the same songs in a degraded form (that is, to simulate a close intruder and a far intruder, respectively). By incorporating both male-female and male-male pairs, I determined whether male-male pairs behaved differently to male-female pairs in a territorial context. I also did this to determine whether kokako use habitat-induced degradation, rather than visual cues or song amplitude, to range conspecifics.

The fourth and final chapter summarises results from the song study and the experiment. Conclusions, theoretical applications, suggestions for future kokako song research and recommendations to managers are discussed.

The thesis is formatted so that the two main chapters, with some modification, can each be submitted as scientific publications. Because each chapter stands as an independent unit, there will be some repetition. However, I have provided a general introduction and a 'conclusions and recommendations' chapter in order to integrate the document as a thesis.

CHAPTER TWO



DIFFERENCES BETWEEN THE DUETS OF MALE-MALE AND MALE-FEMALE KOKAKO PAIRS

Chapter 2

Differences Between the Duets of Male-Male and Male-Female Kokako Pairs

2.1 Introduction

Under captive conditions, two males of some sexually monomorphic bird species can establish what would appear to be a pair bond (Thorpe 1972; Hand 1981; Hultsch 1983). In both appearance and behaviour, these male-male pairs can be virtually indistinguishable from their male-female equivalents, with one bird taking the male role and the other bird taking the female role. For species that sing by duetting between the sexes, this role-playing is also exemplified in the duet (Thorpe 1972; Hultsch 1983).

The endangered North Island kokako (*Callaeas cinerea wilsoni*), henceforth 'kokako', is the only known duetting songbird for which male-male pairing is thought to be common in natural populations. Consequently, this is the only known species in which male-male pairing can be closely studied without using captive animals, or having to resort to an extremely small sample size. However, male-male pairs (together with an excess of single males) are also characteristic of unmanaged declining kokako populations (Innes *et al.* 1996). The fact that male-male pairs are not readily distinguishable from male-female pairs means that the abundance of reproductively viable pairs in unmanaged forests cannot be readily established, and this makes it extremely difficult to determine which populations are most in need of female recruitment. This presents a significant obstacle for conservation management of the kokako. Studies of the behavioural ecology of kokako are therefore urgently required to ensure the survival of mainland populations.

This chapter comprises a detailed study of the duets of kokako and specifically seeks to determine whether any differences exist between male-male and male-female pairs. To introduce the topic, I will review the current literature on avian same-sex pairing, particularly that which describes known cases of male-male pairing. I will then give the evidence for, and characteristics of, male-male pairing in the kokako populations that are currently being monitored. This will be followed by a literature review of the song parameters which distinguish male song from female song in duetting species, so that some predictions can be made about how male-male and male-female duets might differ. I will then finish the introduction by outlining my specific objectives.

2.1.1 Male-male pairing and the North Island kokako

Most cases of avian homosexuality that have been described in the literature involve pairings between females. Female-female pairing has been documented in four gull species (the western gull *Larus occidentalis*, the ring-billed gull *L. delawarensis*, the herring gull *L. argentatus*, and the California gull *L. californicus*), the caspian tern *Sterna caspia*, and the lesser snow goose *Chen caerulescens caerulescens* (see Quinn 1989 for a review). Female-female pairs may arise in a population when two females are unable to find resident mates and so attempt to communally rear offspring from extra-pair fertilisations (Shugart *et al.* 1988).

A supposedly less common form of homosexual pairing in gulls is that which occurs between two males. Male-male pairing has been documented in laughing gulls *L. atricilla* occupying an outdoor aviary in the absence of prospective female mates (Hand 1981). Although the pair performed certain courtship displays, these took place much earlier than they did for any of the captive male-female pairs. Mounting behaviours were also performed, but never completed. Nonetheless, the pair built a nest and were shown to be fully capable of raising and defending a clutch that was provided for them (Hand 1981).

Male-male pairing has also been documented in captivity for two songbird species, the robin chat *Cossypha heuglini* Hartlaub (Hultsch 1983), and the tropical bou-bou shrike *Laniarius aethiopicus major* (Thorpe 1972). Both the robin chat and the bou-bou shrike are sexually monomorphic and both species sing by antiphonal duetting between the sexes (Todt *et al.* 1981; Todt & Hultsch 1982; Wickler & Seibt 1982). In the robin chat study by Hultsch (1983), a male-male pair was formed when a caged male was introduced to a resident male housed in an indoor aviary. The two birds delivered bouts of duetting, with one bird (the caged male) always taking the female component. This female song role was further accompanied by the typical visual displays assumed by females, which include rapid wing beating and a horizontally stretched body position (Hultsch 1983; Todt *et al.* 1981). The caged 'intruder' continued to assume the female role both when the caging situation was reversed, and when both birds were allowed to freely interact (Hultsch 1983).

For the bou-bou shrike study, a male-male pair formed despite the fact that there were several females housed in the same cage at the same time. When one of the pair members died, the remaining bird again paired with another male. As with the robin chat male-male pair, one male consistently took the female song role and adopted the characteristic female body postures, while the other bird took the male role. On two occasions this role playing extended to nest building (Thorpe 1972).

Both the robin chat and the bou-bou shrike male-male pairs responded aggressively and co-operatively towards intrusions from other birds, one of which was a female (Thorpe 1972). However, in neither species was the male-male pair thought to be a long term association. Instead it has been suggested to be an attempt by the subordinate male (the 'female' singer) to pacify the more dominant bird (Hultsch 1983; Thorpe 1972)

An apparently more stable male-male pairing situation occurs in the kokako. Breeding records show that male-male kokako pairs can persist in wild populations for as long as any male-female pair. For example in one population, the Rotoehu forest, a male-male kokako pair stayed together for at least four consecutive seasons before disbanding, while many male-female pairs in the same population have been known to attempt to breed together for just one season before disbanding (J. Innes, unpub. data). Another male-male pair, at the Mapara reserve, has been together for at least seven consecutive seasons despite what is now thought to be an abundance of female birds in the population (I. Flux, in litt.; Bradfield & Flux 1996).

Like the male-male pairs of the robin chat and the bou-bou shrike, male-male kokako pairs are virtually identical to male-female pairs in both appearance and behaviour. Both sexes have a bluish-grey body and a black mask over the eyes, with a pair of fleshy ultramarine wattles that originate from the edges of the gape and extend under the base of the bill. Adult males and females are approximately the same size, around 38 centimetres from bill to tail.

In kokako male-male pairs, one bird takes the male role (the 'primary male'), while the other bird invariably takes on the role of a female (the 'secondary male') (J. Hudson, pers. comm.; J. Taylor, pers. comm.). Male-male pairs at Mapara have been observed to perform courtship feeding and courtship displays (known as the 'Archangel' display, whereby the bird fans its wings and tail for several seconds whilst giving a 'chirr' call), as well as collecting and carrying nesting material (an activity normally confined to females). In all observed cases, the nesting material was soon dropped. However, one non-breeding pair at Mapara (which from leg measurements was likely to be male-male) also built at least one nest, which they immediately deserted (I. Flux, in litt.). Another Mapara pair, which was almost certainly male-male (both birds have since bred with females, however one of the birds was unbanded at the time it was paired to the other male) built a nest and sat on it for highly unusual periods for about three days (I. Flux, in litt.). A male-male pair in the Urewera was also seen to collect and carry nest material, but again like the Mapara pairs, this was soon dropped (J. Hudson, pers. comm.).

Without intensive management, all mainland kokako populations decline due to predation by introduced mammals (Innes *et al.* 1996). Furthermore, it is thought that because of nest predation the sex ratios of such populations may be highly skewed, so that they may be composed almost entirely of male birds (Bradfield & Flux 1996). Many of the birds in declining populations may be established as pairs, however it is now known from observing banded birds in managed populations that a large number of these pairs could be male-male (Innes *et al.* 1996).

In addition to referring to past breeding records, two methods have been devised which can be used to sex kokako. For the Mapara reserve, there is a morphological sexing method that incorporates tarsometatarsus length and body weight data. However, because of geographic variation in adult size ranges, this relationship may not be transferable between populations and even within a population there may be some degree of overlap between the sexes (I. Flux, in litt.; Innes *et al.* 1996). Furthermore, this method requires capturing the birds (either as adults or shortly before fledging) in order to sex them, which can be difficult. Mist netting for adults and sub-adults can be very time consuming and therefore expensive, as is locating nests. Recently, another sexing method was devised which involves taking blood and analysing the CHD-W gene (I. Flux, pers. com.). This method is almost certainly reliable and can be used on birds regardless of their age, yet it still has the same fundamental problem in that it requires being able to capture the birds.

An alternative way of determining the sex of kokako pairs may be found by comparing the behaviours of male-male and male-female pairs, and this might best be done by looking at features of their songs. Song features are easily quantifiable, allowing certain aspects of sound (such as pitch) to be compared directly between different categories of animals (McCracken & Sheldon 1997). Song can also be highly stereotyped (Morton & Page 1992), occur frequently in the birds' daily routines and be relatively easy to induce and observe. In comparison, calls and non-vocal displays have less potential as a sexing tool because they can be extremely context-specific (Morton & Page 1992), and are often much more difficult to hear or observe in dense forest. Many methods for surveying bird populations rely upon counts of singing males, and up to 90 percent of detections are due to song (Gibbs & Wenny 1993; Kroodsma *et al.* 1996).

2.1.2 Features of duet participation by males and females

A common feature of many duetting species is the lack of sexual dimorphism, which has often made it difficult for researchers to determine the sex of individuals (Bertram 1970; Thorpe 1972; Wickler & Sonnenschein 1989; Brown & Brown 1994; Slater 1997). In a study by Brown & Brown (1994) on golden whistlers *Pachycephala pectoralis*, only 12 percent of adult birds could be positively sexed visually or aurally. Other studies have used anatomical methods to sex birds, involving laparoscopy (Slater 1997) and post-mortem examination of the gonads (Thorpe 1972).

Sexual monomorphism may also be expected to interfere with sex recognition between the birds themselves. In duetting species, both the male and the female will, when necessary, actively engage in territorial defence against neighbouring pairs (Farabaugh 1982). During such border disputes, each member of a pair must be able to distinguish its mate from either of the birds in a rival pair to avoid misdirecting their attacks. Furthermore, some species such as the Australian magpie and tropical wrens of the genus *Thryothorus* have strong intrasexual aggression, with attack bouts that are precisely co-ordinated so that each bird only attacks others of like sex (Farabaugh 1982; Levin 1996b; Brown & Farabaugh 1996). Information must therefore be encoded in each bird's behaviour to reveal not only the identity, but also the sex of each singer. This information could be provided in the form of certain short-range, low intensity calls and as non-vocal visual displays, or within features of the song itself (Farabaugh 1982).

Females may have distinct sex-specific duet contributions, and these contributions may occur within a different frequency range to those of the male. Sex-specific song repertoires occur in species where there is strong intrasexual aggression (Levin 1996b; Brown & Farabaugh 1997), such as the robin chat (Todt *et al.* 1981; Hultsch 1983), the tropical bou-bou shrike (Hooker & Hooker

1969), the bay wren *Thryothorus nigricapillus* (Slater 1997), the Indian hill mynah *Gracula religiosa* (Bertram 1970), the Australian magpie (Brown & Farabaugh in press), the barbet *Trachyphonus d'arnaudii emini* (Wickler & Seibt 1982) and in the slate-coloured bou-bou shrike *L. funebris* (Wickler & Seibt 1982; Wickler & Sonnenschein 1989). Sex-specific song frequency ranges occur in the robin chat (Todt *et al.* 1981) and in the rufous-and-white wren *T. rufalbus* (Farabaugh 1982). In robin chats, female song occurs mostly between three and four kilohertz while male songs are pitched between one and three kilohertz (Todt & Hultsch 1982).

A higher singing pitch for females relative to males may be related to morphological differences between the sexes, such as a smaller body size (Lambrechts 1996). In great tit *Parus major* song, males are best able to sing song elements at three to seven kilohertz. That is, great tits can sing at a higher rate and show less song frequency deviation when they sing within this range (Lambrechts 1996). This occupies approximately one quarter of the total frequency range of the individual. However, McCracken & Sheldon (1997) note that fundamental frequency, average number of syllables per vocalization and syllable structure are ultimately constrained by the genetic components controlling syringeal morphology, while other features such as frequency range and first-peak energy frequency are largely determined by habitat. This means that fundamental frequency range, rather than total frequency range, might provide more accurate cues for discriminating sex.

Another feature of some duetting species is that males and females have an unequal participation in the amount and/or the number of sounds used in the duet (Farabaugh 1982). The amount of female song present in the duet is often correlated to the latitudinal position of the species range (Farabaugh 1982). Generally, for many tropical species such as the Cuban red-winged blackbird and the bay wren, females will frequently sing alone and their share of the duet is as large as the males (Whittingham *et al.* 1992; Levin 1996b), while for zebra finches and most other temperate species only the male sings (Brenowitz & Kroodsma 1996). Between these tropical and temperate extremes lie species such as the robin chat, where the female never sings alone and has an intermediate amount of input into the duet (Todt *et al.* 1981). There may also be significant variation between two populations of the same species, as shown for the house wren (Farabaugh 1982) and for the Cuban and North-American populations of red-winged blackbirds (Whittingham *et al.* 1992)

2.1.3 Objectives of study and predictions

This chapter examines the structure of kokako duets, in particular the use of song pitch and duration components by pair members, to identify patterns which may distinguish male-male duets from male-female duets. Due to the decline in kokako numbers in unmanaged areas, there is an urgent need to determine how close these populations are to collapse, and hence, whether or not they can be recovered without recruiting females from other populations. The main objective of this study is therefore oriented towards conservation management, with the specific aim of building on current surveying techniques so that 'new' kokako pairs can not only be counted using song, but also sexed. At the same time, this study is the first to focus solely on male-male pairing and duetting in the wild. Male-male kokako pairs present a unique research opportunity, allowing the dynamics of the male-male pair bond to be studied with regard to the current literature on song and singing behaviour in duetting species.

Based on the literature I have presented above, I propose that male-male pairs will sing differently to male-female because both primary and secondary males may be selected to contribute male-typical song. A major assumption of this hypothesis is that male and female kokako each have quite different song contributions, and this will need to be demonstrated before any of the male-male pairs can be examined with respect to the predictions. If males and females do sing differently, I anticipate two major differences in the structure of male-male duets which may distinguish them from male-female duets. Firstly, the distribution of singing time between pair members may be closer to a 50:50 ratio for male-male pairs. This is because both birds may compete for the same acoustic space, and neither bird will be selected to sing the typical female contribution (which is lower than that of the male's for most species). Secondly, song elements and song pitches that may be typical of female contributions might be represented less in the duets of male-male pairs. This may occur because males are physically less capable of producing female elements. These predictions may be interrelated, since a decrease in the use of female-typical song will reflect on an increase in male song, particularly if the amount of sound per rendition remains constant.

The analysis will be structured so that I will first look for patterns that distinguish male contributions from female contributions. These patterns will then be applied to songs of male-male pairs, in the form of the two predictions described above, to look for features that distinguish them from the songs of male-female pairs.

2.2 *Methods*

2.2.1 Recording Procedure

The songs of North Island kokako pairs and singles were recorded from four widely dispersed populations: the Mapara Reserve in the King Country, the Rotoehu forest in the Bay of Plenty, the northern Urewera ranges near East Cape and the Hunua ranges near Auckland. Each population was comprised of one or more song dialects. Pairs were defined as belonging to a collective dialect when they shared the same song elements, arranged in a very similar order. Songs sampled from Mapara comprised three dialects, Mapara north, Mapara south and Mapara central, while one dialect was sampled from each of the remaining populations.

With my focus being mainly on the confirmed male-male pairs and their male-female neighbours, I recorded the duets of 13 pairs from the Mapara reserve, five pairs from Rotoehu, three pairs from the Urewera, and two pairs from the Hunua ranges. I also recorded the solo songs of males on several occasions, both from unpaired males and from paired males when their mates were not present; in addition, I recorded a single songbout from a captive female at the Otorohanga Kiwihouse. Mr J. Taylor recorded two other male-male pairs from the Hunua Ranges for the study. Confirmed male-male pairs and their confirmed male-female neighbours were given the highest priority for recording, that is they were visited more often than the unconfirmed male-male pairs and their male-female neighbours. An explanation of the criteria met for confirmed male-male and male-female pairs is given in Table 2-1. Appendix 2 presents the total sample of pairs from each location. Appendix 3 shows the distribution of these pairs within each dialect. Note that the Hunua population has just one banded male-female pair. Recordings were made over the twelve months starting just before the 1996/97 nesting season.

Songbouts were recorded onto digital audio tape (DAT ; Sony DT-120 tapes) using an AKG shotgun microphone (C460B) and a Sony DAT Walkman (Digital Audio Tape-Corder TCD-D7), between dawn and noon on settled days. Outside of the breeding season, taped song and calls (from either the focal pair or one of its neighbours) were usually played to attract the birds and to induce them to sing. Each recording began with a short introduction noting the day, time and location, and the name of the pair or single being recorded. During recording, I attempted to identify the contribution made by each bird to the duet by watching one or both of the birds engaging in song, or preferably by listening from a position between the birds. Recording usually continued until the birds moved away and/or stopped singing.

2.2.2 Classification of song components and extraction of song data

The recordings were analysed on a Compaq Contura 400 laptop computer by producing a sonagram with Avisoft Sonagraph Pro software(version 2.5; f_s=8kHz, 16 bit, FFT length: 256, frame size = 100%, Hamming window, overlap = 93.75%). Time-frequency data for selected recordings (usually those which were long and had a large amount of song) were exported by 'Dynamic Data

Table 2-1 Explanation of priorities for recording kokako (see appendix 2 for pair names and sampling locations)

Priority 1 pairs

- Included all confirmed male-male pairs, and at least three confirmed male-female pairs from each of the neighbourhoods where a confirmed male-male pair was recorded.

Criteria used for categorization:

a) *Male-male pairs:*
Pairs of banded birds that had been a pair for at least four seasons without producing any clutches. Evidence on sex was supported by leg measurements, and DNA sexing when available.

Total N = **3 pairs**

b) *Male-female pairs:*
Pairs of banded birds that had produced at least one clutch together and/or pairs of banded birds where one of the birds was known to have bred successfully with another bird which confirms it as being a female. Evidence on sex was supported by leg measurements.

Total N = **12 pairs**

Priority 2 pairs

- Included suspected but unconfirmed male-male pairs and at least one of their confirmed male-female neighbours.

Criteria used for categorization:

a) *Male-male pairs:*
Both birds were banded and had never produced a clutch as a pair, but at least one of the birds had been monitored for less than four seasons. Leg measurements suggested that both birds were male.

Total N = **2 pairs**

b) *Male-female pairs (excluding priority 1 male-female pairs)*:
(Same description as for priority 1 male-female pairs)

Total N = **3 pairs**

Priority 3 pairs

- Included suspected but unbanded male-male pairs and at least one of their confirmed male-female neighbours.

Criteria used for categorization:

a) *Male-male pairs:*
Pairs that had never bred during the seasons over which they have been observed, but at least one of the birds was unbanded. Leg measurements were not available for the unbanded bird(s).

Total N = **4 pairs**

b) *Male-female pairs (excluding priority 1 male-female pairs)*:
(Same description as for priority 1 male-female pairs)

Total N = **1 pair**

Priority 4 singles

- Included one single male, two males whose mates were absent (one in a male-male pair, one paired with a breeding female), and a female at the Otorohanga Kiwihouse (sexed using DNA sexing)

Total N = **4 birds**

Exchange (DDE)' into a Microsoft Excel 6.0 spreadsheet, where song elements were arranged into song cycles or 'renditions'. A rendition was defined as a single cycle of the particular dialects' song. Song renditions were divided into verses, which were usually separated in time by at least the duration of a song verse. Each song verse was divided into song phrases, and then into song syllables. A song phrase was defined as a group of syllables, whereby the timing between each syllable did not change from one rendition to the next. Some phrases may be comprised of a single syllable if they are not produced with other song elements in a temporally consistent fashion. A song syllable was the smallest song unit, and for the purpose of this study it was defined as a continuous trace on the sonagram that did not undergo any sudden or dramatic shifts in frequency (that is, a shift of more than 500kHz in the space of 0.5 seconds). This definition enabled each song element to be quantified without overlooking any minor changes in frequency, therefore giving me an accurate representation of the distribution of frequency use within the song. Hence, when a note sounds continuous it may in fact be composed of more than one syllable. In comparison to song verses, the timing between phrases and syllables was generally much shorter and less variable. Any calls that occurred throughout the song were classified in a similar manner to phrases. Appendix 1 displays sonagrams of each dialect's song together with the calls most often used during songbouts.

For the purposes of this study, I focused my efforts on extracting data which described where the sound energies were most concentrated. Data were collected for each song and call syllable, and included the time at the start of the syllable (lapsed since the start of the first rendition in the songbout), the fundamental frequency of the syllable (taken as the average frequency between the start point and the end point of the trace of strongest energy) and the duration of the syllable (defined as the time at the end of the fundamental trace minus the time at the start).

In order to quantify the production of song at certain fundamental frequencies, I sectioned the frequency range of kokako song (which occurs between approximately 0.45 and 2.95 kHz, including low-intensity calls) into 50 classes.

Each of these classes therefore represented a range of 0.05 kHz. To calculate the time spent singing at each frequency class, I summed the durations of all of the syllables which had a fundamental frequency that fell into the class, and divided this by the total time the bird(s) spent vocalizing. To obtain data which incorporated more than one singer, I took an overall average of each of their respective proportions.

One of the analyses examined the central tendency of song pitch use of male-male and male-female pairs and pair members. The data for the central tendency plots were produced in the same way that the lower quartile, median and upper quartile are estimated for a cumulative frequency distribution. That is, I produced a cumulative graph which plotted frequency classes against the successive summation of the proportions of time spent singing in each frequency class. I then estimated the quartiles (hence the lower, median and upper frequencies) by dropping similar perpendiculars from the intersections of the 25%, 50% and 75% points, and noting the respective song frequencies. The plots (figure 2.3) therefore present the frequencies up to which occurred 25%, 50% and 75% of the total time spent singing. I called these the lower frequency, the median frequency and the upper frequency, respectively. Hence a lower frequency of 1kHz and an upper frequency of 2kHz implies that 25% of the time spent vocalizing in the song occurred at less than 1kHz, while 25% occurred above 2kHz. This is a useful way of seeing how concentrated the use of fundamental frequency is for a pair, pair member or group. I excluded all vocalizations below 0.75kHz because many of these were likely to be low-intensity calls and may have skewed many of the distributions.

2.3 *Results*

2.3.1 General description of the recordings

In total, 312 song renditions were analysed. This constituted approximately 39 minutes of vocalized sound. 60 renditions were analysed for the priority 1 male-male pairs (16-20 renditions per pair), 21 renditions for the priority 2 male-male pairs (5 and 11 renditions per pair, respectively) and 33 renditions for the priority 3 male-male pairs (5-11 renditions per pair). 186 renditions were analysed for the priority 1 male-female pairs (9-20 renditions per pair), and 32 renditions were analysed for other male-female pairs (7-11 renditions per pair). 11 renditions were analysed for the single birds (1-5 renditions per bird).

Of the renditions of male-male pairs, 13 were fully characterised according to each bird's contributions for two of the three priority 1 male-male pairs (5 and 8 renditions respectively). 6 renditions were characterised for one of the two priority 2 male-male pairs, and 7 were characterised for one of the four priority 3 male-male pairs. Of the renditions of male-female pairs, 48 were fully characterised for 10 of the 12 priority 1 male-female pairs (1-11 renditions per pair), and 1 rendition was characterised for one of the four remaining male-female pairs. Some pairs were recorded but not used in the analysis because their songs were too infrequent. The most complete sampling of pairs was from the Mapara North, Mapara South and Hunua dialects. Only a limited proportion of the pairs present in the Mapara Central, Rotoehu and Urewera dialects was used in the analysis.

Figure 2-1 compares the mean rendition lengths of male-male pairs with those of the male-female pairs for each dialect. These data represent the total time spent vocalizing in the renditions, not their overall durations including silent sections. Pair 11 of the Urewera population was excluded from the sample of male-male pairs because I was not able to record the pair with both birds duetting in close range of the microphone. However, I did obtain recordings on separate occasions with one of the birds nearby, and from these I could obtain data on the contributions made by either bird to the duet (but obviously not on the proportion neighbours) but never in the male-male pairs. These include ms1d, mc1c, mn2d and r5c. In addition, phrases u3a and u5a may be absent from the repertoires of the Urewera male-male pair, although the sample size for this pair was small.

2.3.2 Use of fundamental frequency by male-female and male-male pair members

Figure 2-2a shows the distribution of fundamental frequency use for pair members of male-female pairs in the Mapara South, Mapara North, Rotoehu and Hunua dialects. Coverage of the frequency range by males and females appears to vary depending on dialect, however all four of the dialects which have characterised renditions show that females sing more than males at and above frequency classes 33 to 35 (2.05-2.20kHz). For the Mapara North and Hunua pairs, and possibly the Mapara South pairs as well, this frequency range is also where the females concentrate most of their song.

Figure 2-2b shows the distribution of fundamental frequency use for the male-male pair members. None of the secondary males described by the graphs show a concentration of singing time at or above classes 33 to 35 (2.05-2.20kHz). For those male-male pairs which can be compared to the male-female pairs in their own dialect, L-Nino & Racino appears to show the closest similarity to male-female pairs in terms of each pair members' coverage of the frequency range. Almost all of the frequencies used by Gian are concentrated below class 19 (around 1.40kHz), whereas in the Mapara South females the distribution is more widespread over the whole frequency range. This situation is reversed in Halls, which has a much wider coverage of the frequency range than the Hunua female. All secondary males except Racino show prominent peaks in the mid-frequency range.

Figure 2-3 summarises frequency use by members of male-female and male-male pairs by showing where frequency use is concentrated. The figure also shows the extent of variation which occurs between individuals within each group. Primary male pair members of all five male-male pairs have a similar distribution of singing time over the fundamental frequency range to male pair members of females cannot be distinguished from Gian, Matabeelee, 11b or Halls on this basis.

2.3.3 Use of fundamental frequency by male-female and male-male pairs

Figures 2-4, 2-5 and 2-6 show the distribution of the frequencies used by each male-male pair (presented in order of recording priority) compared to the male-female pairs in their respective dialects. Two of the three priority 1 male-male pairs (figure 2-4), Duja & Gian and L-Nino & Racino, show a lower use of the female-typical song pitches (classes 33 to 35; 2.05-2.20kHz). Tracy2 & Wobble show no such reduction. Of the priority 2 male-male pairs (figure 2-5), the songs of Bosnia & Matabeelee (but not pair 11) show this reduction, while for the priority 3 pairs (figure 2-6) the reduction occurs for Hudson & Halls, Cuzzie & Bro and Rise & Shine, but not for Jimmy & Bo. None of the male-male pairs except Hudson & Halls have a maximum song pitch as high as that of the male-female pairs in their respective dialects.

2.3.4 Proportion of time spent singing by females and secondary males in duets

Figure 2-7 displays the mean proportion of time spent vocalizing by females and secondary males for characterised duet renditions, relative to the total time spent vocalizing by the pair. Of the eleven female pair members used in the study, eight contributed less than their mates to their duets. These included the Hunua female and all three of the Mapara North females.

Only three of the secondary males could be compared with the females in their corresponding dialects. Racino was the only secondary male to show a higher mean proportion of time singing than all of its characterised neighbouring females. In comparison to many of the females (particularly those in Mapara South), secondary males are relatively invariable in terms of the proportion of the duet that they contribute.

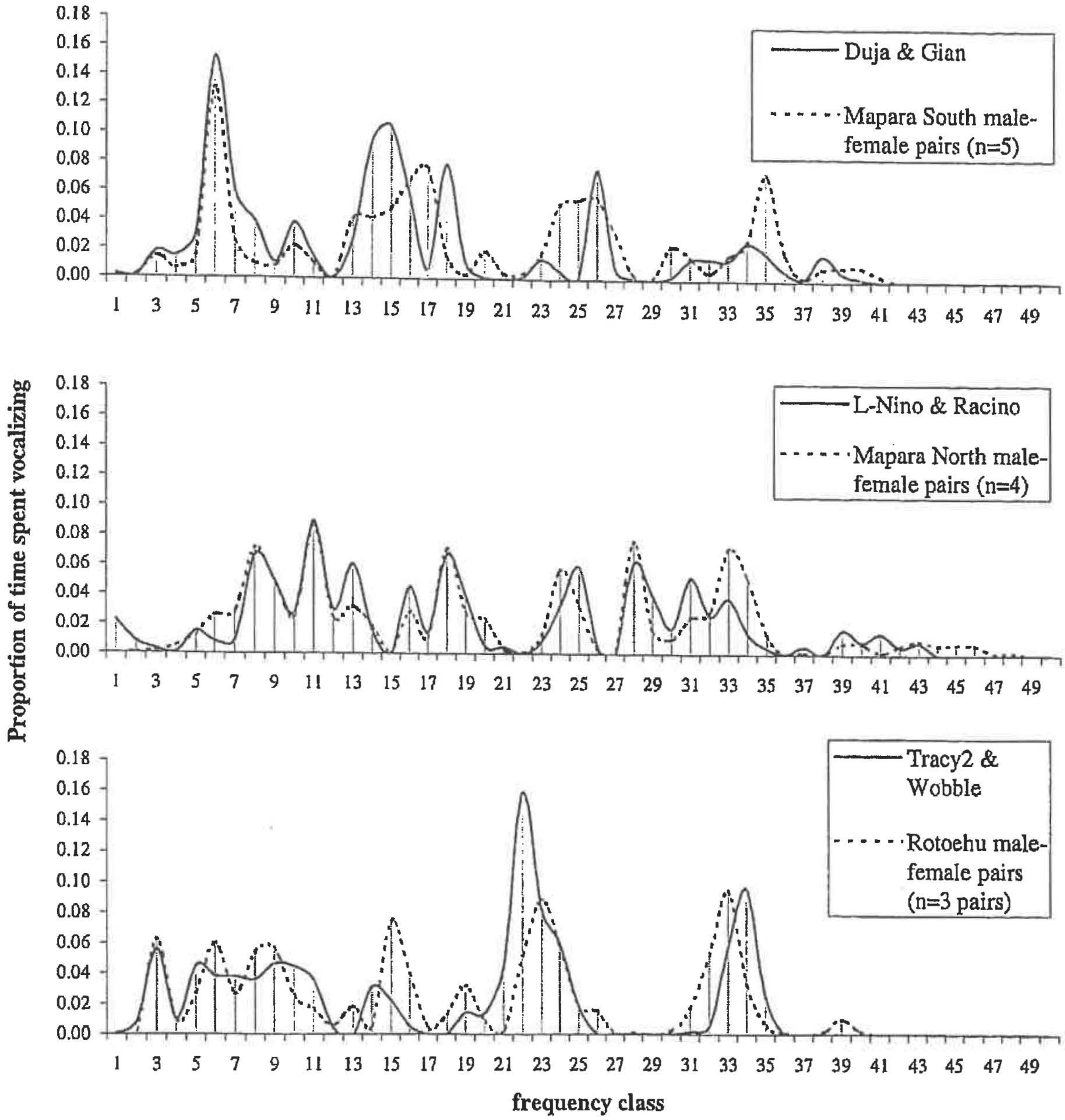


Figure 2-4 Distributions of fundamental frequencies used by priority 1 male-male pairs and local male-female pairs (see Appendix 5 for a list of frequency classes)

2.3.5 Song characteristics of the captive female kokako

Figure 2-8 shows the distribution in the use of fundamental frequency in song renditions of the captive female at the Otorohanga Kiwihouse. Unlike the wild birds, Bruce did not appear to incorporate any low-frequency, low-intensity calls

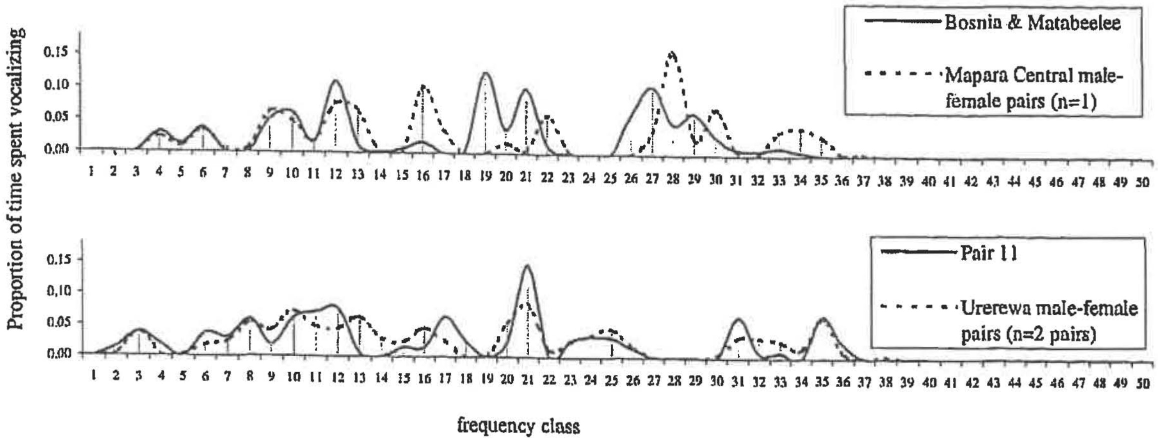


Figure 2-5 Distributions of fundamental frequencies used by priority 2 male-male pairs and local male-female pairs (see Appendix 5 for a list of frequency classes)

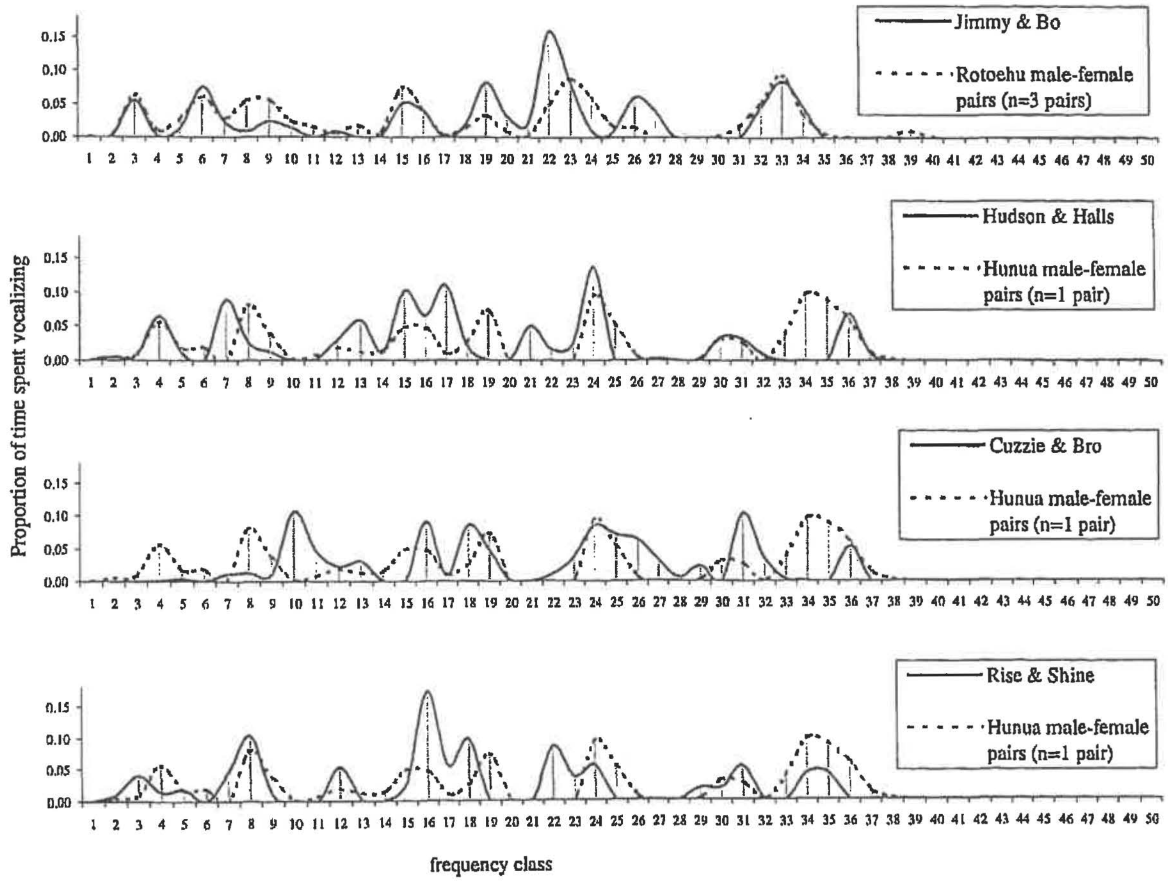


Figure 2-6 Distributions of fundamental frequencies used by priority 3 male-male pairs and local male-female pairs (see Appendix 5 for a list of frequency classes)

2.4 Discussion

Differences between the songs of male-male pairs and male-female pairs can only be expected to occur if males sing differently to females, and from the evidence I have presented it would appear that in most cases they do. Females may sing slightly less in duets relative to males, as was shown for 8 of 11 male-female pairs used in the study, and they also seem to favour a higher singing pitch. However, female song can be highly variable both between and within dialects, and between renditions for the same pair. This variation may place constraints on whether or not male-male pairs can be distinguished from male-female pairs in some dialects.

The greatest differences between males and females were seen for the Hunua and Mapara North dialects, since these dialects had the least variable female contributions. For the Hunua dialect, the female component was restricted to just one song phrase. Although only one female was available from the Hunua Ranges for the study, this phrase is also the only contribution given by the two unbanded Hunua females (J. Taylor, pers. com.). For the Mapara North male-female pairs, females contributed eight song phrases and three high-intensity calls. Females in the Hunua and Mapara North dialects also had a smaller contribution than the males (mean proportion of time spent vocalizing for Hunua females = 0.33; Mapara females = 0.24-0.4), and favoured different phrases to males. These patterns were reflected in their use of fundamental frequency, with males and females favouring different song pitches. The solitary male in the Hunuas was shown to incorporate female song elements into its territorial song (see Appendix 4), but this may not necessarily mean that it is equally capable of producing male and female song. Instead, the use of female song elements by solitary males is probably due to the need to repel neighbouring male-female pairs from their territory. As several studies have suggested (e.g. Hultsch 1983; Hultsch & Todt 1984), solo duet performances may be an attempt by the territory holder to create the illusion that there is more than one bird in residence. However, solo song performance can also occur in paired males, in which case it is thought to represent calling for an absent mate (Wickler & Seibt 1982). This may be why the single Hunua male produced such a large amount of female-typical vocalization, since the recording was made very soon after it disbanded with a female (J. Taylor, pers. com.).

Because males sing differently to females in the Mapara North and Hunua dialects, both of the predictions for male-male pairs that I proposed in the introduction can now be applied to the male-male pairs in each of these dialects. The first prediction was that male-male pairs will divide their songs so that the secondary male will contribute close to 50% of the duet (compared to 24-40% in Hunua and Mapara North females). The second prediction was that the typical female contribution, which is shown to be concentrated between 2.05-2.20kHz, will occur less in the songs of male-male pairs compared to male-female pairs.

Between them, male-male pairs in the Mapara North and Hunua dialects met both of my predictions. For L-Nino & Racino (priority 1), the secondary male contribution was considerably greater than the typical female contribution for the Mapara North dialect, and actually exceeded the size of the primary males contribution. The secondary male maintained the typical female song pitches, but it also sang part of the typical male contribution. For Hudson & Halls (priority 3), the amount of song produced by the secondary male was no greater than that of the local female, but its use of song pitch was considerably more diverse and there was also less use of female-typical song pitches. Hence while L-Nino & Racino only supported the first prediction, Hudson & Halls only supported the second.

Given the small sample size of male-female pairs (especially in the Hunuas), there is a chance that these results could be attributed to random variation between pairs. Therefore, it can only be concluded that the two male-male pairs described above sing differently to the 'average' male-female pair, and each sing in a way that would indicate that both birds are male. However, the advantage of applying the two predictions to the Mapara North and Hunua dialects (as opposed to the other dialects) is that variation between females is low, so it is unlikely that any of the male-female pairs would be easily mistaken for a male-male pair.

Most of the remaining male-male pairs met at least one of the predictions. For Duja & Gian (priority 1), the secondary male showed a strong preference for male song pitches (as opposed to the more general use of song frequencies by Mapara South females) and a decrease in the use of the higher song pitches typical of females, but showed no difference in the size of the contribution. The secondary male in Bosnia & Matabeelee (priority 2) showed both a decrease in the female-typical song pitches of Mapara females, and a contribution of singing time that approximately equalled that of the primary male. Both Rise & Shine and Cuzzie & Bro (each priority 3) showed an overall reduction in their use of female-specific song frequencies. Like Hudson & Halls, these pairs also distribute the song more equally between the pair members than the male-female pair does (J. Taylor, pers. comm.). Pair 11 (priority 2) used female-typical song pitches no less than Urewera male-female pairs, although both the primary and secondary males had a similar preference for male-typical song pitches. For Tracy2 & Wobble (priority 1) and Jimmy & Bo (priority 3) there was no decrease in female-typical song pitch. Given these results, Bosnia & Matabeelee appears to support my first prediction while Duja & Gian, Bosnia & Matabeelee, Rise & Shine, Cuzzie & Bro and pair 11 appear to support the second. Tracy2 & Wobble and Jimmy & Bo showed no evidence that suggested a compliance with either of the two predictions. However, there is a high probability that either or both of these pairs may have disbanded during the time I was in the field, and since I seldom saw their band combinations the more recent recordings may be for male-female pairs. The results for Tracy2 & Wobble and Jimmy & Bo should therefore be examined with discretion.

A particularly interesting feature of song behaviour in the two confirmed male-male pairs from Mapara is the way in which some phrases were split between the pair members. In the male-female pairs of Mapara North, phrases mn2c and mn3b are usually sung by the male alone, although some females will sing the three syllables of mn3b by themselves on occasion. In L-Nino & Racino, however, L-Nino never sings all three syllables of either phrase, and instead leaves the third syllable for Racino to sing. Racino may also sing all three syllables by itself. A similar pattern occurs in Duja & Gian for phrase ms2b. This sequence is always produced with Duja giving the first and last syllables, and with Gian giving the syllables in between. On some occasions (when Gian is presumably distracted), Duja will produce its two syllables but will never give the syllables normally prescribed to Gian. Furthermore, I have never heard either bird give a solo performance of this phrase. In Mapara South male-female pairs, however, either member of the pair can give the full phrase and the syllables are never shared.

When male-male pairs first form there is likely to be significant overlap in each bird's contribution, and this will need to be minimised in order for their duets to resemble those of other pairs and to be able to function in a song ranging context. The ability to range the distance of other pairs, and being able to be ranged by other pairs, is thought to be the basis of territorial defence and maintenance. It requires that each singer has a version of the other bird's song stored in its long term memory (Morton & Page 1992). Rather than an having a total reduction in the contribution of one of the birds, male-male kokako pairs may therefore develop an even partitioning of the song between the pair members. However, this could take some time to refine, which may explain why the song splitting shown in L-Nino & Racino and Duja & Gian did not occur in the Mapara Central male-male pair. While Duja & Gian have been paired for at least seven years and L-Nino & Racino for at least four (but probably seven), Bosnia and Matabeelee are known to have been paired for just three years (I. Flux, in litt.). As a result, they may not have had sufficient time to adapt the duet. If this is true, and assuming that Bosnia & Matabeelee are in fact a male-male pair, then one might expect that in a few years time phrase mc5b will be similarly split.

A possible explanation for male-male pairing in the absence of females in wild kokako populations, is that pairs are generally more effective at defending and maintaining a good quality territory than are single birds. In an experiment by Hultsch & Todt (1984) on robin chats, it was found that single male territory holders confronted an intruding bird by launching an immediate attack, while pairs preferred to display first. From these observations, Hultsch & Todt suggested that pairs may expect intruders to withdrawl, while singles are more at risk of being ousted and choose to actively defend their territory instead. For long-distance encounters with other pairs, an alternative strategy (as mentioned earlier) may be to give a solo performance of the duet in order to sound like two birds. In kokako, solitary males may have difficulties incorporating female song components into their own song repertoires while still being able to match the song rate and singing diversity of their neighbouring pairs. This could be because the female component is hard for a male to produce, or the bird simply gets exhausted by the increased burden of having to produce more song elements in the same space of time as its normal song. This would make them less effective at convincing (and therefore, repelling) rivals, especially if female song has a prominent role in territorial defence. If this is so, then a male-male pair may be more successful at maintaining a territory than a solitary male simply because pairs are better at countersinging with other pairs. A male-male pair can share the contribution of both the male and the female between them, or one can take the female role plus part of the male role. Either way, a male-male pair would certainly be able to sustain song for a longer period and at a higher rate than a single bird, particularly if the female component is especially taxing for a male to produce. Both birds would benefit from the partnership by being more capable of holding and maintaining a territory, which may also be larger or of better quality than that of a single bird.

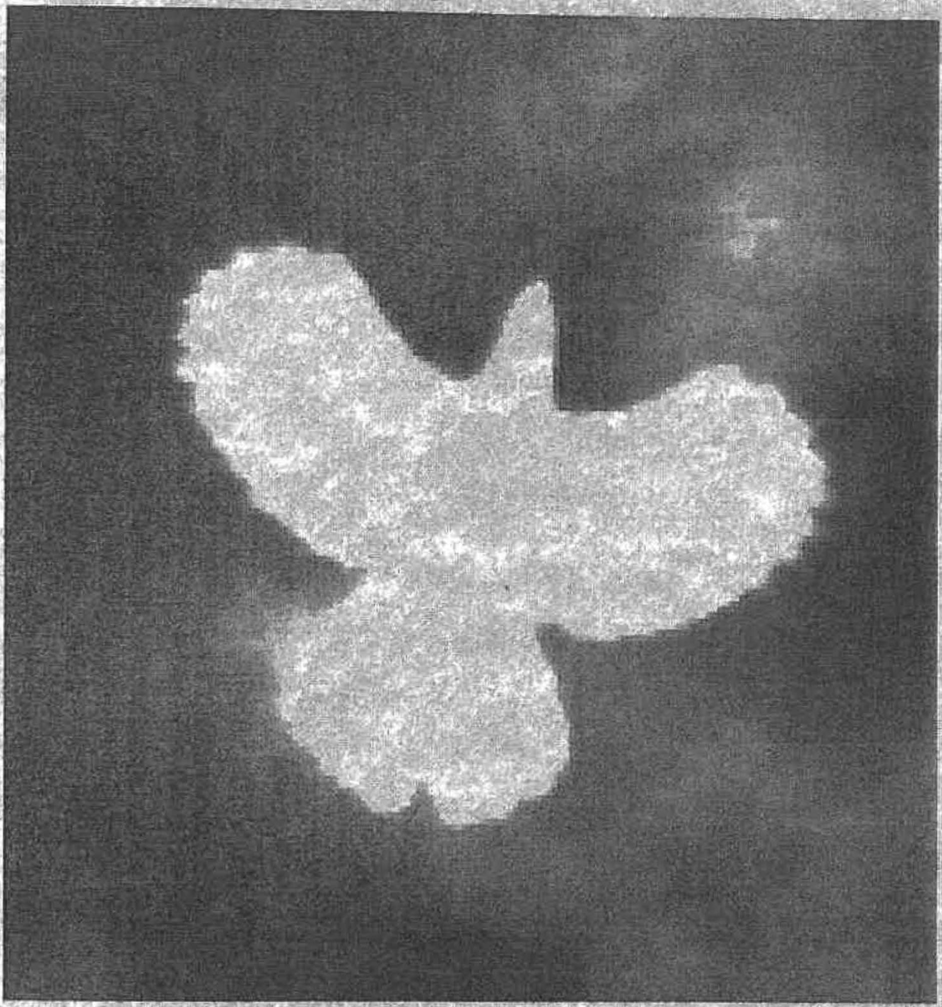
One aspect of male-male pairing which may not be explained by the need to maintain a territory is that male-male pairs occur in populations of low density, where territorial rivals are presumably less abundant and less of a threat. One explanation may be that such male-male pairs were formed when the population density was still relatively high (e.g. at Mapara before pest management began), in which case there will be obvious short term benefits to territoriality. Male-male pairs may then persist simply because there are no immediate detrimental effects associated with the condition.

The reproductive benefits for a male in long-term pairing with another male, despite the presence of potential female mates, is by no means clear. It may be that the primary male is initially deceived by the other birds' behaviour, but this deception might not be expected to persist beyond the first nesting season. If male-male pairing in kokako is the same as it is in the robin chat or the bou-bou shrike, then one would not expect the association to remain stable, particularly when females become available. Yet the main difference that distinguishes male-male pairing in these species from the kokako is that male-male pairing in the kokako occurs in the wild and is relatively stable. Male-male pairs may persist for longer under natural conditions, and with large territory sizes, because each bird is able to avoid the other by simply flying away to another part of the territory.

To conclude, the singing behaviour of male-female kokako pairs led me to make two predictions that could differentiate a male-male pair from a male-female pair. The first prediction was that male-male pairs might divide their song more equally between them than would a male-female pair, while the second was that male-male pairs and pair members might favour a broader and lower range of song pitches. Based on the data available, two male-male pairs (one confirmed, one suspected male-male pair) did not meet either of the predictions. Of the other seven male-male pairs examined, one pair (a suspected male-male pair) met both predictions, one pair (a confirmed male-male pair) met the first prediction, and five pairs (one confirmed, four suspected male-male pairs) met the second prediction. I demonstrated that the predictions can be used to clearly distinguish male-male pairs from male-female pairs, but only in dialects where the female contribution is concentrated at female-typical song pitches.

Because of variation in the size of the female contribution, and the tendency for some females to sing at male-typical song pitches, the predictions may also be met by male-female pairs in some dialects and this could limit the reliability of the technique. Yet it may be possible to apply this technique to pairs in such dialects and still be able to identify male-male pairs with certainty. This could be done by quantifying the extent that either of the two predictions are met for a particular pair, and if the extent to which they meet a prediction exceeds a certain threshold, then this could enable the pair to be classed as male-male. Of the two predictions, the second would appear to be the most definitive in such dialects: although many females may sing equal to or more than 50% of the duet, most females appear to concentrate their song at female-typical song pitches.

CHAPTER THREE



THE USE OF SOUND DEGRADATION IN THE ESTIMATION OF DISTANCE BY MALE-MALE AND MALE-FEMALE KOKAKO PAIRS

Chapter 3

The Use of Sound Degradation in the Estimation of Distance by Male-Male and Male-Female Kokako Pairs

3.1 Introduction

3.1.1 Ranging and the North Island kokako

For many forest bird species, visibility in their habitat is impaired by the density of the vegetation and by diurnal variation in light levels. For territorial songbirds in particular, this has major implications for a bird's ability to estimate the distance between itself and other members of its species. The ability to estimate distance, or 'range', is highly advantageous to a resident bird since it enables it to locate intruders and continue to maintain claim over its territory, without wasting time and energy on unnecessary searches. As a result, territorial songbirds are thought to have evolved the ability to range using sound (Morton 1986).

As a sound travels through its environment it is altered in two ways, both of which may be perceived by a listening bird. Firstly, there is an overall loss of signal amplitude with distance (amplitude attenuation). According to the Inverse Square Law, sound diverges spherically from a source that is small relative to the sound's wavelength (Morton 1975), and in a medium free of acoustic obstacles this accounts for a drop of six decibels for every doubling of distance from the source. The second way in which a sound is altered in its environment is by degradation, and this has been shown to be the main cue by which many bird species are able to range in their natural habitats (Richards 1981; Morton 1982; McGregor & Falls 1984; Morton *et al.* 1986). Degradation occurs by two mechanisms. First, certain sounds or parts of a sound can be absorbed by air, ground and vegetation so that the amplitude of the signal at any particular distance is lower than would be predicted by the Inverse Square Law (Morton 1975). Such a loss of sound energy increases in proportion to the length of the sound propagation path. Second, sound energy can be redirected by diffraction and reflection off ground, branches and leaves. Unlike the first mechanism, sound alteration in this way is disproportional to the length of the sound propagation path (Morton 1975).

Short wavelength sounds are rapidly degraded because they are more likely to be reflected than long wavelength sounds, therefore the excess attenuation effects brought about by most natural environments are directly related to sound frequency (Morton 1975; Mathevon & Aubin 1997). As a result, the higher frequency components of birdsong will generally attenuate within a shorter distance than lower frequency components. Furthermore, degradation causes a loss of syllable detail, particularly for songs with rapid frequency and amplitude modulations. Loss of syllable detail is caused by reverberation and echo, which lengthens the duration of the stronger elements and hides the quieter elements (Morton 1975; Naguib 1996b), as well as concealing information encoded by amplitude modulation (Richards & Wiley 1980).

Accurate ranging is thought to be achieved by comparing the degradation in the perceived signal with an undegraded version stored in the perceiver's long-term memory, often referred to as a 'standard' (Morton & Page 1992). Standards are derived from songs learnt from the bird's parents, and from its territorial neighbours (Morton *et al.* 1986). Great tits *Parus major* show an ability to range when the perceived songtype is present in the bird's own repertoire, but this effect is much reduced when birds are presented with unused songtypes (McGregor *et al.* 1983). In contrast, western meadowlarks *Sturella neglecta* may still range songs which are sung by their neighbours but which are absent in their own repertoires (McGregor & Falls 1984). A need to range the songs of neighbours is thought to be one reason why males of many bird species learn more songs than they actually sing (McGregor *et al.* 1983; McGregor & Falls 1984).

An ability to range was recently demonstrated for the dusky antbird *Cercomacra tyrannina* (Morton & Derrickson 1996). A major difference between this and any of the other species for which ranging has been shown (e.g. Carolina wrens *Thryothorus ludovicanus* (Richards 1981), great tits (McGregor *et al.* 1983), western meadowlarks (McGregor & Falls 1984)) is that dusky antbirds are suboscines (suborder Passeriformes, family Tyranni). This implies that song learning is not necessarily a prerequisite for ranging, since it is thought that suboscines do not learn their songs. Furthermore antbirds do not have dialects. Another difference between this study and any of the previous ranging studies is that antbirds sing by duetting between the sexes, a feature not apparent in most temperate species where only the male sings (Farabaugh 1982).

The North Island kokako *Callaeas cinerea wilsoni* (henceforth kokako), is a sexually monomorphic passerine which is found only in native forest on the North Island of mainland New Zealand and on nearby predator-free islands. Kokako defend permanent year-round territories, either as pairs or single males (Hay 1980). These territories are large, sometimes up to 30 hectares in size, and are often characterised by dense vegetation together with deep gullies and sharply rising spurs (Innes *et al.* 1996). This means that for kokako, visual cues alone must play only a minor role in the long distance monitoring of conspecifics. The most likely medium for this purpose is their song, which carries extremely well on settled mornings. On one occasion, a particular song was heard from more than a kilometre from where the singer's territory was known to be located (J. Hudson, pers. com.). Like the dusky antbird, both sexes sing by duetting (Hughes 1981).

Territorial borders in kokako are well defined and are maintained through a combination of mutual avoidance, song advertisement and occasional physical interactions (Hay 1980). Certain aspects of kokako territoriality and song behaviour may indicate that kokako are able to range. Firstly, kokako have dialects (Hughes 1981). These occur as distinct populations separated by distance, although additional divisions can also exist within the same interbreeding population (pers. obs.; J. Hudson, in lit.). Hence there is a significant amount of song sharing between neighbouring birds. Secondly, during song interactions, adjacent territory holders appear to sing in order to deliberately 'fit in' with each other's song sequences so that a considerable portion of time within songbouts may be spent listening (Hughes 1981). This behaviour resembles the countersinging interactions described for temperate species, whereby two birds reply to each other with the same songtype. Countersinging is thought to be a major component of ranging as it facilitates the exchange of reliable distance information between the singers (McGregor & Falls 1984; McGregor 1994). Kokako also sing from elevated song perches, a feature which is often associated with countersinging since it improves vocal propagation and also makes the singers more conspicuous to each other (Hughes 1981; Mathevon & Aubin 1997). Lastly, sonagrams of kokako songs (Appendix 1) reveal features that could predispose song elements to varying degrees of degradation (Morton 1975; Richards & Wiley 1980). Such features include song patterns with rapid amplitude modulation (for example, calls mnCall7 and msCall5, and song phrases mn2a and mn4e (Appendix 1B), long pure tone notes accompanied with numerous harmonics and abrupt breaks (for example, mc5a (Appendix 1D)), and low frequency low-intensity song sequences (for example, ms1b, mn1a and r1b (Appendix 1A, 1B and 1C, respectively)).

In this chapter, I looked at the response of wild kokako pairs to their own song played to them at an equal amplitude in a 'less degraded' form (re-recorded from 5 metres) and in a 'more degraded' form (re-recorded from 100 metres away). This allowed me to determine whether kokako pairs can range familiar song based solely on degradation cues, or whether they rely more on other methods such as visual cues. Because ranging by habitat-induced degradation is thought to be the most energy-efficient means of locating intruders, determining the extent to which kokako pairs rely on degradation cues will provide insights into the importance of song and territoriality in the daily energy expenditure of this species.

The study may also reveal differences between the affiliative behaviour of two very different types of kokako pairs. A particularly important feature of kokako reproductive and territorial behaviour is the occurrence of male-male pairs. As yet, no study has been conducted for any songbird which experimentally examines the territorial behaviour of male-male pairs versus male-female pairs.

3.1.2 Kokako conservation and male-male pairing

For the kokako and some other bird species, male-male pairs may exist because there is a shortage of available females (Thorpe 1972; Hand 1981; Hultsch 1983; Innes *et al.* 1996). For the kokako, which is currently listed as endangered (Collar *et al.* 1994), male-male pairing presents a serious obstacle for conservation management because males are visually indistinguishable to females. This makes it very difficult to assess the status of an unmanaged population since although birds may be established as pairs, it cannot be known from casual observation how many of these pairs are capable of breeding. Although efforts can now be made to effectively restore declining populations through intensive pest management, many of these populations urgently require the recruitment of females from other populations if they are to survive beyond the next decade. Being able to distinguish male-male pairs from male-female pairs is also necessary for determining when to re-introduce pest control to previously managed populations in which management has ceased. Nothing has yet been identified which enables male-male and male-female pairs to be readily distinguished on the basis of behaviour, although there may be differences in song (Chapter 2).

The male-male pair bond may be expected to differ functionally in some aspects to the male-female pair bond, and these differences could be reflected by their respective behaviours towards a simulated territorial intrusion. In another duetting species, the robin chat (*Cossypha heuglini* Hartlaub), territorial alliance is thought to be expressed by certain non-vocal displays, one in particular being close perching (Todt *et al.* 1981; Hultsch & Todt 1984). Close perching is thought to signal territorial alliance to an intruder because the distance to which two individuals tolerate each other provides information about their familiarity, and therefore shows their willingness to co-operatively defend the territory (Hultsch & Todt 1984). Hence if the kokako male-male pair alliance is little more than two birds sharing a territory, then male-male pair members may respond to an intruder more independently than would the members of a true male-female pair, and this could be reflected in their spacing.

In this study, I looked at whether kokako pairs were able to range familiar song based on degradation cues alone. By incorporating both male-female and male-male pairs, I also looked at whether there were any differences in the way that these types of pairs behaved in a territorial context.

3.2 Methods

3.2.1 Selection of experimental pairs and processing of songs

The songs of 12 pairs of North Island kokako were recorded from three widely separated populations in the central and upper North Island of New Zealand during the spring, summer and winter of 1996/1997. Of these pairs five were known to be, or suspected to be, 'male-male': two confirmed male-male pairs and a suspected male-male pair from the Mapara Reserve; one suspected male-male pair from the

Rotoehu Forest; and one suspected male-male pair from the Hunua Ranges. The remaining seven pairs were all confirmed male-female pairs: four from the Mapara Reserve, two from the Rotoehu Forest, and one from the Hunua Ranges (see Table 3-1). Each male-female pair was selected on the basis of being located near, but not immediately adjacent to, a male-male pair. This was to ensure that the male-female pairs being used in the experiment had songs that were representative of the male-

Table 3-1 Male-male and male-female pairs used in the experiment, listed with respect to location (see footnote for definitions of confirmed and suspected pair types)

	Pair Type	Confirmation
Mapara Reserve		
North Block		
L-nino and Racino	confirmed male-male[1]	both banded
Serpens and Botswana	confirmed male-female	both banded
Pyrosia and Gossum	confirmed male-female	both banded
South Block		
Duja and Gian	confirmed male-male	both banded
Vishnu and Huhu	confirmed male-female	both banded
Cirrus and Batagooli	confirmed male-female	both banded
Central Block		
Bosnia and Matabeelee	suspected male-male[2]	both banded
Rotoehu Forest		
Jimmy and Bo	suspected male-male	only one banded
Merlin and Bakano	confirmed male-female[3]	both banded
Trevor and Kawi	confirmed male-female	both banded
Hunua Ranges		
Hudson and Halls	suspected male-male	only one banded
Bob and E.T.	confirmed male-female	both banded

[1] Pairs of banded birds that had been a pair for at least four seasons without producing any clutches. Evidence of sex was supported by leg length and weight measurements.

[2] Both birds were banded and had never produced a clutch as a pair, but at least one of the birds had been monitored for less than four seasons. Leg measurements suggested that both birds were male.

[3] Pairs of banded birds that had produced at least one clutch together and/or pairs of banded birds where one of the birds was known to have bred successfully with another bird which confirms it as being a female. Evidence on sex was supported by leg length and weight measurements.

male pair neighbourhoods, as well as being far enough apart so that one trial could not directly interfere with another. Appendix 3 shows the distribution of experimental pairs and their approximate territory locations for the 1996/97 breeding season. The sample of experimental pairs initially consisted of seven male-male pairs, with an additional male-male pair from Rotoehu and another from the northern Te Urerewa National Park (the confirmed and suspected male-male pairs 'Tracy2 & Wobble' and 'Pair 11,' respectively). However, both of these pairs disbanded prior to the sampled nesting season and so could not be included in the experiment. Recordings were made onto digital audio tape (DAT ; Sony DT-120), using an AKG shotgun microphone (C460B) and a Sony DAT Walkman (Digital Audio Tape-Corder TCD-D7). Only songbouts recorded during settled weather were used for the experiment. Three song renditions (a 'rendition' being defined as a single cycle of the particular dialects' song from start to finish (Appendix 1)) were chosen on the basis of clarity from the recordings of each pair. Whenever possible, each song rendition was taken from a different day. Song renditions were sampled at 48000 hertz (16 bit) to a laptop computer (Compaq Contura 400, with a New Media WAVjammer audio adapter) and filtered to remove low-frequency background noise (highpass, 150 hertz; Avisoft Sonagraph Pro, version 2.5). All silences greater than three seconds in duration were deleted (not cut) to remove unwanted background noise. Other features of the song renditions, such as the timing of song components and the occurrence of calls and wingbeats, were left unmanipulated. As a result, the durations of the song renditions were quite variable, even though the amount of sound in each was fairly consistent (mean rendition lengths: Mapara 55.5s ± 19.8s ; Rotoehu 43.4s ± 4.3s ; Hunua 56.8s ± 6.9s).

The processed songs, called 'source songs', were transferred at equal amplitudes onto a minidisk (MD ; Sony MDW-60). The maximum amplitude was standardised using a Radioshack sound level meter (Cat. No. 33-2050).

3.2.2 Kokako amplitude measurements and degradation of song

The maximum natural amplitude of kokako song over several song renditions was measured (using the Radioshack sound level meter) from two male-female pairs, and a male-male pair at the Mapara Reserve, and from a captive bird at the Otorohanga Kiwi House outdoor aviary. Amplitude readings at Mapara were taken during calm mornings at distances of around 10 and 15 metres from the singing birds. Amplitude readings were taken from the Otorohanga captive bird at distances of one and three metres. Readings taken at distances greater than one metre were back-calculated to obtain the approximate maximum amplitudes from one metre, on the principle that amplitude decreases by six decibels for every doubling in distance from the source. The amplitude readings from the captive bird were deemed to be more accurate approximations of the maximum natural amplitude of kokako song, since the bird was clearly facing the sound meter and was singing from a much closer distance. The maximum natural amplitude at one metre was therefore estimated at 98 decibels. Table 3-2 shows the peak amplitude readings of all tested birds.

Source songs were grouped with regard to their source populations. The populations each had quite different climates and vegetation assemblages, which may combine to give each habitat different acoustical properties. Each group of source songs was therefore degraded separately near the population of its source, on a clear settled night a few days prior to the first experiment. Song degradation was carried out across flat terrain, in a forest tract away from any of the study pairs. The first attempts to degrade songs at Mapara were made during the morning, however the frequent intrusions of other noises from birds and traffic (the Mapara Reserve lies in the path of a major airline route) prevented me from getting clean recordings and from completing the session in less than two hours. It was therefore decided to degrade the songs at around midnight and avoid such intrusions, even though there may be certain atmospheric conditions associated with the dawn chorus which did not occur at this time.

Table 3-2 Peak amplitude readings of kokako song for three wild kokako pairs and a single captive female

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Songs of Mapara birds

Vishnu and Huhu (male-female), measured 7/7/97:
max @ 15m = 66dB
= ~90dB @ 1m
Serpens and Botswana (male-female), measured 8/7/97:
max @ 15m = 65dB
= ~89dB @ 1m
L-nino and Racino (male-male), measured 8/7/97:
max @ 10m = 70dB
= ~87dB @ 1m

Song of captive bird Bruce (female), recorded 20/8/97:

max @ 1m = 95dB
max @ 3m = 88dB
= 98dB @ 1m

The number of source songs for each session was divided into two sets, and each set was degraded alternately (see below). This was to ensure that if any increase in atmospheric turbulence occurred during the degradation session, then the effects would have been distributed more evenly among the songs than they would have if the songs were degraded in one continuous block. Both the speaker and the microphone were mounted on three metre long poles with the microphone aimed at the speaker. Degradation of the source songs was carried out with the help of an assistant, so that each set of source songs was played at 98 decibels (amplified using a TOA CA200 car stereo amplifier) through the forest, and re-recorded onto DAT at either 5 metres or 100 metres. The first half of songs were re-recorded with the microphone positioned 100 metres away from the speaker. The microphone was then moved to 5 metres from the speaker, and the second and first half of songs were re-recorded, respectively. The microphone was then repositioned 100 metres from the speaker and the second half of songs were re-recorded. The degraded and undegraded song versions were then filtered using the sound analysis and editing system (highpass, 150 hertz) to remove low-frequency background noise as before, and then transferred in the appropriate order onto MD. These songs were called the 'stimulus songs'.

3.2.3 Site Selection and Experimental Procedure

Playback sites were positioned approximately 50 metres inside a pair's territorial boundary. To determine territorial boundaries, I referred to territory maps from the 1996 walk-through surveys which were conducted by Department of Conservation (DOC) employees just prior to the 1996/97 nesting season (territory boundaries are relatively stable from one season to the next). For the Hunua Ranges, selection of appropriate playback sites was made under the guidance of Mr J. Taylor, while Mr P. Bradfield and Mr I. Flux helped determine sites for the Mapara pairs. Playback sites were selected on the basis of being away from any neighbouring territories to avoid the direct interference of other pairs. Sites also had to have good visibility and a fairly continuous canopy (either fully closed or evenly patchy), and I avoided areas where broadcasts were likely to be impaired by major landforms such as sharply rising spurs. For each site, trees within a 40 metre radius of the speaker were tagged at certain distances with ties of orange tape. This divided the sites into four circular zones : 0-5m, 5-10m, 10-20m, and 20-40m. Tags were aligned in the four main compass directions.

Pairs were presented with their own stimulus songs on settled mornings during the winter and early spring of 1997. The pair's own songs were chosen because it was assumed that they would be the most familiar to the birds (regardless of how long the pair had been together and of how experienced they were at singing), and therefore the most 'rangeable' for distance-estimation. Furthermore, avoiding the presentation of another pair's songs eliminated the effects that any previous interactions with the birds may have had. Kokako are also highly responsive to playback of their own songs (pers. obs.). Playback was broadcast from three metres above ground level with the speaker mounted on a pole.

Each pair was exposed to the two treatments (degraded and undegraded song). The second treatment was given at approximately the same time of the morning as the first treatment. Up to three trials took place in one day, during either early-morning, mid-morning or late-morning. Late-morning trials were started no later than 1030 hours, while early-morning trials usually began as soon as there was enough light to be able to see the birds and their band combinations. I often had to work around the weather as well as an increasing daylength, therefore I could not adhere to an exact timetable. Mid morning trials generally began at around 0830 to 0900hrs. Trials were not started in wind or rain, since this not only interfered with sound recording and propagation, but also made locating the birds very difficult. Treatments on a given pair were separated by at least one week (usually more than two), and alternated in order between the different pairs. If a pair failed to respond to a trial (see below for the definition of a non-response), then the pair was given the same treatment type at the same place at least a day later, but at a different time of the morning. If the pair failed to respond after three trials of their first treatment, then a new playback site was chosen using the same criteria as before. Depending on the terrain, new sites were selected either 50 metres further into the territory, or along a different edge of the territorial boundary. Table 3-3 shows the allocation of treatments between pairs and the times that they received their trials.

Each trial began with a five-minute pre-playback observation period, used to establish the position of the birds, either by sight or by their vocalisations. These observations were recorded to DAT as a running commentary. The pre-playback period was followed by a presentation of one of the three stimulus songs. The order of the stimulus songs was randomised to eliminate the effects of any seasonal or day-to-day variability that might have been carried over in the source songs. The first presentation was followed by two minutes of continuous observation which was again recorded to DAT.

Table 3-3 Experimental Schedule (male-male pairs presented in **bold**)

Pair Name	Treatment order	Time	Days
L-nino & Racino	Undegraded ; Degraded	early morning	14/9, 4/10
Serpens & Botswana	Degraded ; Undegraded	early morning	8/8, 1/9
Pyrosia & Gossum	Degraded ; Undegraded	mid morning	10/8, 1/9
Duja & Gian	Degraded ; Undegraded	early morning	5/8, 2/9
Vishnu & Huhu	Undegraded ; Degraded	mid morning	4/9, 16/10
Cirrus & Batagooli	Undegraded ; Degraded	mid morning	9/8, 4/9
Bosnia & Matabeelee	Degraded ; Undegraded	early morning	17/9, 18/10
Merlin & Bakano	Undegraded ; Degraded	mid morning	27/9, 21/10
Trevor & Kawi	Degraded ; Undegraded	early morning	27/8, 21/10
Jimmy & Bo	Degraded ; Undegraded	early morning	29/9, 22/10
Bob & E.T.	Undegraded ; Degraded	early morning	22/9, 12/10
Hudson & Halls*	Degraded ; Undegraded	mid morning	25/9, 30/10

* Note that the results for the second treatment of Hudson & Halls were lost due to theft

At the end of the observation period, a second presentation was given. This was followed by another observation period in the same manner as before. Presentation/observation periods continued until the first approach was made by a bird to within 40 metres of the speaker, and then two more presentation/observation periods were given. However, if neither bird entered the 40-metre zone after three presentation/observation periods, then no more presentations were given and the trial was deemed a non-response.

Once the bird(s) arrived within the observation area, their movements were tracked so that whenever a bird moved more than approximately three metres to a new place and remained there for at least three seconds, a site number was recited into the recording (e.g. 'bird 1 at site 2'). This location was indicated on an aerial map of the speaker zones. If either of the birds approached within 20 metres of the speaker during the presentation/observation period, the observation period was extended by ten minutes from the time that they entered the 20-metre zone. However, if both birds moved beyond the 20-metre zone during that ten minutes, the observation period was reset to two minutes from the time that they left.

The last presentation/observation period was followed by a ten-minute post-playback observation period, with observations again recorded to DAT. For each experiment, I was accompanied by a helper who controlled the playback apparatus and remained motionless while I stood and watched the birds. Both myself and my helper wore dark clothing to minimise drawing the bird's attention.

3.2.4 Data entry

To describe the time spent by birds at positions relative to the speaker, the maps which illustrated the pairs movements were divided into three sections: 'in front of speaker' (the facing direction of the speaker, bearing 315-45 degrees), 'behind speaker' (opposite to the facing direction of the speaker, bearing 135-225 degrees) and 'adjacent to speaker' (either side of the speaker, bearings 45-135 and 225-315 degrees, combined). For each time period, I took the amount of time spent by each bird in each zone, and divided this total by twice the duration of the time period. This gave the mean time spent by the pair in each zone (for example, if one bird stayed in zone 1 and the other stayed in zone 2, then the pair spent 50% of its time in zone 1 and 50% in zone 2). To combine pairs, I took an average of their corresponding frequencies.

A similar method was used to determine the time spent by the pairs at certain spacing distances (<1 metre, 1-5 metres, 5-10 metres, >10 metres). Each time one of the birds moved, I estimated the distance between the pair members by referring to the maps used above. Then, for each time period, I divided the total time spent at each distance class by the duration of the time period.

3.3 Results

3.3.1 Responsiveness of Experimental Pairs

Five pairs did not respond after being exposed to three of their first treatments, and were re-tested at new playback sites. For two of these pairs, Jimmy & Bo and Bakano & Merlin, the new site was set up 50 metres further towards the middle of the territory, while for L-Nino & Racino, Bosnia & Matabeelee and Vishnu & Huhu the new site was set up along a different side of the territory boundary (Appendix 3). All pairs responded in some way to playback at either their first or second playback sites.

Out of all of the initially successful tests, six pairs responded to their first trial for both treatments (L-Nino & Racino, Duja & Gian, Bosnia & Matabeelee, Jimmy & Bo, Bakano & Merlin, Serpens & Botswana). The remaining five pairs required more than one trial for their first treatment. Four of these pairs then responded to the first trial of their second treatment (Pyrosia & Gossum, Vishnu & Huhu, Cirrus & Batagooli, Trevor & Kawi), while the remaining two pairs (Hudson & Halls, Bob & E.T.) required more than one trial for both of their treatments.

For the second treatment of Bob & E.T. and for both treatments of Trevor & Kawi, the birds did not approach to within 40 metres of the speaker during the experiment; however, they were often in sight just outside of the playback zone and they did respond by singing. Trevor & Kawi eventually responded to their first treatment by entering and moving through the playback zone, but this occurred a few minutes after post-playback.

During the pre-playback period for 17 of the 24 trials, I could not hear any song being given in the neighbourhood, which meant I was often not able to initially locate the pairs. On two occasions I heard or saw the experimental pair while travelling to the site and so was able to point the speaker in their direction, and for Serpens & Botswana the pair were already within 40 metres of the speaker at the beginning of both of their trials. For the remaining pairs, I assumed they were located near the middle of their territory.

Because I was rarely able to see the birds from the very start of the first presentation, I had few data to describe the first playback and observation period. This did not necessarily indicate a lack of responsiveness, since the birds may have heard the presentation and could have been moving towards the speaker. Furthermore, although I had collected around ten minutes of observation data for 35 of the 69 presentations, I could not assume that the birds were still responding to the presentation by the end of the ten minutes. After the first few playbacks, there were often other birds in the singing in the neighbourhood which the experimental pair may have been responding to as well. Hence, for all of the analyses apart from the cases of birds singing during the playback, I decided to use only the data for the second and third presentations and the first two minutes of their respective observation periods. Post playback data were taken for the ten minutes immediately following the third 2-minute observation period.

3.3.2 Degraded versus undegraded song

Figure 3-1 shows examples of degraded and undegraded verses. Both versions of each verse were derived from the same source song. The sonagrams show that the 100 metre song degradation procedure resulted in both a loss of harmonics at higher frequencies (all harmonics above the second harmonic in the last three traces in verse B, and all harmonics above the first harmonic in the two middle traces in verse C) and an extensive echo effect for many song elements. Reverberation has also caused a lengthening of the fundamental frequency (hence the prominent trailing of the final trace in verse A) and an overall loss of definition (particularly for the first trace in verse B and the last trace in verses C and D).

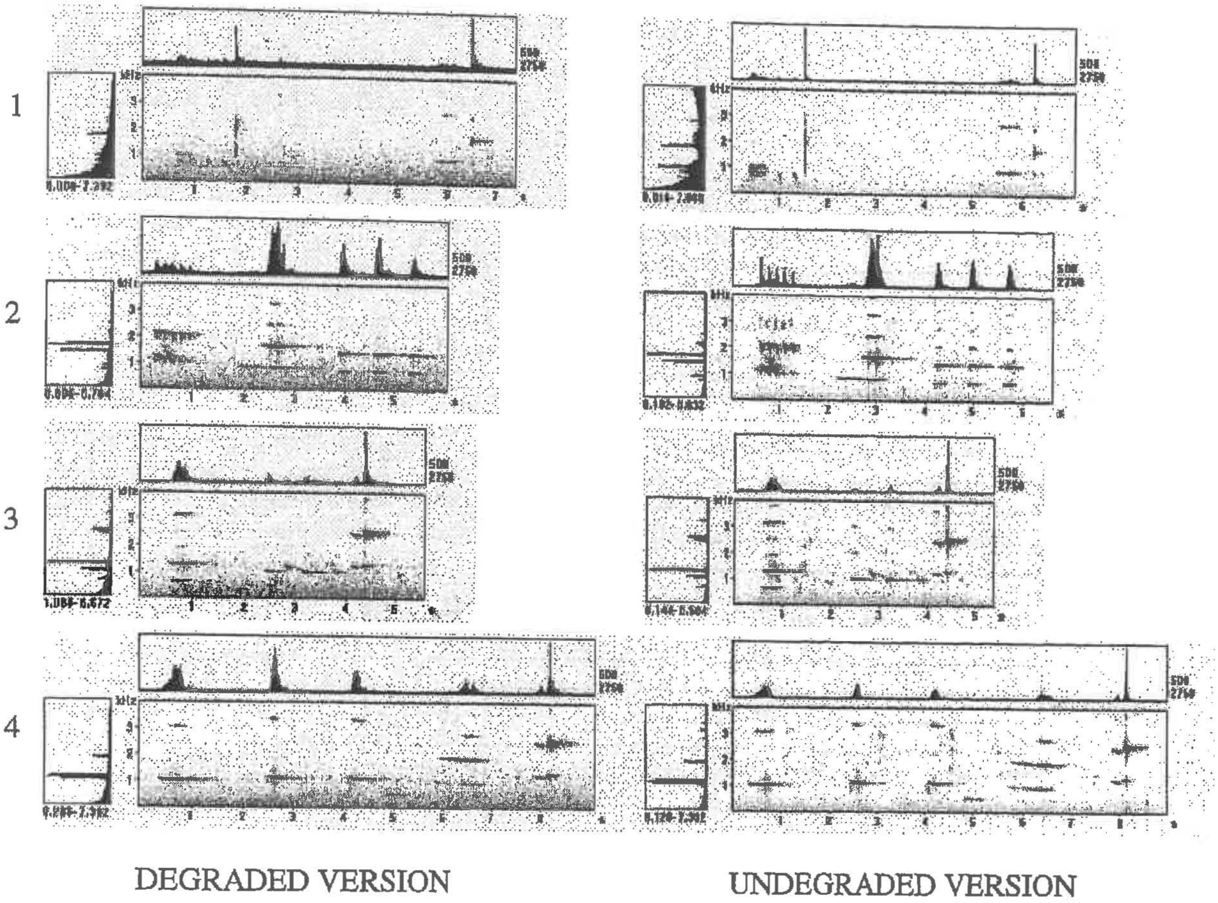


Figure 3-1 Effects of degradation procedure (L-Nino & Racino stimulus song verses 1-4: Main windows show sonagrams; smaller windows directly above and to the left of the main windows show the distributions of amplitude, averaged over frequency and time, respectively)

Figure 3-2 shows the proportions of time spent by male-female and male-male pairs in each zone around the speaker, for the second and third presentations and for the ten minute post-playback period. I have omitted error bars from the presentation because they were usually extremely large (up to 0.14), so the small variation between the bars is not likely to be meaningful. Nevertheless, for both degraded and undegraded tests, the figure shows that pairs spent the most amount of time in front of the speaker and the least time behind the speaker; approximately equal time was spent above and adjacent to the speaker (mean proportions of time spent

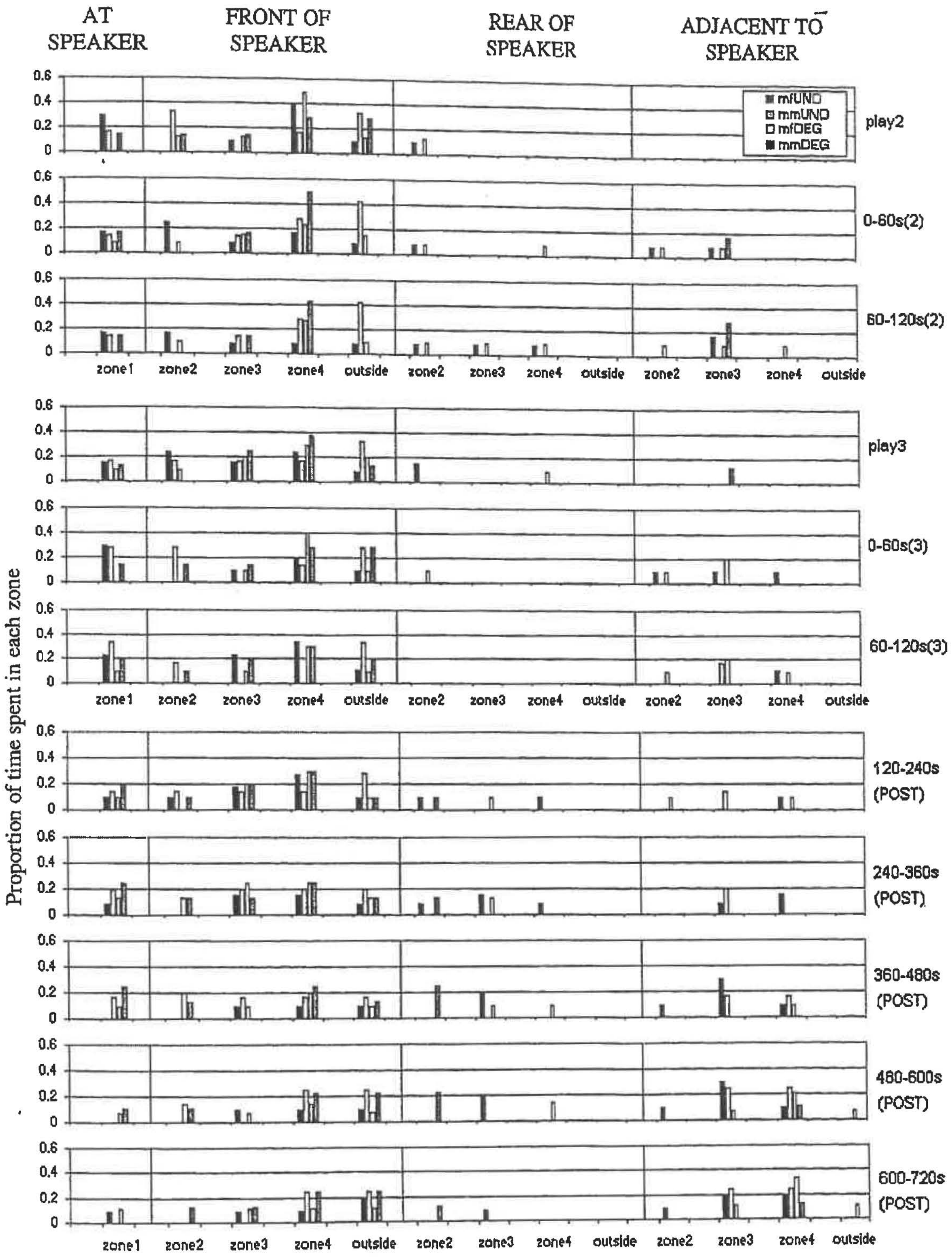


Figure 3-2 Time spent by pairs in each zone surrounding the speaker during and after the second and third presentations and during post-playback (zone1= 0-5m from speaker ; zone2= 5-10m ; zone3= 10-20m ; zone4= 20-40m ; outside= >40m)

(undegraded, degraded): above = 0.15, 0.11; front = 0.56, 0.63; rear = 0.10, 0.10; adjacent = 0.19, 0.15).

More time appeared to be spent by some pairs behind the speaker for the second presentation than for the third, however pairs were no more likely to move beyond the speaker for degraded song than they were for undegraded song (mean proportions of time spent behind speaker (undegraded, degraded treatments): second presentation = 0.05, 0.06; third presentation = 0.01, 0.02).. There was similarly no tendency for pairs to move beyond the speaker for degraded treatments during post-playback, with pairs staying mainly in front of the speaker (mean proportions of time spent during post-playback (undegraded, degraded treatments): above = 0.03, 0.07; front = 0.21, 0.31; rear = 0.06, 0.07).

Figure 3-3 shows the ways that male-male and male-female pair members were spaced during and following the second and third playback presentations. Pairs seemed to spend considerably more time at a spacing of less than one metre apart than they spent at either 1-5 metres, 5-10 metres or >10 metres apart. This spacing occurred whether they were played degraded song or undegraded song, and did not change during the two minutes that followed either of the playbacks. Pairs were also closely spaced throughout the post-playback period for both degraded and undegraded song presentations.

Figure 3-4 shows the time taken for pairs to begin singing in response to playback, and the number of verses sung by the pair during the 2 minutes immediately following each playback. On five occasions, pairs continually recited verse 1 but never proceeded to verse 2. Hence, in order to avoid giving weighting to these incomplete songs (which did not represent the full vocal repertoire), I only counted verses once if they occurred more than once in succession. Both song measures also exclude any vocalisations that occurred during the actual playback. Furthermore, some pairs did not sing at all during the observation period, so for these I assigned a latency which song may have been produced by all pairs for the undegraded song presentation, but this difference was not significant for either the second (t=1.51, n.s.) or third presentation (t=1.21, n.s.).

Figure 3-5 shows the time taken for either of the pair members to move since the start of playback, and the total number of moves made by the pair members. Pairs did not move at all during or after the playback for 13 presentations, and again for these I assigned a latency that was higher than the longest latency observed for the pairs (200 seconds, maximum latency = 197s). Pairs did not move sooner, or move more, for either treatment in comparison to the other.

3.3.3 Male-female versus male-male pairs

Figure 3-2 shows that some male-male pairs spent more time above and in front of the speaker than male-female pairs during the presentations. No male-male pairs moved behind the speaker for either presentation (mean proportions of time spent (male-male, male-female pairs): above = 0.18, 0.13; front = 0.76, 0.59; rear = 0, 0.12; adjacent = 0.06, 0.16).

Figure 3-3 shows no differences between male-male and male-female pairs in terms of their spacing, apart from an absence of cases where male-male pairs were spaced at less than five metres apart during the two minutes following their second presentation of undegraded song.

Figure 3-4 suggests that male-male pairs may have sung sooner than male-female pairs after being given undegraded song. However, this difference was not significant for the second presentation (t=1.11, n.s.) nor the third presentation (t=1.68, n.s.). There do not appear to be any differences between male-male and male-female pairs in terms of the amount of song given.

Figure 3-5 shows that male-female pairs may have moved more times on average than male-male pairs for their first presentation of undegraded song. However, this difference was again not significant (t=1.30, n.s.).

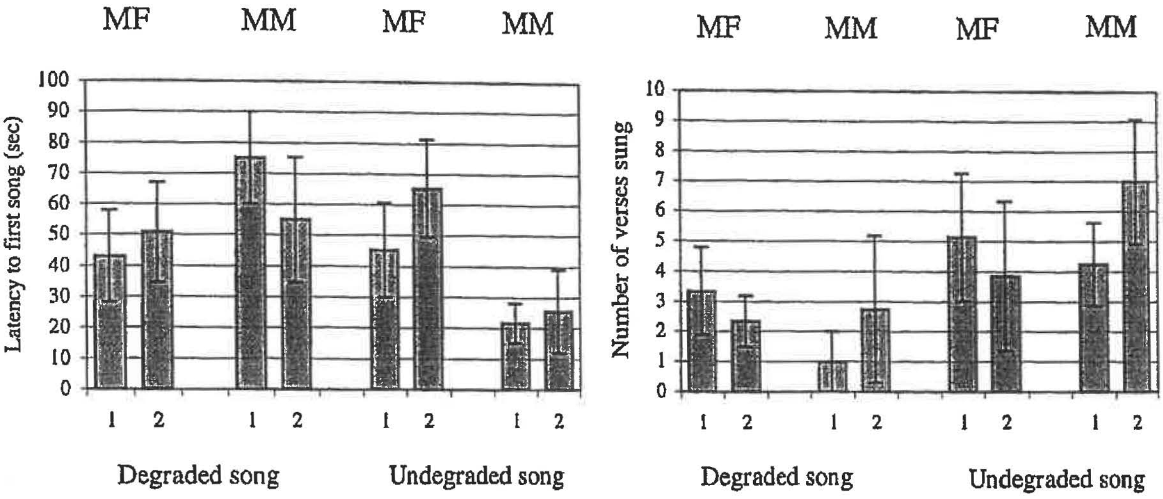


Figure 3-4 Length of time until male-male and male-female pairs sang, and the amount they sang (mean ±SE), after two playbacks of degraded and undegraded song (measures taken from the end of playback onwards)

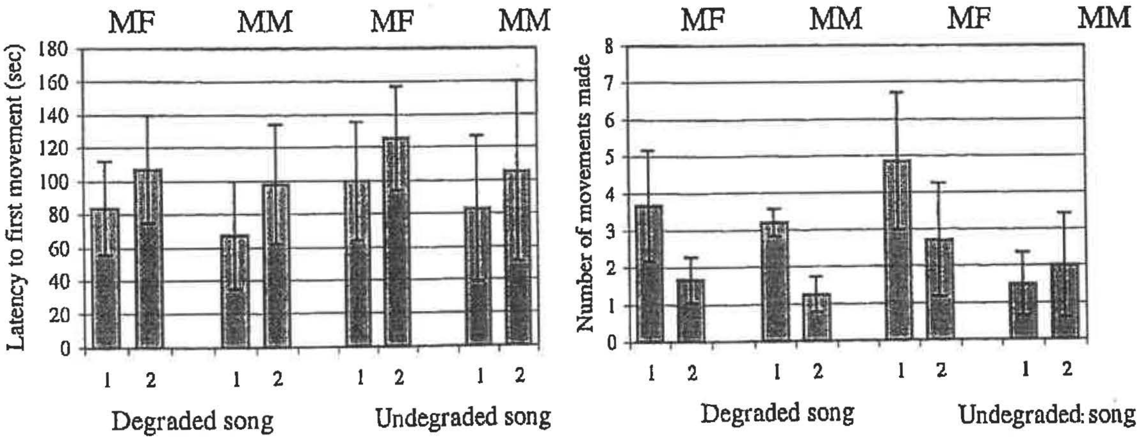


Figure 3-5 Mean latency to move and number of movements (±SE) of male-female and male-male pairs during and after two playbacks of degraded and undegraded song

3.3.5 Second versus third presentations

In figure 3-5, both male-male pairs and male-female pairs showed a longer mean latency to move since the onset of playback for both treatments, and also made fewer movements for the third presentation compared to the second. However, neither of these differences were significant (t=1.63, n.s.).

3.4 Discussion

3.4.1 Degraded versus undegraded song

I found no differences in the response of kokako pairs to degraded versus undegraded song in terms of the time spent within each speaker zone. Pairs moved directly towards the speaker for both treatments, and on no occasion did a pair move beyond the speaker without spending a large amount of time directly above or at a short distance in front of the speaker. These results do not agree with those of published studies in which song degradation influenced ranging. For a study on Carolina wrens, males responded to degraded song by countersinging and occasional theme matching, whereas they responded to undegraded song with an immediate cessation of singing, flying over the speaker, and occasionally by attacking the speaker (Richards 1981). Dusky antbirds approached sooner and closer to undegraded song than to degraded song, and also sang sooner and displayed for a greater length of time to undegraded song (Morton & Derrickson 1996). There are several aspects of the singing behaviour of kokako that suggest a capacity to range (such as the occurrence of dialects, countersinging, and the use of elevated song perches), but ranging was not apparent here. Because of the obvious limitations of sample size, the results of this experiment should not, however, be used to rule out the likelihood that kokako possess this ability.

Certain features of kokako song appear to be more susceptible to degradation than others, and this could enable the song to be used in ranging. In fact, Hughes (1981) identified several kokako song elements that were highly susceptible to reverberation and reflection. These included phrases with 'double-voicing', whereby the same bird is able to produce two discrete elements at the same time. The amplitude of the two elements is inversely coupled, so that when one is loud the other is soft, making the latter element more susceptible to degradation. Hughes (1981) also noted several cases of rapid frequency modulation and long, tonal frequency sweeps. Frequency sweeps are highly susceptible to reverberation and are most common in open-habitat species that range (Anderson & Conner 1985; Naguib 1996a). Rapid frequency modulation is rare in kokako song (Hughes 1981), and neither this, frequency sweeping nor double voicing were obvious features of any of the dialects that I recorded. Nonetheless, sonagraphic analysis of two of the stimulus songs showed that some of the song syllables in this study may also be highly influenced by degradation.

Observer presence may have been a major problem in the design of this experiment, particularly since all of the pairs used in the study had interactions with humans in the past, and may well have learnt to associate human presence with playback. Although I wore dark clothing and avoided sudden movements, the birds would have certainly heard my voice and were probably aware of my presence. Furthermore, the understorey was very sparse for many playback sites so I was often in full view of the birds. Eliminating this problem (by hiding or distancing myself from the speaker) would, however, have affected the accuracy and detail of my observations during the trials.

The results strongly suggest that the birds knew exactly where the sound was originating from. Even though they often matched certain parts of the playback and appeared to search for intruders, the birds usually stayed well within the 40 metre speaker zone. In fact, during playback both birds would regularly position themselves on one of the closest available perches and directly face the speaker whilst singing or giving calls. Allowing birds to have close-range experiences with speakers is a common but fundamental flaw in the design of song degradation experiments (Naguib 1996a). Continual playback complicates the birds' perception of the stimulus, since they will hear the signal from several different directions as they move throughout the speaker zone, and in doing so will localise the source of the sound by simple deduction. This problem can be solved by stopping playback before the birds approach the speaker: if the birds were forced to range on the basis of only a small presentation of song, then they may be encouraged to speed up decisions on how and towards whom to react (Naguib 1996a). However, this protocol assumes that variable-length portions of the same song will encode the same message, and will have a similar influence on the bird's behaviour. This may be true for species that have songtypes (such as many temperate bird species) since their songs are often comprised of the same elements repeated in rapid succession. Yet for kokako, which have a song length of almost a minute (often without any repeated elements), a song excerpt of 10 seconds may not have the same meaning to the receiver as a full rendition of song. One could implement this design in a kokako ranging experiment, but it would require a very large sample of pairs to ensure that the effects of degradation are not distorted or outweighed by the effects of presentation length.

Presenting the pairs with three consecutive presentations from the same position may have further complicated their perception of the stimulus, and this could have allowed them to deduce the exact source of the sound by the third presentation. Consecutive playbacks might have also cause a general waning of response strength from the first presentation to the third, even though I attempted to minimise this effect by giving them a different song rendition each time.

Another problem may have been a high level of wide-band background noise on some of the stimulus songs. Wide-band noise was caused by wind and running water, and although it was reduced by highpass filtering it could not be completely removed. In the Hunua Ranges it was especially difficult to record the source songs without the sound of nearby streams, and this effect was exaggerated during the degradation process. Wide-band noise had the effect of hiding some of the quieter song elements, and may have made some songs generally less detectable to pairs. The high level of background noise on the playback and at the playback site could be why Hudson & Halls needed more than one trial for both of their treatments. Also, because of the loss of detail on the recording, these songs may have lacked some species-specific releasing stimuli (McGregor 1994; Naguib 1996a), which would have reduced the bird's ability to recognise the stimulus songs.

For close-range encounters with the speaker, background noise may also have provided the birds with a cue for localising the origin of the signal. For some of the degraded stimulus songs, there may have been up to a second of noise before the first song syllable occurred and this often appeared to be just as effective at attracting the bird's initial attention as the actual playback. The importance of wide-band background noise in an experiment such as this can be tested quite easily by incorporating it as an additional treatment in itself.

Even if all of these factors were to be controlled, certain features of kokako ecology in general may make them difficult to work with in a degradation experiment. The dense nature of the mid- to upper-canopy for many of the playback sites, and the generally poor flying ability of kokako, meant that the birds were unable to make long unobstructed flights over the speaker. The distance that a bird flies beyond the playback speaker provides an immediate indication of how far away it estimates the stimulus to be, and it is therefore one of the most pertinent and measurable responses (Naguib 1996a). However, the way that kokako run through the canopy may allow them to take frequent pauses to periodically assess the stimulus to decide on where it is sourced. Again, this problem could be reduced by stopping playback before the birds approach.

3.4.2 Male-male versus male-female pairs

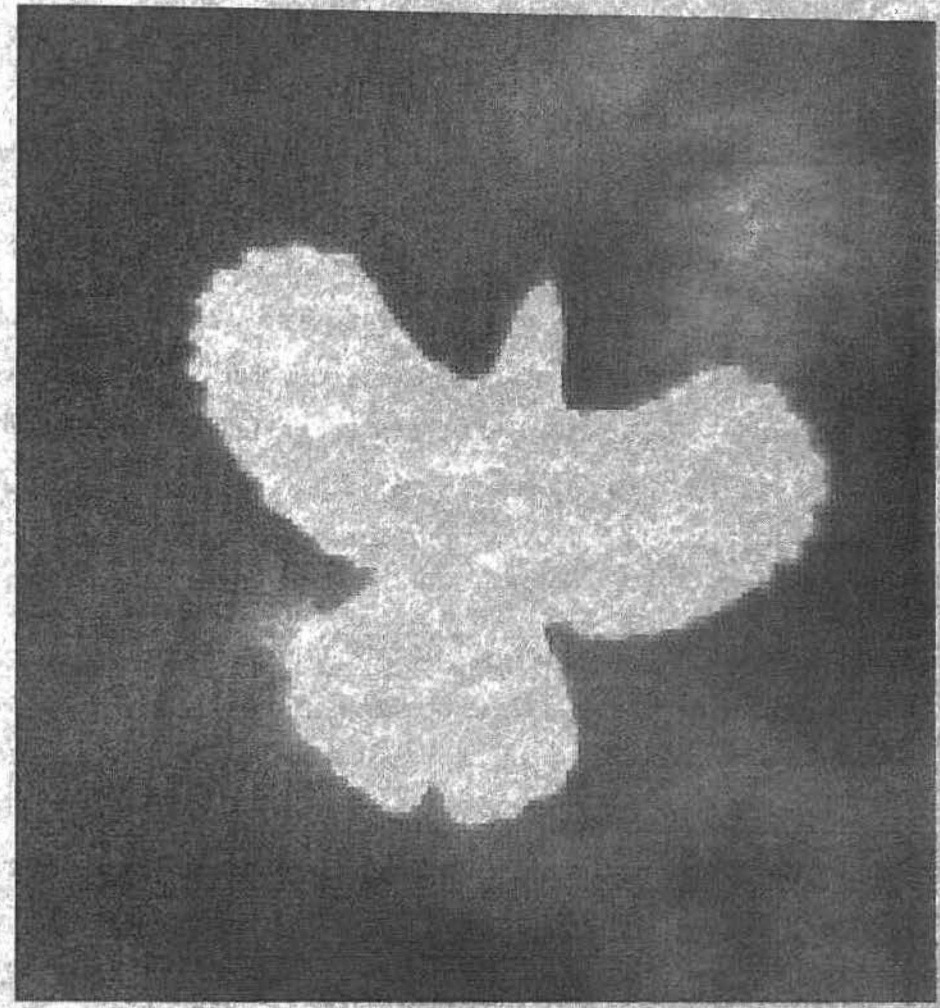
The experiment showed no obvious behavioural differences that distinguish male-male pairs from male-female pairs in a territorial context. However, this does not necessarily imply that male-male pairs behave identically to male-female pairs. It is quite possible that behavioural differences do exist, but they are likely to be very difficult to observe and/or they may require a much larger sample size of pairs to be adequately represented.

Male-male pair bonds may have a different function to male-female pair bonds, and this could be reflected in their intra-pair spacing distance: if the members of a male-male pair are simply sharing a territory, then they may respond to an intruder more independently than would a male-female pair. This is because the distance to which the birds tolerate each other gives an indication of their willingness to co-operate (Hultsch 1984). Although the experiment revealed no significant differences between male-male and male-female spacing distances, it did suggest that male-male pairs may have a tendency to space themselves more widely than male-female pairs in certain contexts. The spacing distance of a male-male pair may depend on how much of a threat it perceives an intruder as being. This could explain why the male-male pairs used in this study were widely spaced after the second playback of undegraded song, but came together during and after the third playback.

Another difference may arise in the form of displays used during actual border disputes. When more than one pair is present, it is important that each bird can recognise its mate to avoid misdirecting its attacks. The performance of sex-specific behaviour is an important feature of territorial defence in many duetting species, because it allows each pair member to recognise which bird is its mate, and which is its intended target (usually of the same sex as itself) (Farabaugh 1982). Sex-specific behaviours may include visual displays and high-frequency, low-intensity vocalizations for short-range communication, as well as certain song components (Farabaugh 1982). If behaviours that enable sex recognition are important in kokako territorial defence, then male-male pairs might be expected to adopt either a different strategy (which does not require sex-recognition behaviour), or the same strategy with one of the birds assuming the female role. As discussed in Chapter 2, male-male pairs may occur with one bird taking the female song role and the other bird taking the male role, and this in itself may provide a strong enough cue to enable each bird to recognise another's sex during territorial disputes. Yet there may also be other less obvious female-specific behaviours which a secondary male does not perform. However, because of the difficulties of observing birds in dense forest I was not able to measure the occurrence of any kokako behaviours, apart from their song.

To conclude, there was no evidence from the responses of kokako pairs to degraded versus undegraded song that showed an ability to range, neither were there found to be any differences between male-male and male-female pairs in terms of their response to the simulated intrusions. Differences may, however, be found in both cases if a larger sample size were to be used, and if the pair's close range experience with the speaker during playback was to be eliminated by stopping playback before the birds move into the vicinity. The number of presentations given to a pair during each trial may also need to be reduced to show ranging, although this could limit the potential to observe the less obvious behavioural differences between male-male and male-female pairs. Again, this problem could be solved by a larger sample size.

CHAPTER FOUR



CONCLUSIONS & RECOMMENDATIONS

Chapter 4

Conclusions & Recommendations

Male-male pairing is a characteristic feature of declining mainland kokako populations, and because kokako are sexually monomorphic, male-male pairing makes it difficult to estimate the number of viable breeding pairs. The main focus of my study was therefore to examine variation in the song and territorial behaviour of kokako male-male and male-female pairs, so that managers could distinguish between the different pair types and determine the number of pairs in a population that are capable of breeding. In addition, I examined whether kokako use habitat-induced degradation for ranging familiar song.

In chapter two, I firstly identified differences in the duet contributions of males and females. 8 out of 11 males sang more than their female mates, and all females concentrated their song at a higher pitch than their mates. From these differences, I was able to make predictions about the most likely song features male-male pairs might be expected to show. One confirmed male-male pair met my first prediction, that the vocal contribution of the secondary male will exceed that of local females. Five male-male pairs (one confirmed, four suspected) met my second prediction, that song pitches most used by local females will be under-represented in the duets of male-male pairs. Of the remaining three male-male pairs, one suspected male-male pair met both predictions, while two male-male pairs (one confirmed, one suspected) met neither. Although male-male pairs sang differently to 'typical' male-female pairs, females in some dialects incorporated male-like song pitches into their songs.

In chapter three, I was unable to show any differences in the territorial behaviour of male-male and male-female pairs, when presented with degraded or undegraded song. Nor were any general differences seen in the response of kokako pairs to these two treatments. I attributed both of these results to an insufficient sample size, and the fact that the birds had considerable close-range experience with the speaker, which may have provided them with an obvious cue for locating the source of the sound.

Some male-female pairs could be mistaken for male-male pairs on the basis of their duets and territorial behaviour. This is a major obstacle in being able to reliably estimate the proportion of non-breeding pairs in a population. Nonetheless, females that sing male-typical song may retain components of female-typical song, and this may enable male-male pairs to be distinguished. Further research is required on this issue.

4.1 Theoretical contributions

The kokako is the first species in which male-male pairing has been observed in the wild. Male-male pairing has been shown to occur in captivity for laughing gulls *Larus atricilla* (Hand 1981), and for two duetting species, robin chats *Cossypha heuglini* Hartlaub (Hultsch 1983) and tropical bou-bou shrikes *Laniarius aethiopicus major* (Thorpe 1972). Only a few male-male pairs were described for these species, yet for kokako, male-male pairing is known to be relatively common.

Whether kokako are the only passerine in which wild male-male pairs occur remains to be seen. Many studies in the past which described detailed aspects of duetting have used unbanded birds (for example, Diamond & Terborgh 1968; Hooker & Hooker 1969; Wickler & Seibt 1982) and authors may have misidentified the sex of pair members simply because they did not expect male-male pairing to occur. Similarly, observations of kokako song by Hughes (1981) were mainly on unbanded birds, and were made well before the existence of male-male pairing in kokako was first reported (Innes *et al.* 1996). As a consequence, some of the male-female kokako pairs whose duets Hughes had characterised may have been male-male pairs (one case of male-male pairing may have been the 'Pikiariki Road (site 1) pair', which divided up their song differently (and more evenly) when compared to a neighbouring pair (site2)). The occurrence of male-male pairing in other duetting species may therefore be more common than is currently thought, particularly in species where factors that limit female abundance (such as nest predation) mean that there is potential for a highly skewed sex ratio.

Male-male kokako pairs behave similarly to male-female pairs, and this has also been shown for the bou-bou shrike and robin chat male-male pairs (Thorpe 1972; Hultsch 1983). Hence, for the three species in which male-male pairs have been described so far, male-male pairing occurs so that one bird (whom I have called the secondary male) appears to assume the female duet role. However, in the current study, secondary males also assumed characteristics of the male-typical song role, such that the song was divided more evenly between the birds. Furthermore, in two male-male pairs (one which has been confirmed using DNA tests), the division of song elements even occurred within phrases of song, a feature not seen in any of the local male-female pairs. This feature, which I called 'phrase splitting', could contribute towards the stability of these two male-male kokako pairs, at least one of which is known to have been in existence for more than seven years. Phrase splitting may enable male-male pairs to divide the duet more equally between them, so that the range of male-typical song pitches sung by each pair member remains constant from one rendition to the next.

In the absence of potential female mates, male-male pairing in kokako may enable two (otherwise single) males to share the energetic costs associated with the production of full song and territory maintenance. Permanent pairing and year-round territoriality, both characteristics of kokako, could be favoured by intraspecific competition if pairs are more successful than singles at maintaining territories (Hultsch & Todt 1984). Single males are thought to try to counteract this effect by 'solo singing', whereby the bird incorporates both male and female song components into its territorial song to create the illusion of a pair in residence (Hultsch 1983; Hultsch & Todt 1984). However, if female song is difficult for a male to incorporate into his own song, then two males could be collectively more effective at territorial defence than a single male: by duetting, they may be able to sustain more song over a longer period and/or at a higher rate than a single bird, and be more capable of equaling the song output of neighbouring pairs.

4.2 Suggestions for future song research

A large amount of information regarding the long-term dynamics of kokako pair bonds may be gleaned from their songs. It would be very interesting to know whether the songs of particular pairs change to any large extent over time, and how quickly coordination between pair members develops from the time that they first come together. One feature of particular interest to the male-male pair study was the phrase-splitting shown by the two confirmed male-male pairs at Mapara. If phrase-splitting represents a way to divide the quantity and diversity of song more equally, then it could be a widespread feature of long-term male-male pairing. As mentioned in chapter two, this possibility could be further explored by taking periodic recordings of Bosnia & Matabeelee (a relatively 'new' male-male pair) over the next several years, and seeing whether the duet becomes similarly specialized.

In chapter two, I proposed that male-male pairing may allow two males to hold a territory when either or both birds are unable to defend a territory by themselves. This theory could be tested relatively easily by a mate removal experiment, perhaps using birds whose mates have been captured and transferred to other populations during the course of management. Alternatively, one could compare the song performance of solitary males to that of male-female pairs and male-male pairs, and relate this to territory size or quality. Song measures could include the percentage of time spent singing, song completeness (i.e. the proportion of the full duet that is actually sung), and the amount of song given that is usually produced by the female.

In chapter three, I tested the ability of kokako pairs to range familiar song, and determined if male-male and male-female pairs respond differently to playback. This was the first time anyone has attempted to quantify the response of kokako to playback under an experimental regime. I was unable to identify any distinctive patterns that could distinguish the pair types or the responses to each treatment, and I suggested reasons why this was so. I also emphasized the risk of making assumptions about song portions of different lengths, in that a small segment of song may not have the same meaning to the birds as a longer segment: each rendition of kokako song may be up to a minute in length and is composed of many different types of phrases.

If kokako song can reveal information about the internal motivational state of the bird, then there is a potential for a large amount of information to be revealed in the course of a single song rendition. I suggest that future song studies with kokako should first work towards attaining a thorough understanding of the structure of the song itself, before testing whether the 'classic' functions of song in unrelated species can apply to kokako.

Certain aspects of kokako song are unusual, such as the double-voicing phenomenon described by Hughes (1981), and the way in which the song is structured may also be very different to most temperate species. A great deal of information may be initially obtained by recording bouts of countersinging between neighbouring pairs and distinguishing the singers and their contributions. This could best be done using two microphones, one situated close to each singing bird or pair. One could then examine the dynamics of countersinging between different types of singers, such as male-male pairs, male-female pairs and single males. Simple observational studies such as these may reveal information on the importance of song context (such as the influence of song matching and the use of particular phrases in high- versus low-intensity interactions).

Interactive playback is an important tool, whereby playback is finely coordinated with the focal bird so that the effects of song matching and synchronised song switching can be explored (for an example, see Nielsen & Vehrencamp 1995). For playback experiments on kokako, such a technique could be used to determine the effects of song matching of particular phrases (or types of phrases), and may reveal important information about their use. Other studies could examine the effects of song rate, song sequencing or song completeness. All of these are likely to be important aspects of countersinging interactions, and should be thoroughly understood before any assumptions are be made about the song's meaning, or lack thereof.

Another area that should be examined is song learning. I have recordings of a recently paired male-female pair at Mapara North (Omania & Bettyblubitz), which I made on several occasions over about three months from the time that the female first appeared on the territory. The female was unbanded, was thought to have been quite young (P. Bradfield, pers. comm.), and showed little coordination between her own contributions and those of the male. Her vocalizations also sounded very 'wavery' in comparison to the other local females. If duets have a vital function in ranging, then newly-established pairs such as these may be less willing to engage in territorial defence, and may need to frequently 'practice' in order to perfect their song. Furthermore, there are suggestions that some species which duet may require a significant learning period in order for the song to be perfected and for the pair bond to be established, and this could be a necessary prerequisite to breeding (Wickler 1980). It would be interesting to determine the level of precision that is required before the first breeding attempt, both for young 'novice' kokako pairs and for newly established pairs comprised of older birds. Given the particularly high turnover of pair bonds in kokako, some pairs are likely to be particularly unstable, and this instability could be reflected in their songs.

The formation and maintenance of dialects is an area that also warrants close study. A number of the sonagrams presented by Hughes (1981) were of Mapara South songs, and all of the syllables he presented appear to have persisted, unchanged, to the present day (a span of around 17 years). This may not be entirely surprising, given that the lifespan of kokako is long, but it does demonstrate that kokako song dialects are extremely stable. The Mapara Reserve, with its ease of access and high density of banded birds, presents the perfect research setting to study such dialects in close detail. Furthermore, because Mapara has undergone intensive management, the genealogy of many Mapara kokako is now well known. This makes it possible to determine whether the maintenance of contiguous kokako song neighbourhoods is related to the genetics of the birds that reside within them.

4.3 Recommendations to managers

4.3.1 Distinguishing male-male pairs from male-female pairs

Chapter two revealed that there are differences in the duets of male-male and male-female pairs. However, some females may be mistaken for males if they have a large contribution to the duet. By examining the pitch of song more closely, it may be possible to identify finer differences between females and secondary males. However, given the relatively small sample size of both male-male and male-female pairs used in this study, and the high level of variation in the female contribution between and within dialects, there may well be numerous male-male and male-female pairs in other populations that cannot be distinguished using these measures. This places limitations on whether my two predictions (i.e. that male-male pairs divide the duet more evenly, and that male-male pairs sing less at female-typical song pitches) can be used widely as a surveying tool.

The song features I have identified should be used with some discretion. I have therefore provided three suggestions which I think would improve the use of my predictions, when incorporated with current surveying methods:

a) The two criteria for identifying male-male pair songs should only be used to determine the sex of pairs which are not attempting to breed.

By focussing only on the non-breeding pairs during the nesting season, one could significantly lower the risk of encountering a 'male-like' female, since many male-female pairs will be preoccupied with breeding. In contrast, male-male pairs are often just as vocal during the nesting season as at any other time (pers. obs.; J. Taylor, pers. comm.), and this could make possible non-breeding pairs easier to locate and record. One should still obtain recordings of the songs of breeding pairs, however, as these will provide models against which the recordings can be compared (as demonstrated in chapter 2).

b) The rate of turnover of song features in dialects needs to be determined

It is possible that the song features which I identified in chapter 2 are relatively transient features which may not persist for more than a few years. By comparing my own sonagrams of Mapara South with those of Hughes (1981) from 17 years ago, however, it would appear that dialects may be highly stable over time. If this is true, then patterns in the songs of male-male and male-female pairs may also remain unchanged from one season to the next. This is important if the sexing criteria are to be used in conjunction with the 'pulsing' system of pest management which will be implemented in many kokako populations, since this type of management will require population estimation techniques which are applicable in the long-term.

c) Managers and surveyors should become familiar with song differences that distinguish male-male pairs from male-female pairs

It may be extremely beneficial for surveyors to familiarize themselves with differences between the male-male and male-female pairs in their particular dialect. Because of the extremely simple female component in the Hunua Ranges, surveyors for the Hunua dialect may well be able to identify male-male and male-female pairs by ear. For dialects where the differences are not so obvious, a simple sonagraphic analysis could be used to examine the use of song pitch and quantity with more precision.

4.3.2 Improving kokako responsiveness to surveying tapes

My experience with kokako song throughout the course of this thesis has provided me with several insights on how to improve the general responsiveness of kokako to song playback. The experimental protocol described in chapter 3, in which a rendition of the pair's own song was played towards the middle of the territory at 2 minute intervals, proved to be very effective at drawing the birds into the playback zone: after I had established playback sites within the territories, six pairs approached the speaker on the first day I gave them playback, while the remaining five pairs responded on either the second or third day of playback. I do not know why some pairs responded while others did not. However, by giving the pair its next playback at a different time of the morning, I may have been able to lower the likelihood of another non-response. This may be because the pairs were present in a different part of their territory than for the previous trial and so were better able to hear the tape, and/or they may have been involved in different activities.

Another feature of the experiment which I believe was of importance to playback responsiveness, was ensuring that the pairs can recognise the source song. For each playback, I not only presented the birds with their own song (which, for many territorial songbird species invokes one of the strongest responses (see Searcy *et al.* 1982)), but by having some knowledge of the sequencing of the song I was also able to give them coherent song renditions. Playing the birds a full rendition of the local song may have presented them with a more realistic situation than playing them random sequences of song. Furthermore, I used three different song renditions for each pair, which may have further enhanced the realism of the presentations and decreased the likelihood of habituation. For the dialects I have described in this thesis, I suggest that the sonagrams in Appendix 1 be examined by managers and that the sequencing of the song be thoroughly understood, so that the potential responsiveness of kokako to playback can be maximised. For this purpose, I have made a tape which provides named examples of each song phrase.

4.4 Summary

This thesis has addressed two related aspects of kokako behaviour (singing and territorial responses), in order to identify differences between male-male and male-female pairs. A major part of the first study was conducted to identify trends in the distribution of song pitch and in the size of the song contributions of males and females. For females, these trends included a higher song pitch and a smaller song contribution, while males had lower song pitches which occurred over a wider range. However, females in some dialects incorporated some male-like song pitches into their vocalizations, and their contributions sometimes exceeded the size of the male's. Characterized male-female songs were then used to make predictions about the most likely song features that male-male pairs might show. The first prediction was that male-male pairs will sing so that the duet is divided equally between the birds, while the second prediction was that the female-typical frequency components will be under-represented in the male-male duet. These predictions were then tested using the nine available male-male kokako pairs, of which three were 'confirmed' by leg measurements, an absence of breeding, and, in one case, DNA testing. Of the nine male-male pairs, one met the first prediction, five met the second prediction, one met both predictions and two met neither prediction. It is possible that the recordings of the two latter pairs were of male-female pairs, since one pair included an unbanded bird, and the other pair was later found to have broken up sometime during the recording period so that the remaining occupant had re-paired.

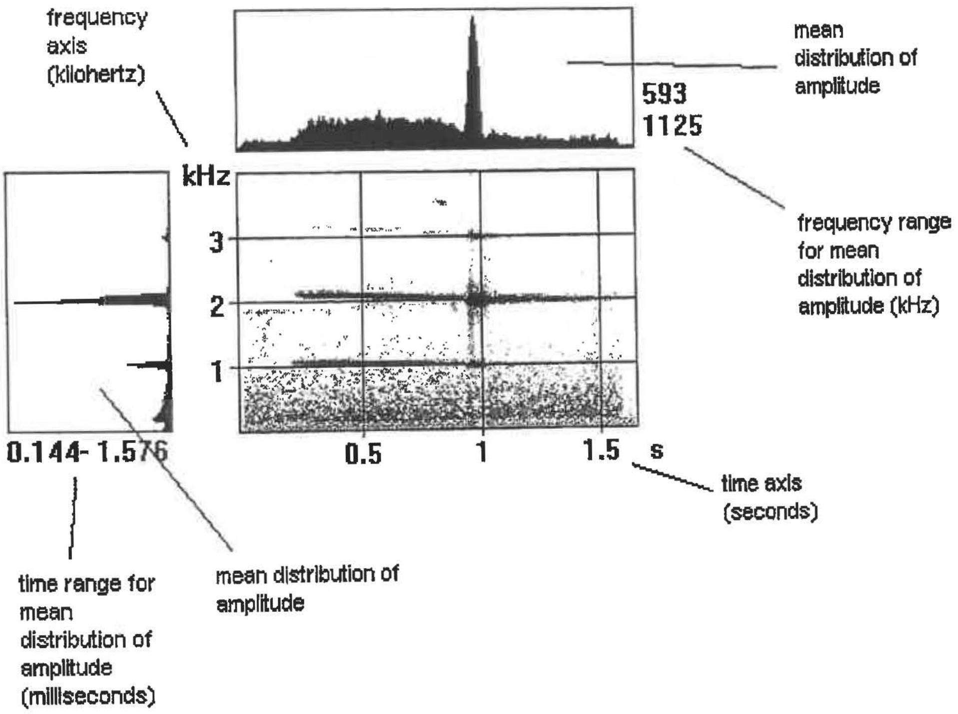
A playback experiment was also conducted to determine whether male-male and male-female kokako pairs were equally capable of ranging song based solely on habitat-induced degradation. Pairs were presented with their own songs from near the edge of the territory, either in an undegraded form or in a degraded form. This study revealed no differences between the responses of the pairs to the two treatments, nor between male-male and male-female pairs. This was possibly due to an insufficient sample size, and the fact that the birds had considerable close range experience with the speaker, which may have provided them with an obvious cue in locating the source of the sound.

Lastly, recommendations to managers were given, so that the information obtained from the research could be used to expand and improve on current kokako surveying techniques. The results of the first study were interpreted as having identifying male-male pairs on the basis of song. This would lower the risk of misinterpreting a particularly vocal female for being a member of a male-male pair. Another, more general, recommendation (which was not directly derived from either study, but had relevance to certain areas) was that the reliability of playback tapes used in surveying could be improved if full renditions of local song were used, rather than small random sequences.

APPENDIX

Appendix 1 Sonagrams of the songs of each dialect used in the study

This section presents sound spectrograms (sonagrams) of each type of song component in the dialects which I have studied. These images were produced using Avisoft Sonagraph Pro version 2.5 software (f_s=8kHz, 16 bit, FFT length: 256, Frame size = 100%, Hamming, Overlap = 75%). Given below is a description of the sonagram window and an explanation of the notation I have used for classifying the song elements. Refer to Chapter 1 for more details about the song.

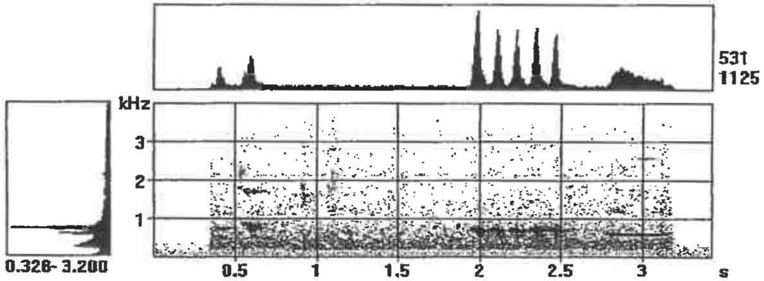


Explanation of song element notation:

r1b(i-ii) Denotes: Rotoehu dialect (r)
verse 1, phrase b (1b)
syllable numbers one to two (i-ii)

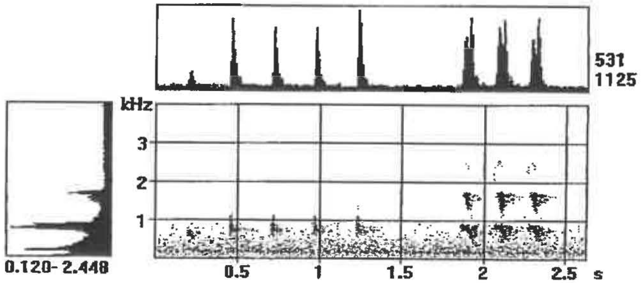
On the right of each phrase name I have presented data which describes the mean occurrence of the phrase in the contributions made by pair members to the characterised renditions of male-female and male-male pairs. The top row ('m') gives the male and 'primary male' contributions. The bottom row ('f') gives the female and 'secondary male' contributions.

Appendix 1-A Mapara South sonagrams



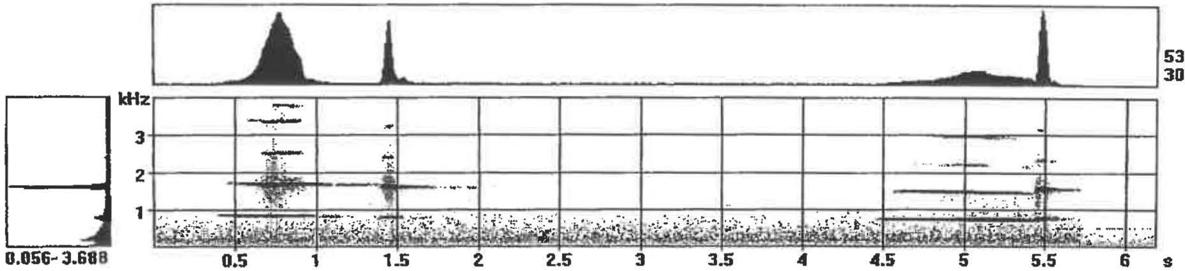
ms1a(i-ii) m: 0.1 ; 0.6
f: 0.0 ; 0.4

ms1b(i-vi) m: 0.3 ; 0.6
f: 0.1 ; 0.2



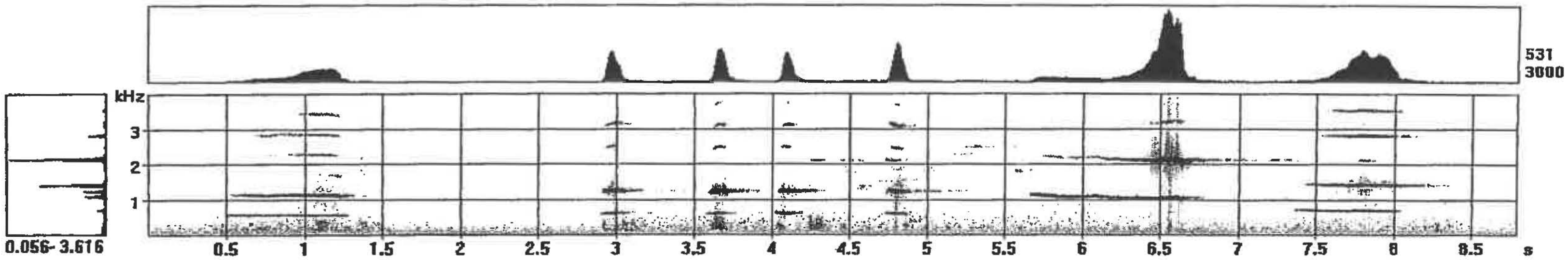
msCall1(i-v) m: 0.0 ; 0.6
f: 0.3 ; 1.0

ms1c(i-iii) m: 0.3 ; 0.0
f: 0.1 ; 0.0



ms1d(i-ii) m: 0.6 ; 0.0
f: 0.3 ; 0.0

ms1e(i-ii) m: 0.6 ; 0.8
f: 0.2 ; 0.0



ms2a m: 0.3 ; 1.0
f: 0.2 ; 0.0

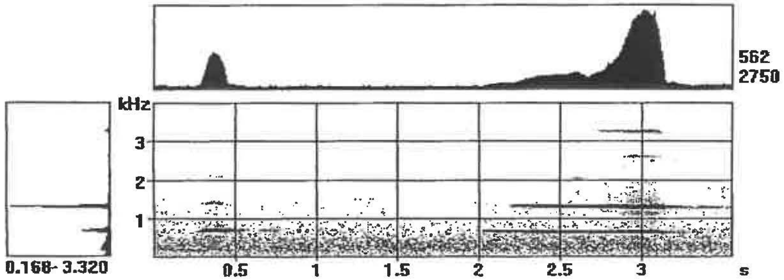
ms2b(i) m: 0.7 ; 1.0
f: 0.3 ; 0.0

ms2b(ii-iv) m: 0.8 ; 0.0
f: 0.4 ; 0.8

ms2c(i-ii) m: 0.5 ; 0.0
f: 0.4 ; 0.2

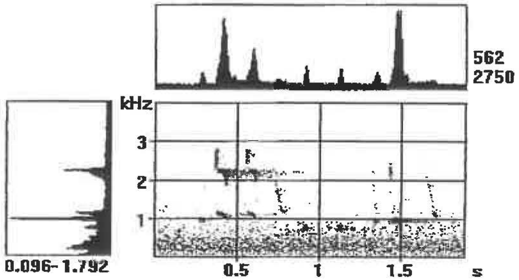
ms2d m: 0.0 ; 0.0
f: 0.1 ; 0.0

Appendix 1-A Mapara South sonagrams (cont'd)

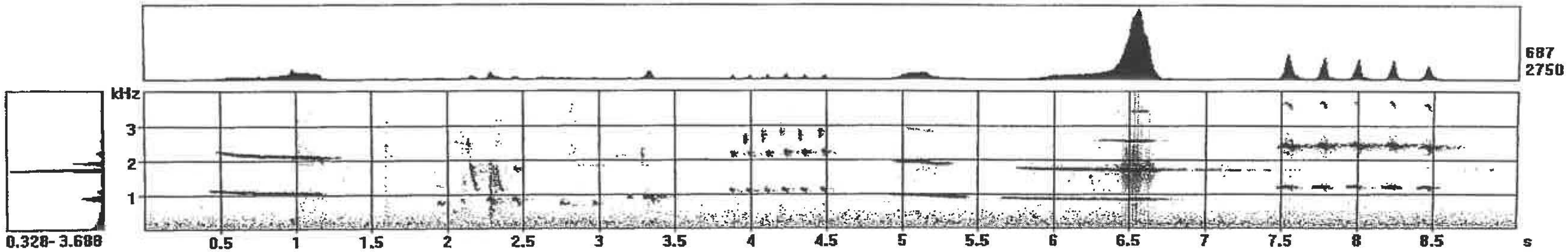


ms3a m: 0.4 ; 0.6
f: 0.2 ; 0.0

ms3b m: 0.3 ; 0.6
f: 0.2 ; 0.0



ms4b m: 0.7 ; 0.8
f: 0.3 ; 0.0



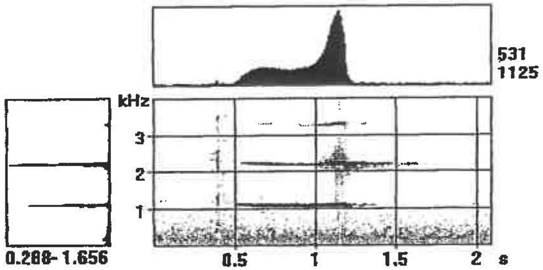
msCall2 m: 0.0 ; 0.0
f: 0.4 ; 0.0

ms4c(i-viii) m: 0.2 ; 0.0
f: 0.1 ; 0.6

msCall5 m: 0.0 ; 0.0
f: 0.3 ; 0.0

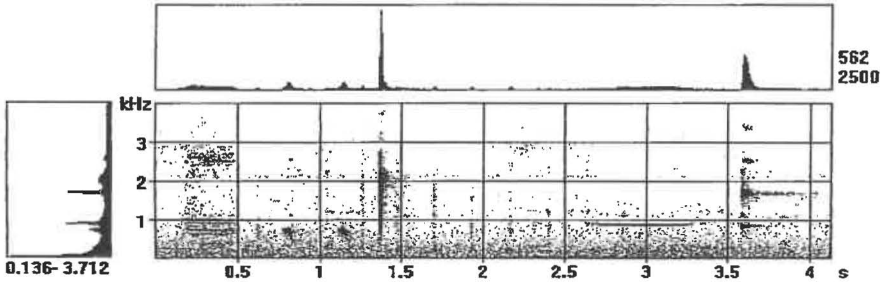
ms4d(i-ii) m: 0.7 ; 0.4
f: 0.1 ; 0.0

ms4e(i-v) m: 0.1 ; 0.0
f: 0.3 ; 0.0



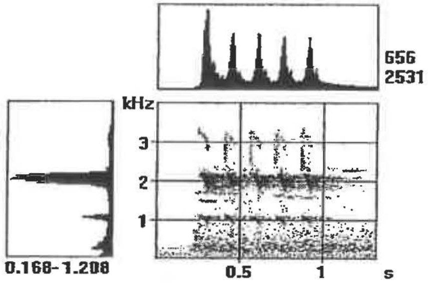
ms4f(i-ii) m: 0.0 ; 0.0
f: 0.1 ; 0.0

Appendix 1-B Mapara North sonagrams

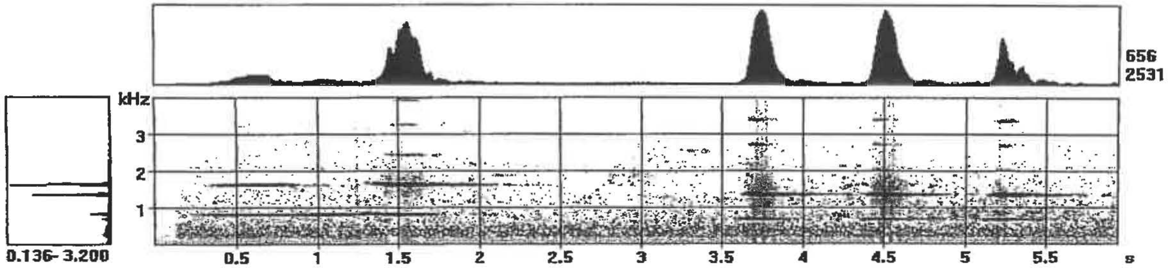


mn1a(i-iv) m: 0.4 ; 0.0
f: 0.9 ; 1.1

mn1b(i-ii) m: 0.7 ; 0.3
f: 0.1 ; 0.6



mn2a(i-v) m: 0.6 ; 0.5
f: 0.0 ; 0.5

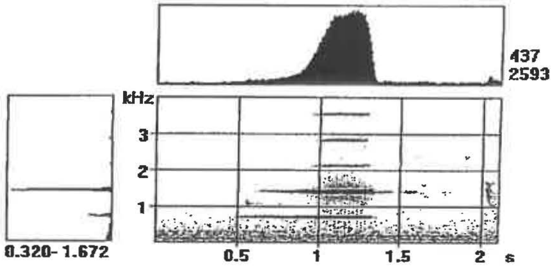


mn2b(iii) m: 0.0 ; 0.4
f: 0.2 ; 0.0

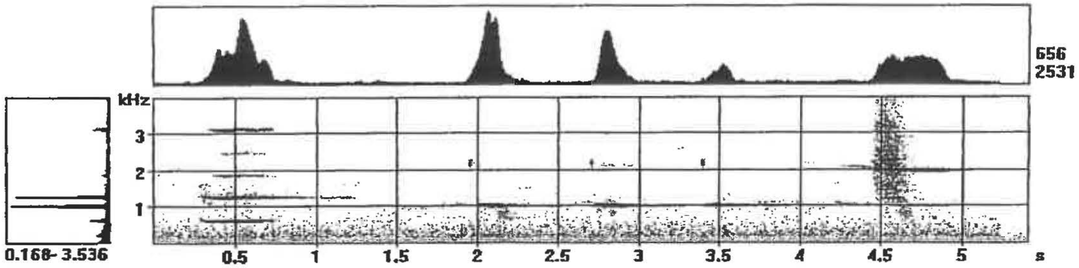
mn2b(i-ii) m: 0.9 ; 0.1
f: 0.3 ; 0.9

mn2c(i-ii) m: 0.8 ; 0.8
f: 0.0 ; 0.3

mn2c(iii) m: 0.6 ; 0.0
f: 0.0 ; 1.0



mn2d m: 0.1 ; 0.0
f: 0.3 ; 0.0

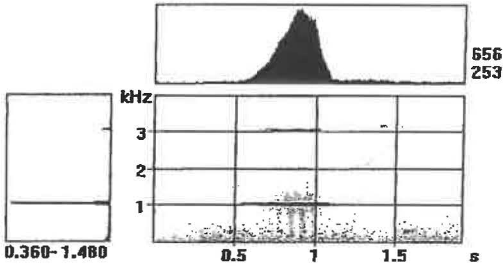


mn3a m: 0.5 ; 0.4
f: 0.0 ; 0.6

mn3b(i-ii) m: 0.4 ; 0.6
f: 0.3 ; 0.0

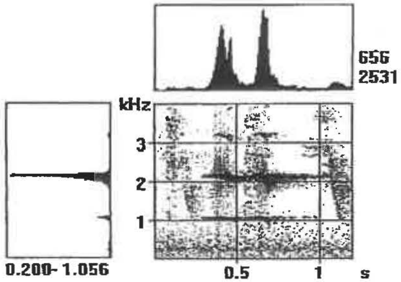
mn3b(iii) m: 0.2 ; 0.0
f: 0.3 ; 0.4

mnCall2 m: 0.3 ; 0.0
f: 0.3 ; 0.0

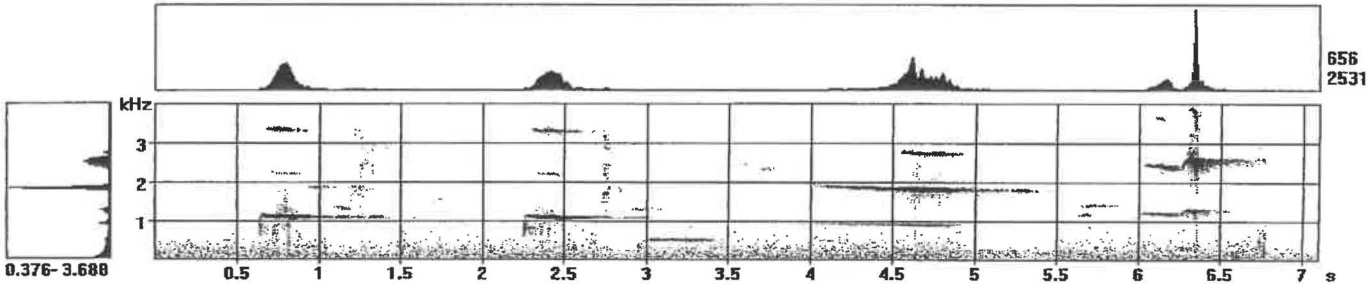


mn4a(i) m: 0.9 ; 0.0
f: 0.0 ; 0.3

Appendix 1-B Mapara North sonagrams (cont'd)



mn4a(ii-iii) m: 0.4 ; 0.0
f: 0.5 ; 0.4

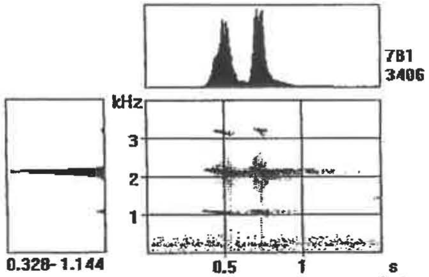


mn4a(iv) m: 0.9 ; 0.5
f: 0.0 ; 0.1

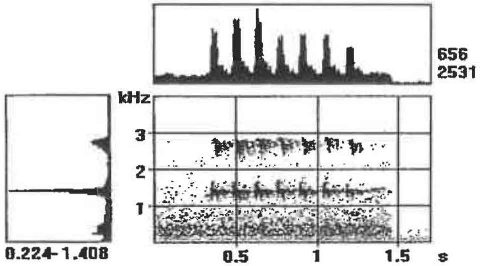
mn4a(v-vi) m: 0.2 ; 0.6
f: 0.0 ; 0.0

mn4b(i) m: 0.7 ; 0.8
f: 0.0 ; 0.0

mnCall1(i-ii) m: 0.0 ; 0.0
f: 0.2 ; 1.0

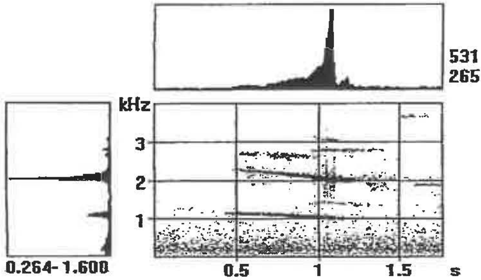


mn4b(ii-iii) m: 0.0 ; 0.0
f: 0.7 ; 0.0

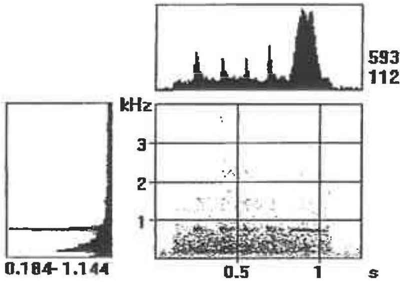


mnCall7 m: 0.0 ; 0.0
f: 0.1 ; 0.3

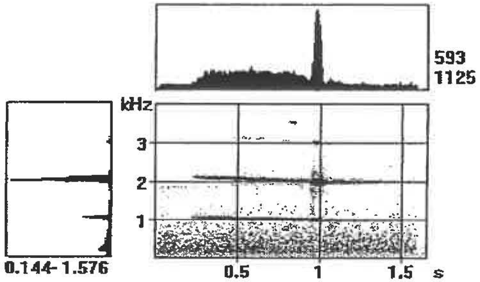
Appendix 1-C Rotoehu sonagrams



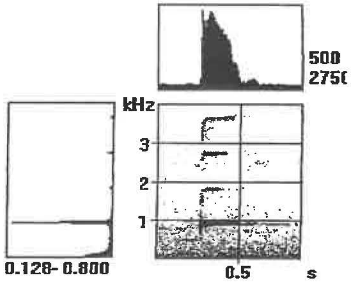
rCall4 m: 0.5 ; -
f: 0.0 ; -



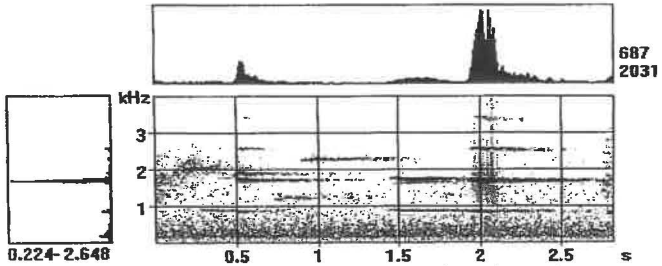
r1a(i-v) m: 0.8 ; -
f: 0.0 ; -



r1b(i-ii) m: 0.0 ; -
f: 0.8 ; -

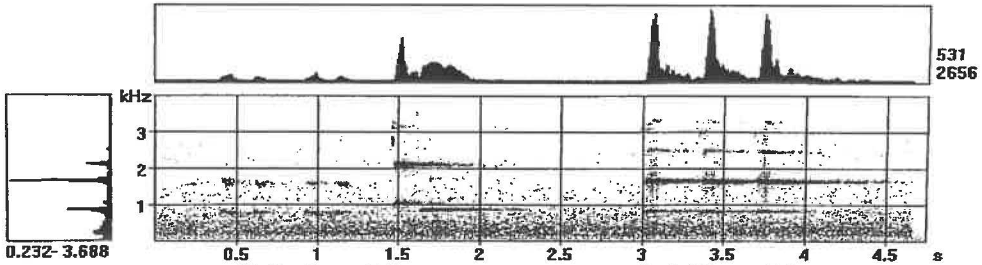


r2d m: 0.5 ; -
f: 0.0 ; -



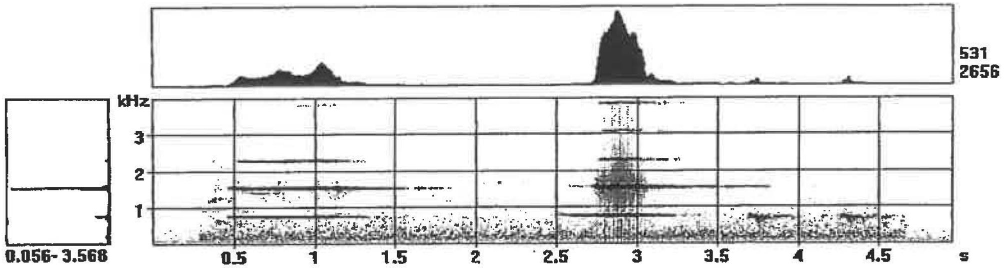
r2a(i-ii) m: 0.3 ; -
f: 0.0 ; -

r2a(iii-iv) m: 0.3 ; -
f: 0.0 ; -



r2b(i-vi) m: 0.0 ; -
f: 0.0 ; -

r2c(i-iii) m: 0.0 ; -
f: 0.0 ; -

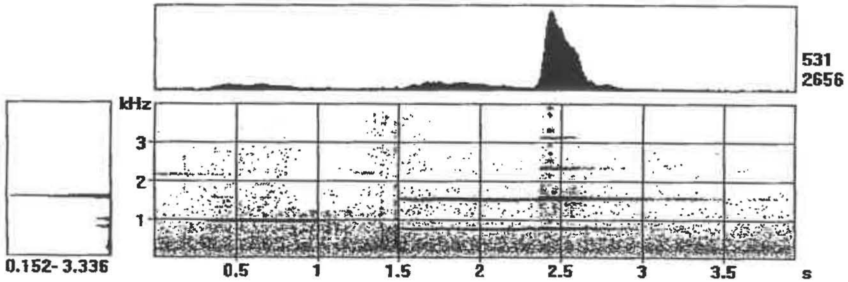


r3(i) m: 0.8 ; -
f: 0.0 ; -

r3(ii) m: 0.8 ; -
f: 0.3 ; -

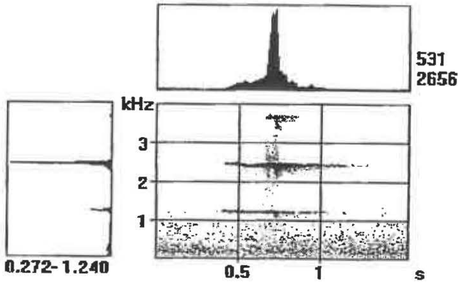
r3(iii-iv) m: 0.8 ; -
f: 0.0 ; -

Appendix 1-C Rotoehu sonagrams (cont'd)

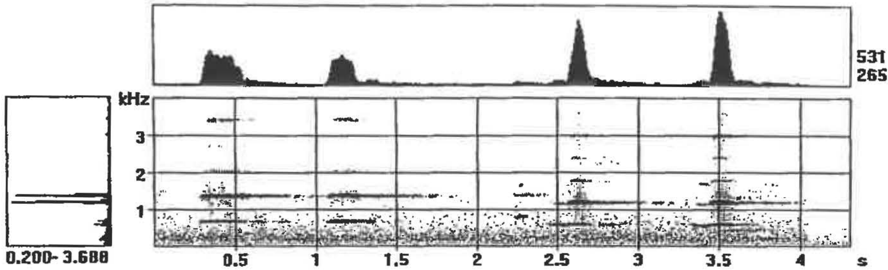


r4(i) m: 0.0 ; -
f: 0.8 ; -

r4(ii-iii) m: 0.0 ; -
f: 0.8 ; -

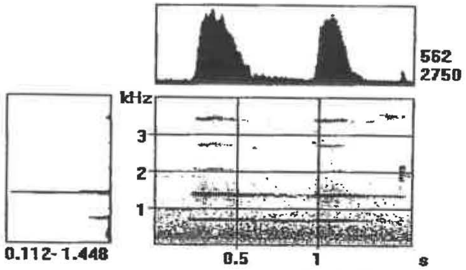


rCall5 m: 0.0 ; -
f: 0.0 ; -

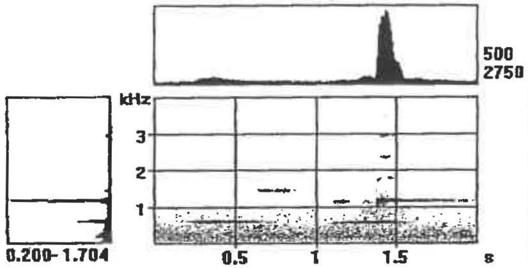


r5a(i-ii) m: 0.3 ; -
f: 0.0 ; -

r5b(i-v) m: 0.0 ; -
f: 0.8 ; -

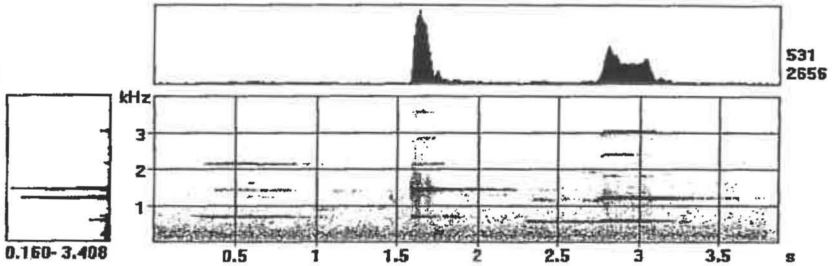


r5c(i-iii) m: 0.5 ; -
f: 0.0 ; -



r6a(i) m: 0.0 ; -
f: 0.0 ; -

r6a(ii-iii) m: 0.0 ; -
f: 0.0 ; -

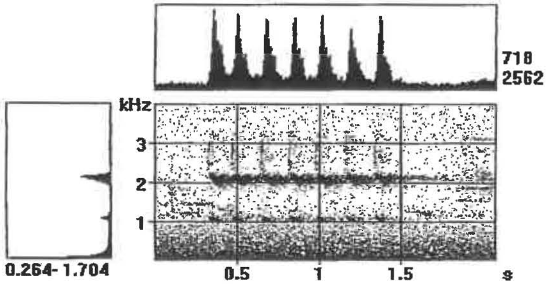


r6b(i) m: 0.3 ; -
f: 0.0 ; -

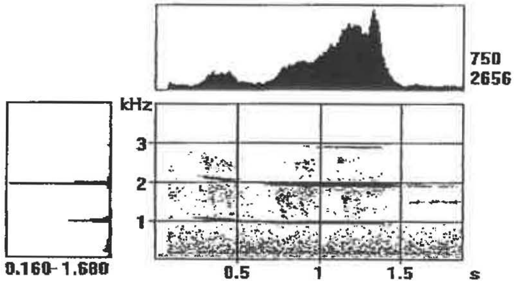
r6b(ii) m: 0.3 ; -
f: 0.0 ; -

r6b(ii-iv) m: 0.3 ; -
f: 0.0 ; -

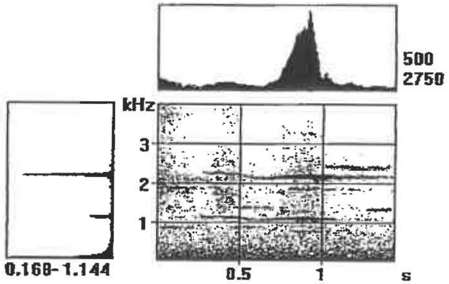
Appendix 1-D Mapara Central sonagrams



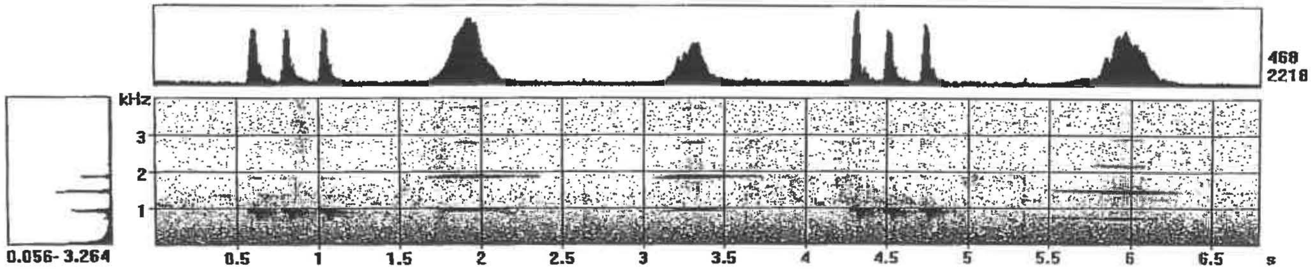
mc1a(i-vii) m: - ; 0.2
f: - ; 0.0



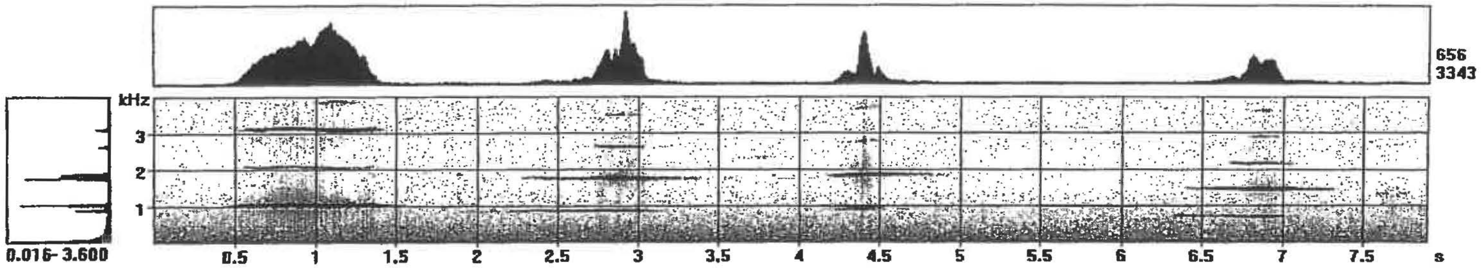
mc1b(i-ii) m: - ; 0.5
f: - ; 0.0



mc1c(i-ii) m: - ; 0.0
f: - ; 0.0

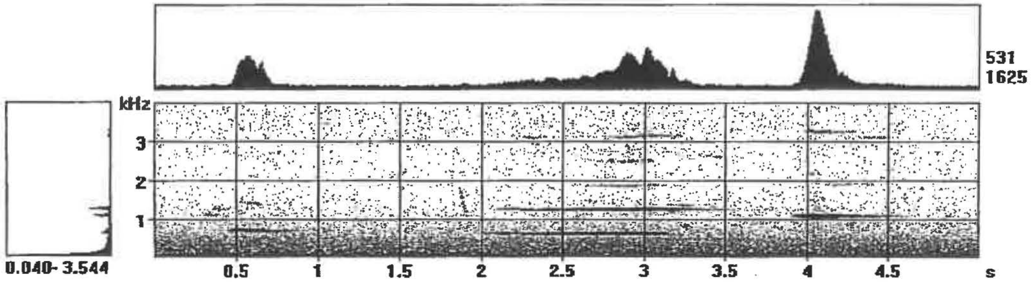


mc2a(i-iii) m: - ; 0.7 **mc2b(i)** m: - ; 0.2 **mc2b(ii)** m: - ; 0.0 **mc2c(i-iii)** m: - ; 0.3 **mc2d** m: - ; 0.2
f: - ; 0.0 f: - ; 0.7 f: - ; 0.3 f: - ; 0.0 f: - ; 0.3



mc3(i) m: - ; 0.5 **mc3(ii)** m: - ; 0.5 **mc3(iii)** m: - ; 0.0 **mc3(iv)** m: - ; 0.0
f: - ; 0.0 f: - ; 0.0 f: - ; 0.5 f: - ; 0.5

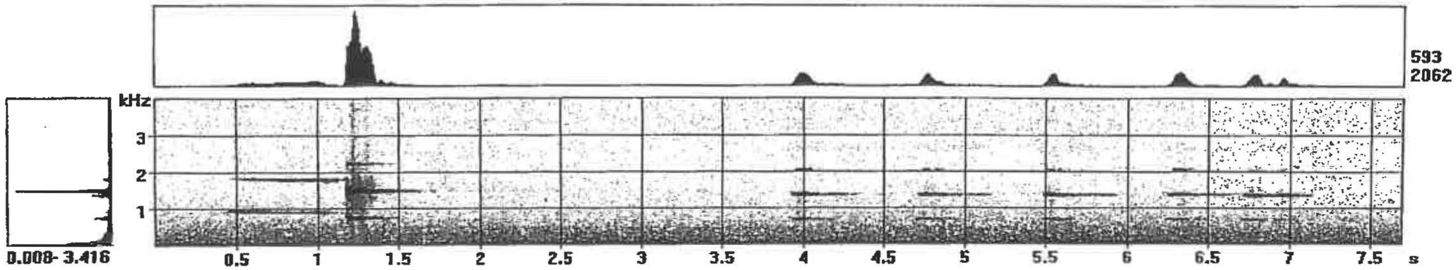
Appendix 1-D Mapara Central sonagrams (cont'd)



mc4a(i) m: - ; 0.0
f: - ; 0.0

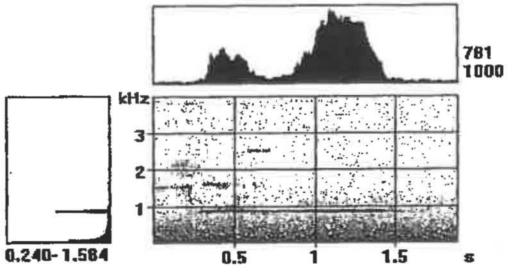
mc4a(ii) m: - ; 0.0
f: - ; 0.2

mc4b m: - ; 0.2
f: - ; 0.0



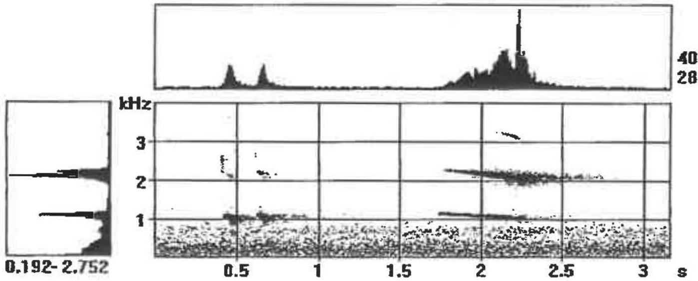
mc5a(i-ii) m: - ; 0.8
f: - ; 0.0

mc5b(i-vi) m: - ; 0.0
f: - ; 1.0



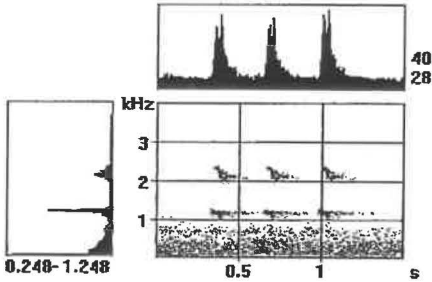
mc5c(i-ii) m: - ; 0.0
f: - ; 0.2

Appendix 1-E Urewera sonagrams

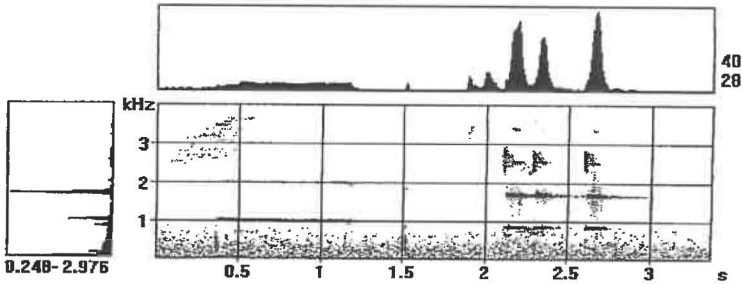


u1a(i-iii) m: - ; 1.0
f: - ; 0.0

u1b m: - ; 1.0
f: - ; 0.0

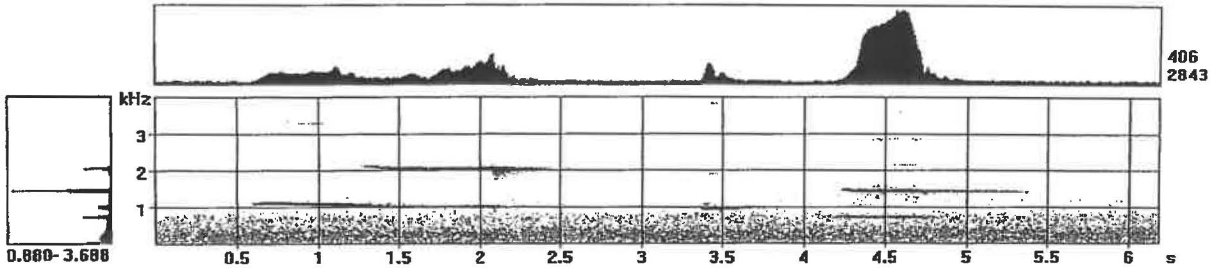


u1c(i-vi) m: - ; 0.5
f: - ; 0.0



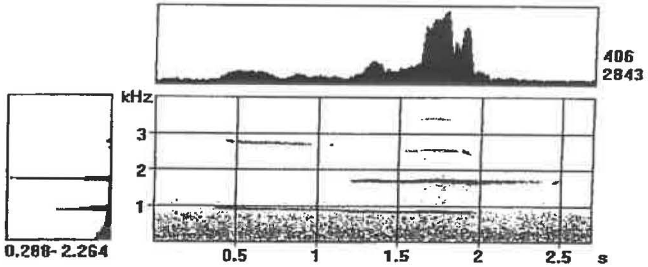
u1d(i) m: - ; 0.5
f: - ; 0.5

u1d(ii-iv) m: - ; 0.5
f: - ; 1.0

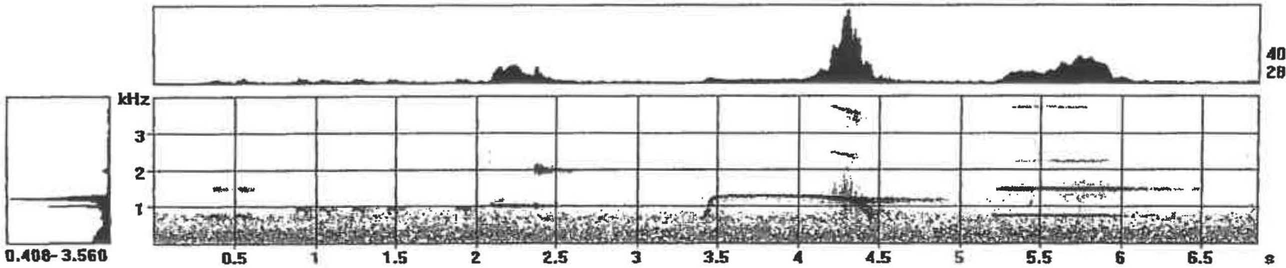


u2a(i-ii) m: - ; 0.0
f: - ; 0.0

u2b(i-ii) m: - ; 0.0
f: - ; 0.5



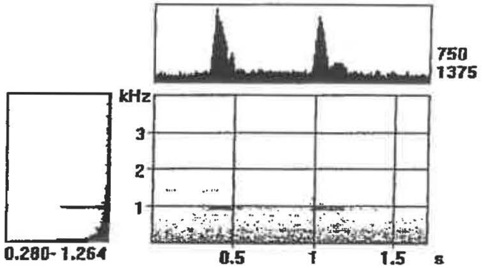
u3(i-iii) m: - ; 0.0
f: - ; 0.0



u4a(i-ix) m: - ; 1.0
f: - ; 0.0

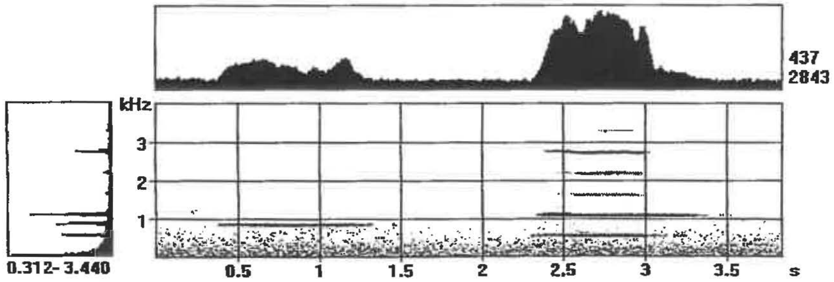
u4b(i-iii) m: - ; 0.5
f: - ; 1.5

u4c(i) m: - ; 0.0
f: - ; 1.0



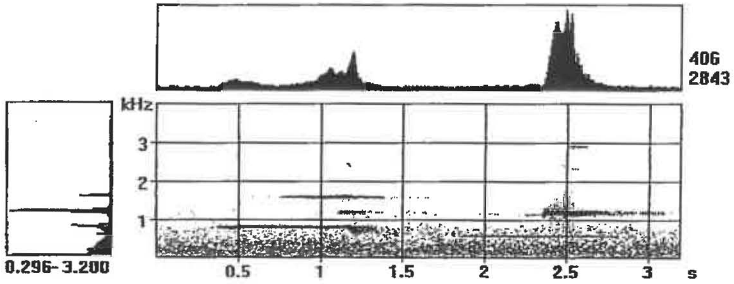
u4c(ii-iii) m: - ; 0.0
f: - ; 0.0

Appendix 1-E Urewera sonagrams (cont'd)



u5a m: - ; 0.0
f: - ; 0.0

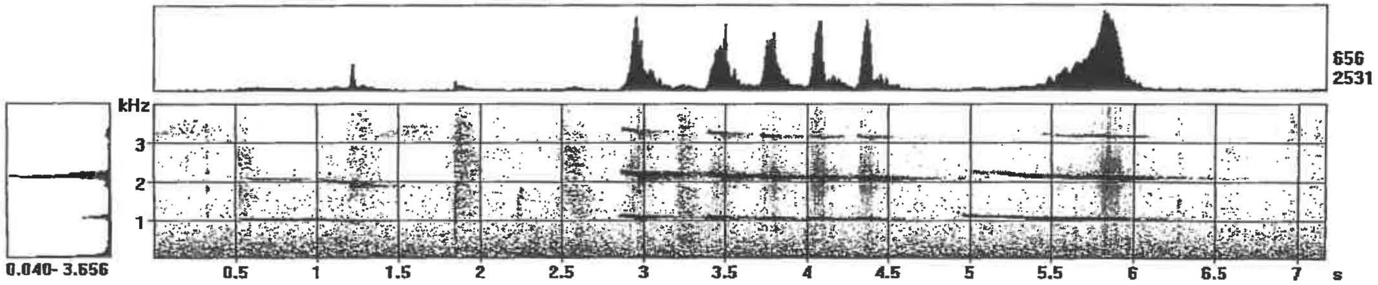
u5b m: - ; 0.0
f: - ; 0.0



u5c(i-ii) m: - ; 0.5
f : - ; 0.5

u5d(i-ii) m: - ; 0.5
f: - ; 0.5

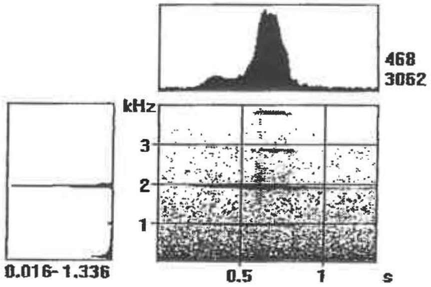
Appendix 1-F Hunua sonagrams



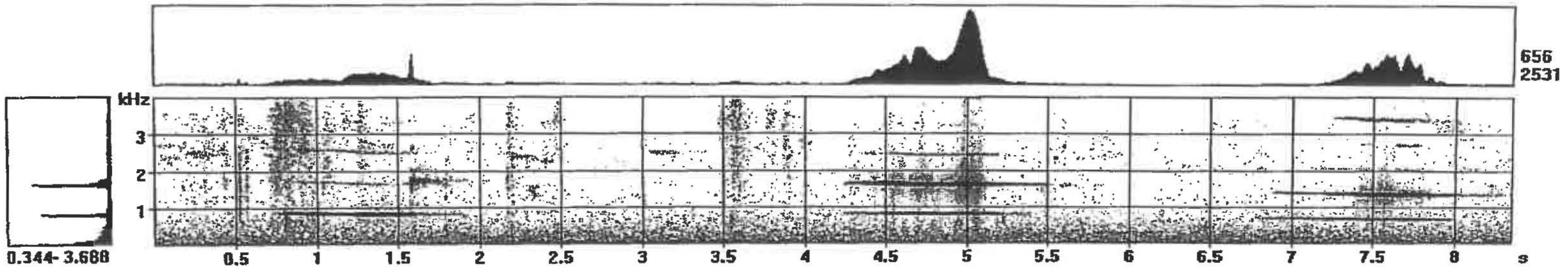
h1a(i-ii) m: 1.0 ; 0.4
f: 0.0 ; 0.3

h1b(i-v) m: 0.0 ; 0.0
f: 2.0 ; 0.0

h1b(vi) m: 1.0 ; 0.9
f: 0.0 ; 0.0



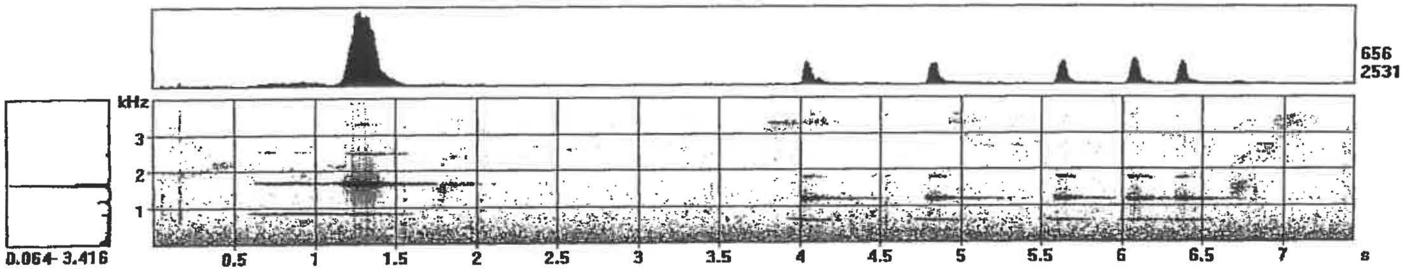
h1c m: 0.0 ; 0.0
f: 0.0 ; 0.4



h2a(i-ii) m: 1.0 ; 0.0
f: 0.0 ; 0.0

h2b m: 1.0 ; 0.0
f: 0.0 ; 0.6

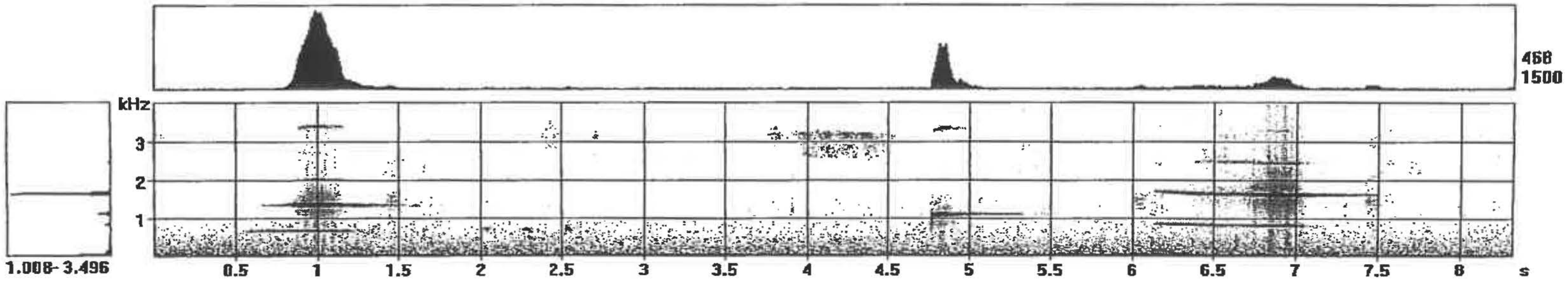
h2c m: 1.0 ; 0.4
f: 0.0 ; 0.0



h3a(i-ii) m: 1.0 ; 0.1
f: 0.0 ; 0.1

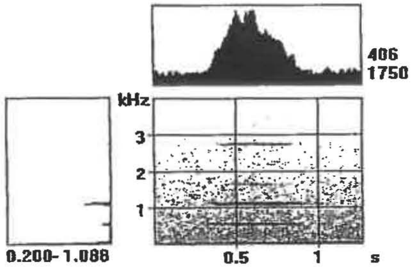
h3b(i-x) m: 1.0 ; 1.3
f: 0.0 ; 0.0

Appendix 1-F Hunua sonagrams (cont'd)

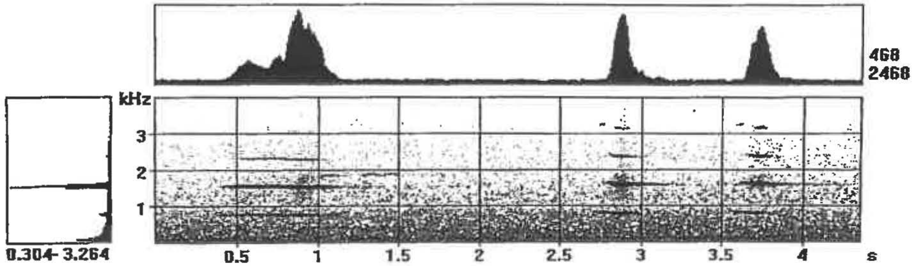


h4a(i-ii) m: 0.5 ; 0.9
f: 0.0 ; 0.1

h4b(i-ii) m: 0.5 ; 0.7
f: 0.0 ; 0.7



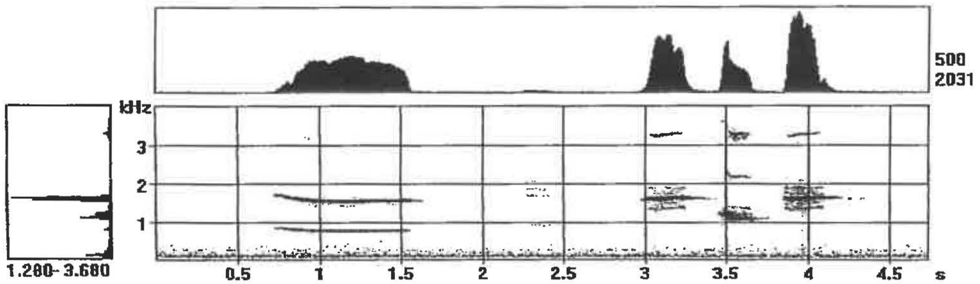
h4b(iii) m: 0.0 ; 0.3
f: 0.0 ; 0.0



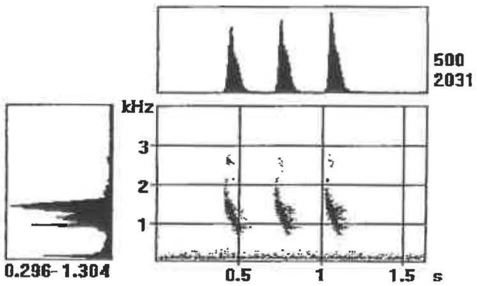
h5a m: 0.0 ; 0.4
f: 0.0 ; 0.0

h5b(i-iv) m: 0.0 ; 0.4
f: 0.0 ; 0.0

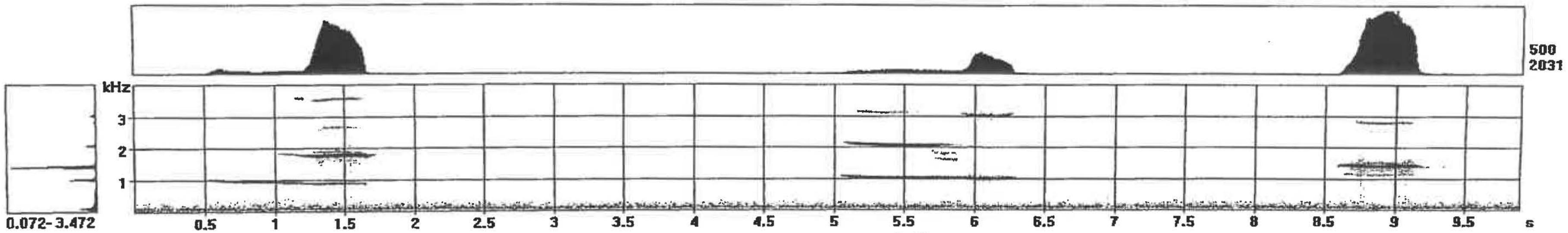
Appendix 1-G Otorohanga sonagrams



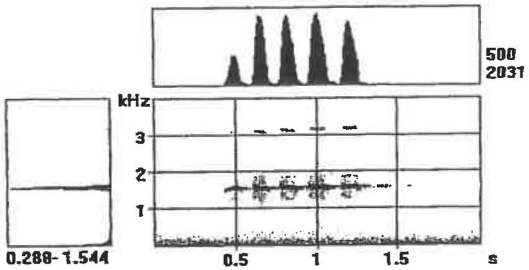
o1a(i-ii) o1b(i-iii)



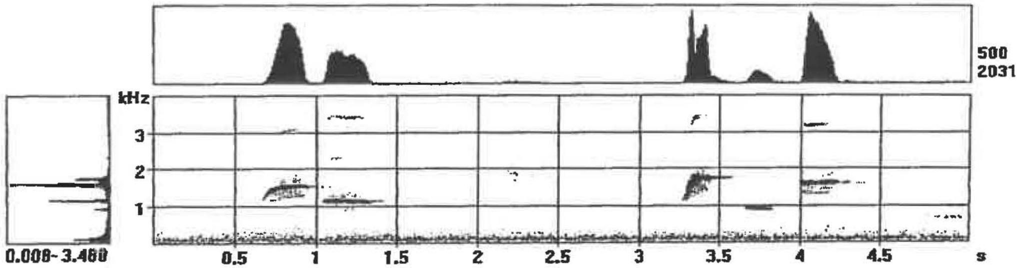
o2d(i-iii)



o2a(i-ii) o2b(i-ii) o2c



o3a(i-v)



o3b(i-iii) o3c(i-iv)

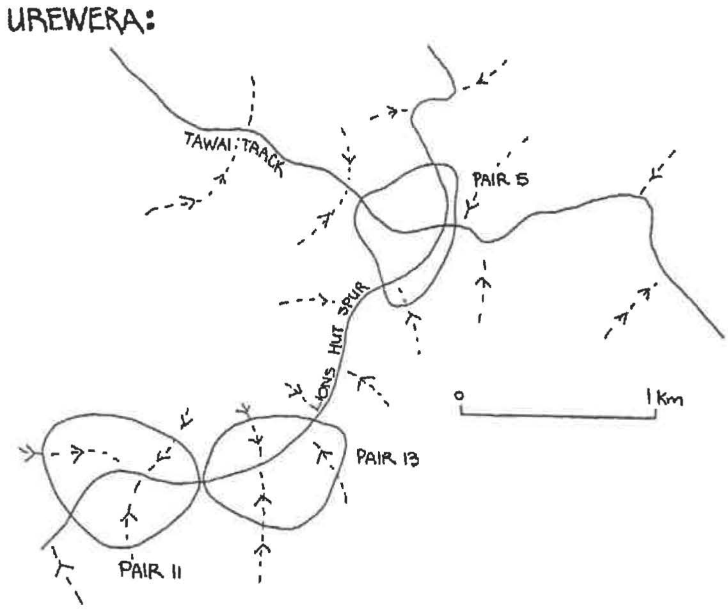
Appendix 2 Kokako recorded for the study, listed with respect to location **(male-male pairs presented in bold)**

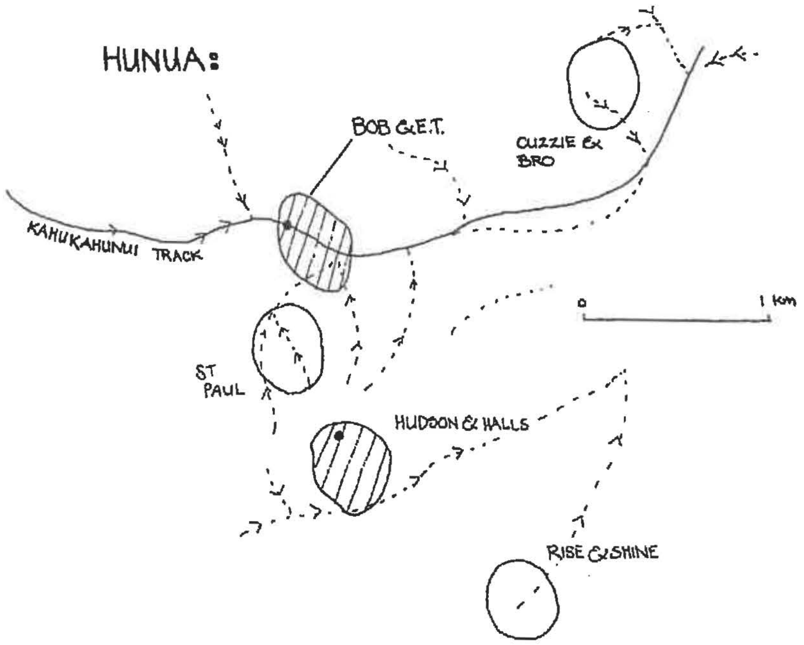
Pair Name and Location	Gender[a]	Priority[b]
MAPARA SOUTH:		
Duja & Gian	male-male	1
Cirrus & Batagooli	male-female	1
Vishnu & Huhu	male-female	1
Vulpec & Fleaphrey	male-female	1
Tui & Menorah	male-female	1
Nice 'n' Sleazy	male-female	1
Vishnu	male	4
MAPARA NORTH:		
L-nino & Racino[c]	male-male	1
Serpens & Botswana	male-female	1
Pili & Opiki	male-female	1
Ojibiway & Solitaire	male-female	1
Pyrosia & Gossum	male-female	1
MAPARA CENTRAL:		
Bosnia & Matabeelee	male-*male*	2
Ezama & Etombi	male-female	2
ROTOEHU:		
Wobble & Tracy2	male-male	1
Jimmy & Bo	male-*male*	3
Trevor & Kawi	male-female	1
Sonyam & Wissel	male-female	1
Bakano & Merlin	male-female	1
TE UREWERA:		
11a & 11b	*male-male*	2
13a & 13b	male-female	2
5a & 5b	male-female	2
11a	*male*	4
HUNUA:		
Hudson & Halls	*male-male*	3
Cuzzie & Bro[d]	*male-male*	-
Rise & Shine[d]	*male-male*	-
Bob & ET	male-female	3
Saint Paul	male	4
OTOROHANGA KIWIHOUSE OUTDOOR AVIARY:		
Bruce	female	4

[a] Birds for which the sex is unconfirmed are given in italics; unbanded birds are underlined. [b] See Table 2.1 for explanation. [c] Sex confirmed by DNA testing. [d] Recorded by J. Taylor.

Appendix 3 Territory locations of study birds (cont'd)

(indicative only; territory sizes and boundaries may not be to scale)

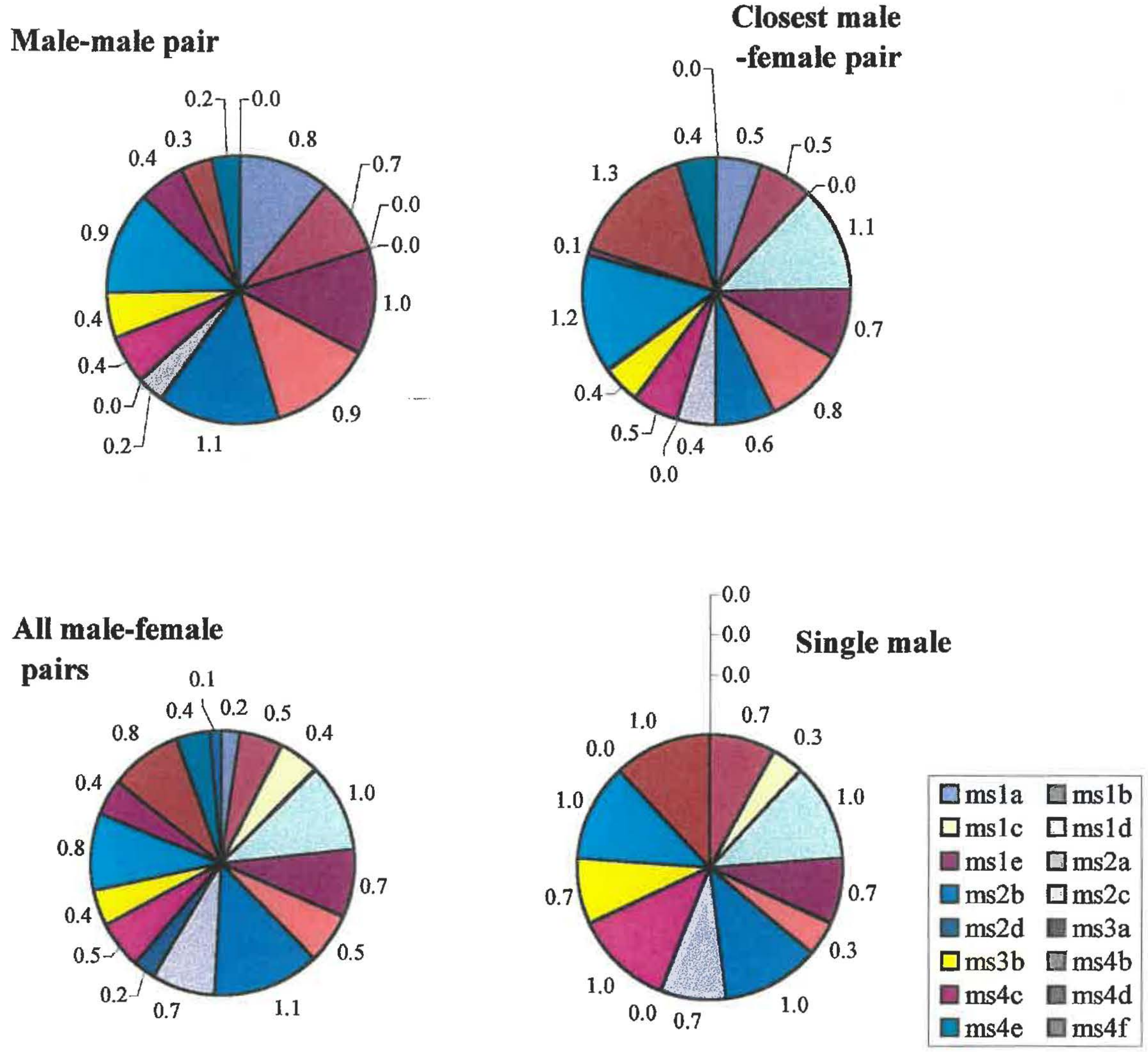




(Artist: L. Hartley)

Hatched territories represent those pairs which were used in the ranging experiment; dots show the locations of playback sites (1, 2 = initial and revised playback sites). Dashed lines and arrows show the basic layout of the topography (arrows point uphill).

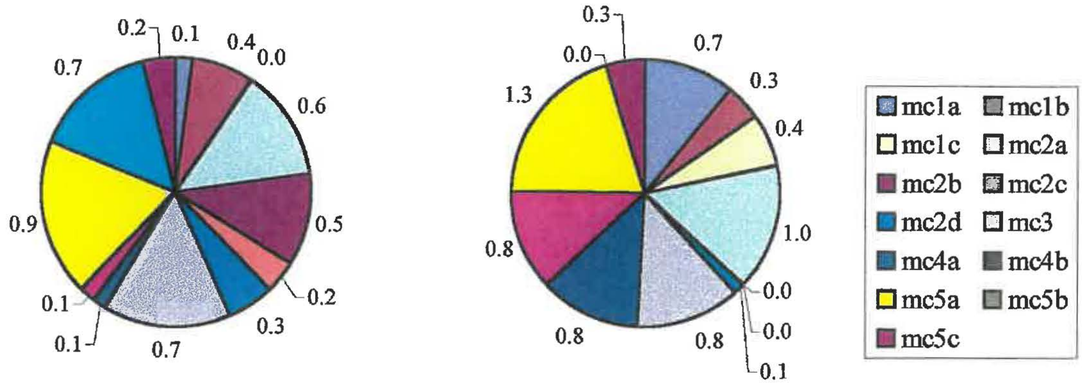
Appendix 4-A Use of phrases by Mapara South birds (numbers depict average occurrence of phrases per rendition of song)



Male-male pair: **Duja & Gian** (n=21 renditions)
Closest male-female neighbour: Nice 'n' Sleazy (n=15 renditions)
Single male: Vishnu (n=3 renditions)

All male-female pairs combined: n=5 pairs, 15+14+10+11+15 renditions

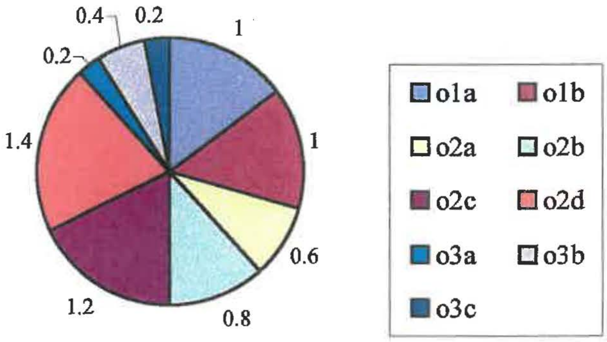
Appendix 4-B Use of phrases by Mapara Central birds (numbers depict average occurrence of phrases per rendition of song)


Male-male pair

Closest male-female pair

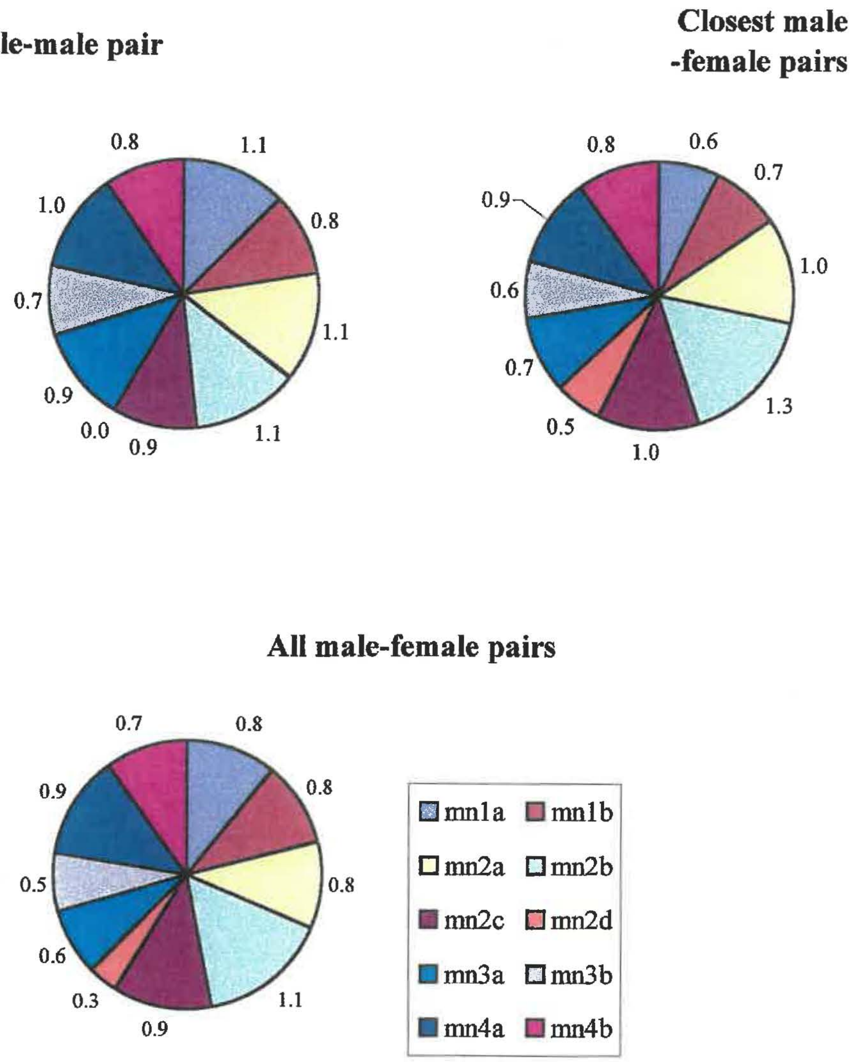
Male-male pair: **Bosnia & Matabeelee** (n=10 renditions)
Closest male-female neighbour: Ezama & Etombi (n=10 renditions)

Appendix 4-C Use of phrases by the captive female (numbers depict average occurrence of phrase per rendition of song)


Captive female

Captive female: Bruce (n=5 renditions)

Appendix 4-D Use of phrases by Mapara North birds (numbers depict average occurrence of phrases per rendition of song)


Male-male pair

Closest male -female pairs

All male-female pairs

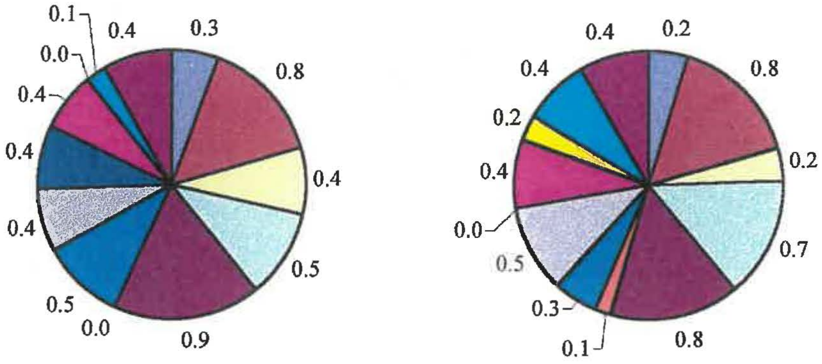
Male-male pair: **L-Nino & Racino** (n=16 renditions)
Closest male-female neighbours: Ojibiway & Solitaire and Pili & Opiki (n=20+10 renditions)

All male-female pairs combined: n=4 pairs, 14+10+20+14 renditions

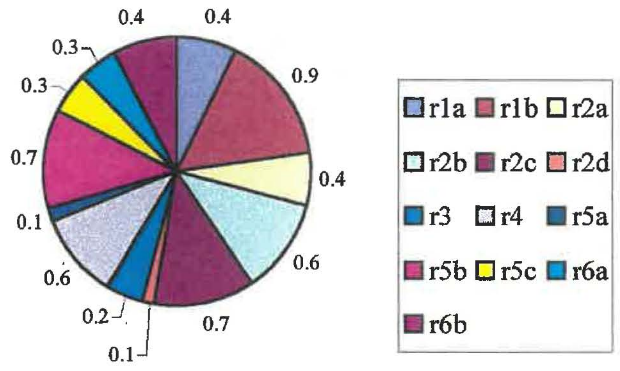
Appendix 4-E Use of phrases by Rotoehu birds (numbers depict average occurrence of phrases per rendition of song)

Male-male pair

Closest male -female pairs



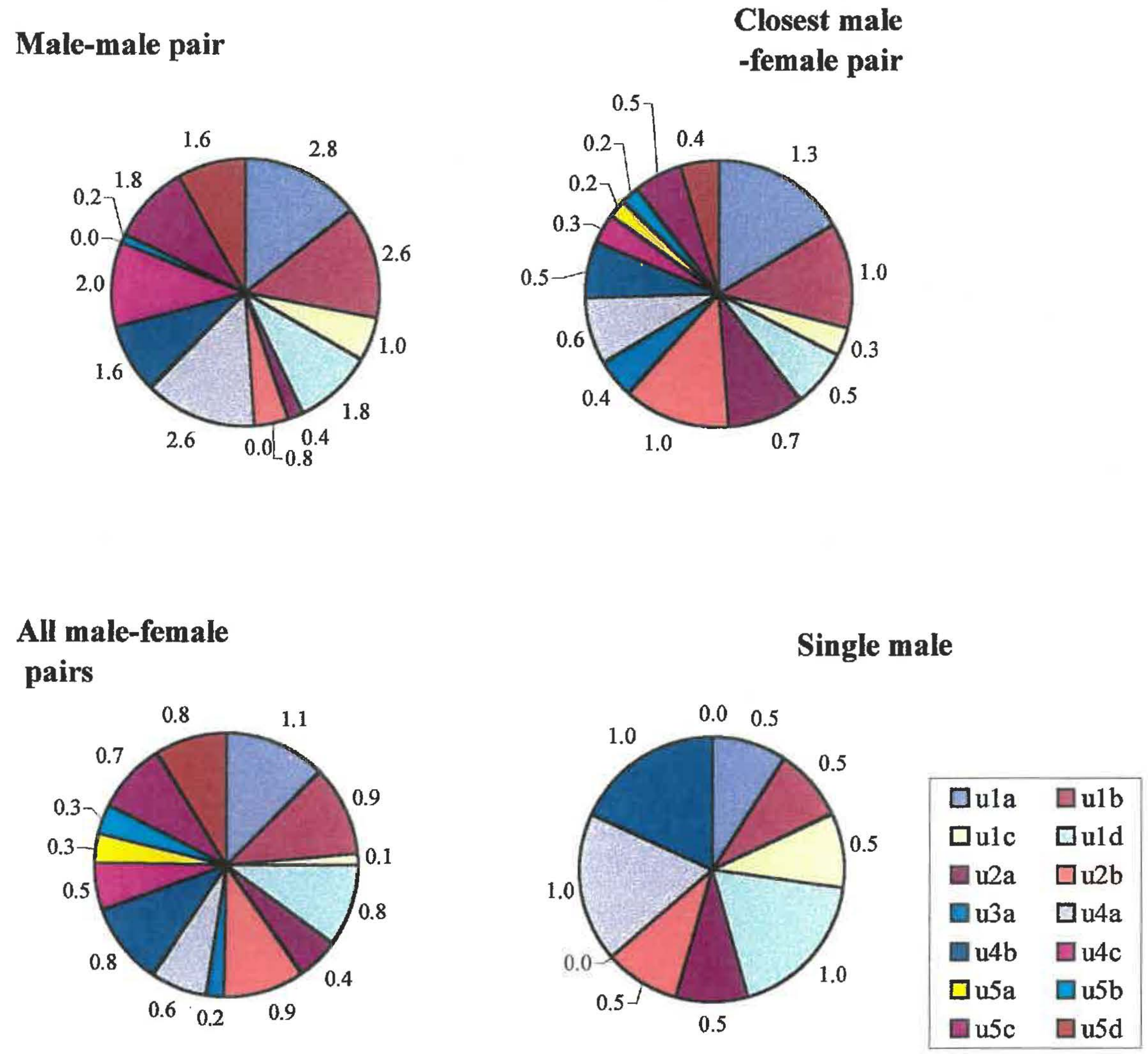
All male-female pairs



Male-male pairs: **Tracy2 & Wobble, Jimmy & Bo** (n=20+11 renditions)
Closest male-female neighbours: Sonyam & Wissel and Trevor & Kawi (n=9+20 renditions)

All male-female pairs combined: n=3 pairs, 9+20+14 renditions

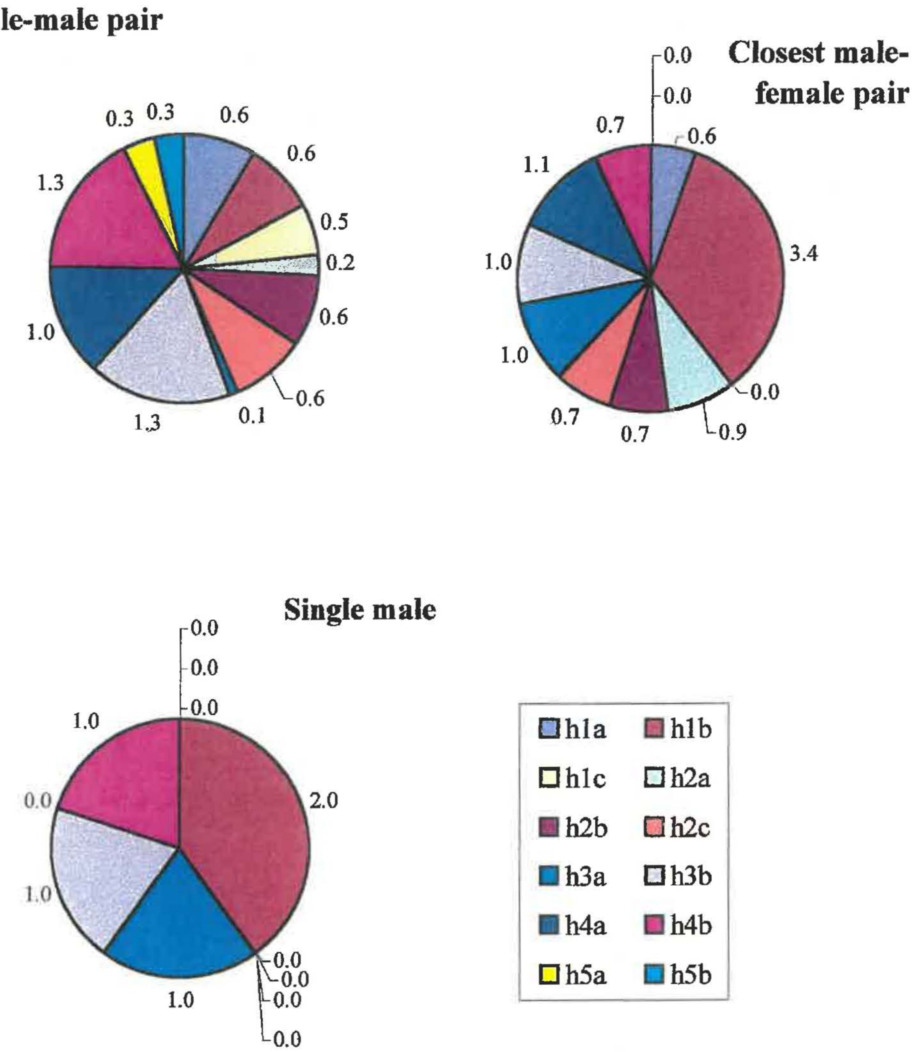
Appendix 4-F Use of phrases by Te Urewera birds (numbers depict average occurrence of phrases per rendition of song)



Male-male pair: **Pair 11** (n=5 renditions)
Closest male-female neighbour: Pair13 (n=11 renditions)
Single male: 11a (n=2 renditions)

All male-female pairs combined: n=2 pairs, 11+7 renditions

Appendix 4-G Use of phrases by Hunua birds (numbers depict average occurrence of phrases per rendition of song)



Male-male pair

Closest male-female pair

Single male

Male-male pair: **Hudson & Halls** (n=11 renditions)
Closest male-female neighbour: Bob & E.T. (n=7 renditions)
Single male: St Paul (n=1 rendition)

Appendix 5 List of frequency classes

class	frequency range (kHz)
1	0.45-0.50
2	0.50-0.55
3	0.55-0.60
4	0.60-0.65
5	0.65-0.70
6	0.70-0.75
7	0.75-0.80
8	0.80-0.85
9	0.85-0.90
10	0.90-0.95

class	frequency range (kHz)
11	0.95-1.00
12	1.00-1.05
13	1.05-1.10
14	1.10-1.15
15	1.15-1.20
16	1.20-1.25
17	1.25-1.30
18	1.30-1.35
19	1.35-1.40
20	1.40-1.45

class	frequency range (kHz)
21	1.45-1.50
22	1.50-1.55
23	1.55-1.60
24	1.60-1.65
25	1.65-1.70
26	1.70-1.75
27	1.75-1.80
28	1.80-1.85
29	1.85-1.90
30	1.90-1.95

class	frequency range (kHz)
31	1.95-2.00
32	2.00-2.05
33	2.05-2.10
34	2.10-2.15
35	2.15-2.20
36	2.20-2.25
37	2.25-2.30
38	2.30-2.35
39	2.35-2.40
40	2.40-2.45

class	frequency range (kHz)
41	2.45-2.50
42	2.50-2.55
43	2.55-2.60
44	2.60-2.65
45	2.65-2.70
46	2.70-2.75
47	2.75-2.80
48	2.80-2.85
49	2.85-2.90
50	2.90-2.95

Appendix 6 List of phrases for which pairs matched the presentation playback sequence (male-male pairs in **bold**; see section 3.3.4 for details)

PAIR NAME & PRESENTATION No.	MATCHED SYLLABLES	BIRDS LOCATIONS BIRD1	BIRD2
Duja&Gian (UND3)	ms3a	outside(f)	outside(f)
L-Nino&Racino (UND2)	mn2a(i-v)	zone3a	zone3a
L-Nino&Racino (UND2)	mn2b(i-ii)	zone2a	zone3a
L-Nino&Racino (UND2)	mn3a	zone1	zone3a
L-Nino&Racino (UND2)	mn4a(iv)	zone1	zone3a
Bakano&Merlin (UND1)	r3(i-iv)	outside(f)	outside(f)
Serpens&Botswana (UND2)	2d	zone1	zone1
Serpens&Botswana (UND2)	3a	zone1	zone1
Serpens&Botswana (UND2)	3b(i)	zone1	zone1
Serpens&Botswana (UND2)	3b(ii)	zone1	zone1
Serpens&Botswana (UND2)	Call2	zone1	zone1
Trevor&Kawi (UND1)	3(i)	outside(f)	outside(f)
Trevor&Kawi (UND1)	3(ii)	outside(f)	outside(f)
Trevor&Kawi (UND2)	3(i)	outside(f)	outside(f)
Trevor&Kawi (UND2)	Call5	outside(f)	outside(f)
Trevor&Kawi (UND2)	6b(ii)	outside(f)	outside(f)
Trevor&Kawi (UND2)	Call5	outside(f)	outside(f)
Trevor&Kawi (UND3)	2b(iii)	outside(f)	outside(f)
Trevor&Kawi (UND3)	2c(i)	outside(f)	outside(f)
Trevor&Kawi (UND3)	3(i)	outside(f)	outside(f)
Trevor&Kawi (UND3)	3(ii)	outside(f)	outside(f)
Trevor&Kawi (UND3)	6b(ii)	outside(f)	outside(f)
Duja&Gian (DEG2)	ms1d(ii)	zone4f	zone4f
Duja&Gian (DEG2)	ms3a	zone4f	zone4f
Duja&Gian (DEG2)	ms4d	zone4f	zone4f
Duja&Gian (DEG3)	2b(i)	zone4f	zone4f
Duja&Gian (DEG3)	2b(ii)	zone4f	zone4f
Duja&Gian (DEG3)	2b(iii)	zone4f	zone4f
Duja&Gian (DEG3)	2b(v)	zone4f	zone4f
Duja&Gian (DEG3)	4b(ii)	zone4f	zone4f
Duja&Gian (DEG3)	4d(i)	zone1	zone4f
Trevor&Kawi (DEG2)	Call5	zone4f	zone4f
3)	3a	zone3f	zone3f
3)	2c(ii)	zone1	zone1

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