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Vocalisations of the Great Spotted Kiwi (*Apteryx haastii*): an Assessment of Vocal Individuality

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Jennifer May Dent

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Abstract of a dissertation submitted in partial fulfilment of the requirements for the Degree of Bachelor of Science (Honours)

Vocalisations of the Great Spotted Kiwi: an Assessment of Vocal Individuality

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Kiwi (*Apteryx* spp.) vocalisations are routinely used as part of a nationwide monitoring programme in which call-rate is used to infer population density. The ability to individually identify kiwi would drastically improve the accuracy and quality of monitoring programmes. One potential avennue to achieve this is through acoustic identification. In many vocally active species, vocalisations have been shown to encode information about the identity of the caller (vocal individuality). This has proven extremely useful in monitoring rare, nocturnal and cryptic bird species. In this study, vocal individuality was assessed with regard to a population of great spotted kiwi (*Apteryx haastii*) residing in the Hawdon Valley, Canterbury, New Zealand. Acoustic recorders were installed near the breeding den sites of seven great spotted kiwi pairs between November 2012 and March 2013. In total 303 whistle vocalisations were recorded during this time. A range of temporal and spectral parameters were measured from the highest quality recordings. These measurements were taken at a whole call and individual syllable level. Call parameters were; number of syllables, syllable rate and syllable duration. Syllable parameters were; minimum frequency (Hz), maximum frequency (Hz), bandwidth (Hz), duration (sec) and peak frequency (Hz). These variables were used to describe and classify calls using one-way repeated measures ANOVAs and stepwise discriminant function analysis.

Male and female syllables are sexually dimorphic, however, the pattern of temporal and spectral variation within calls is consistent between sexes. Discriminant function analysis indicated that great spotted kiwi vocalisations were highly individualised. Male individuals were were classified with an accuracy of 95.7% on the basis of seven parameters. Females were classified with an accuracy of 90% on the basis of five call parameters. In both analyses spectral parameters were shown to be most important for individual discrimination. This is the highest degree of vocal individuality in *Apteryx* species reported to date. Such a high degree of individuality indicates that great spotted kiwi vocalisations could be utilised for individual identification purposes. The next step is to assess the temporal stability of this phenomenon.

Keywords: vocal individuality, *Apteryx haastii*, Hawdon Valley, whistle call, fundamental frequency, autonomous acoustic recording, acoustic monitoring, call-rate, vocal dimorphism

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Chapter 1

Literature Review

1.1 General Introduction

Kiwi are a family of ratites (Apterygidae) belonging to the order Struthioniformes (Sales 2005). It was once presumed that New Zealand's moa and kiwi evolved from a common ancestor, however, recent phylogenetic analysis suggests that kiwi are in fact, most closely related to the Australian and African ratites (Trewick & Gibb 2010). Although the taxonomy of Apterygidae has been widely debated, at present five species of kiwi are formally recognised; the North Island brown kiwi (*Apteryx mantelli*), rowi (*A. rowi*), tokoeka (*A. australis*), great spotted kiwi (*A. haastii*) and the little spotted kiwi (*A. owenii*) (Sales 2005; Holzapfel et al. 2008). All five species are endemic to New Zealand and share a number of unusual traits.

One of the most distinctive traits of kiwi is that they are flightless, having only vestigial wings and no external tail (Sales 2005). Flightlessness is thought to have arisen as a consequence of evolution in an environment free of mammalian predators (Sales 2005). Isolation from terrestrial mammals has also led kiwi to occupy a generalist niche in terms of foraging strategy and habitat selection (Fuller 1990). Kiwi are largely nocturnal birds, they spend much of the night foraging and retreat into burrows and dens during the day (Fuller 1990; McLennan & McCann 1991). Presumably due to this nocturnal habit, kiwi possess small, poorly developed eyes and complex, enlarged olfactory structures (Reid et al. 1982). Such a highly developed olfactory system is unusual amongst avian species. The kiwi situation is made even more unique by the nostril positioning at the tip of the bill (Sales 2005)

Social and breeding behaviour is known to vary quite substantially between kiwi species; however, there are some unifying traits (Sales 2005). Most kiwi species are monogamous; they form long term partnerships with high partner fidelity (Fuller 1990). These pairs are highly territorial, defending home range areas which range in size from 2–3 ha up to 100 ha depending on the species, habitat type and population density (Heather & Robertson 2005). Kiwi are regarded as K-selected species as they have slow rates of reproduction (McLennan 1988; Butler & McLennan 1991). Clutch size is typically small (1-2 very large eggs) and the incubation period is prolonged (lasting 65-85 days) (Sales 2005). Juveniles also grow slowly, often taking 3-5 years to reach sexual maturity (McLennan et al. 2004). Kiwi have a relatively long life expectancy for bird species: between 25-50 years, depending on the species (Heather & Robertson 2005). Though unified by these characteristics, each species of kiwi has its own unique traits. The species of particular interest to this study is the great spotted kiwi.

1.2 Great Spotted Kiwi (Roroa)

Unfortunately information concerning great spotted kiwi is scarce. They are the largest of the five kiwi species; females have an average weight of about 3000g and although males are slightly smaller, they still reach an average weight of about 2200g (McLennan & McCann 2002). Aside from their size, they are distinguished from other kiwi by their plumage which is predominantly mottled grey with a distinctive patch of chestnut on their back (Fuller 1990, Figure 1.1).

Figure 1.1: Great spotted Kiwi (source: www.KiwisforKiwi.org)

Great spotted kiwi are monogamous; they form long-lasting pair bonds which may last several breeding seasons or their entire lives (Fuller 1990; McLennan & McCann 1991; Taborsky and Taborsky 1999). Each pair will defend a territory together (Sales 2005). Great spotted kiwi territories are quite large with an average home range size of 29.5 ha (Keye 2008). They predominantly occupy subalpine and alpine habitats in the North West of the South Island and are most numerous in high rainfall, forested areas, 700-1000m above sea level (Fuller 1990). There are thought to be four main populations of great spotted kiwi in the wild: Northwest Nelson, Nelson Lakes National Park, Paparoa Range and Arthurs Pass-Hurunui (Figure 1.2; McLennan & McCann 2002). The largest of these populations resides in Northwest Nelson, where an estimated 12,000 kiwi occupy an area of coastal foothills and mountains spanning 2600km^2 (McLennan & McCann 2002). Population density is thought to vary drastically between these main populations, ranging from 6-8 birds per square kilometre in Northwest Nelson to 2-3 birds per square kilometre in the Arthurs Pass-Hurunui grouping (McLennan & McCann 2002).

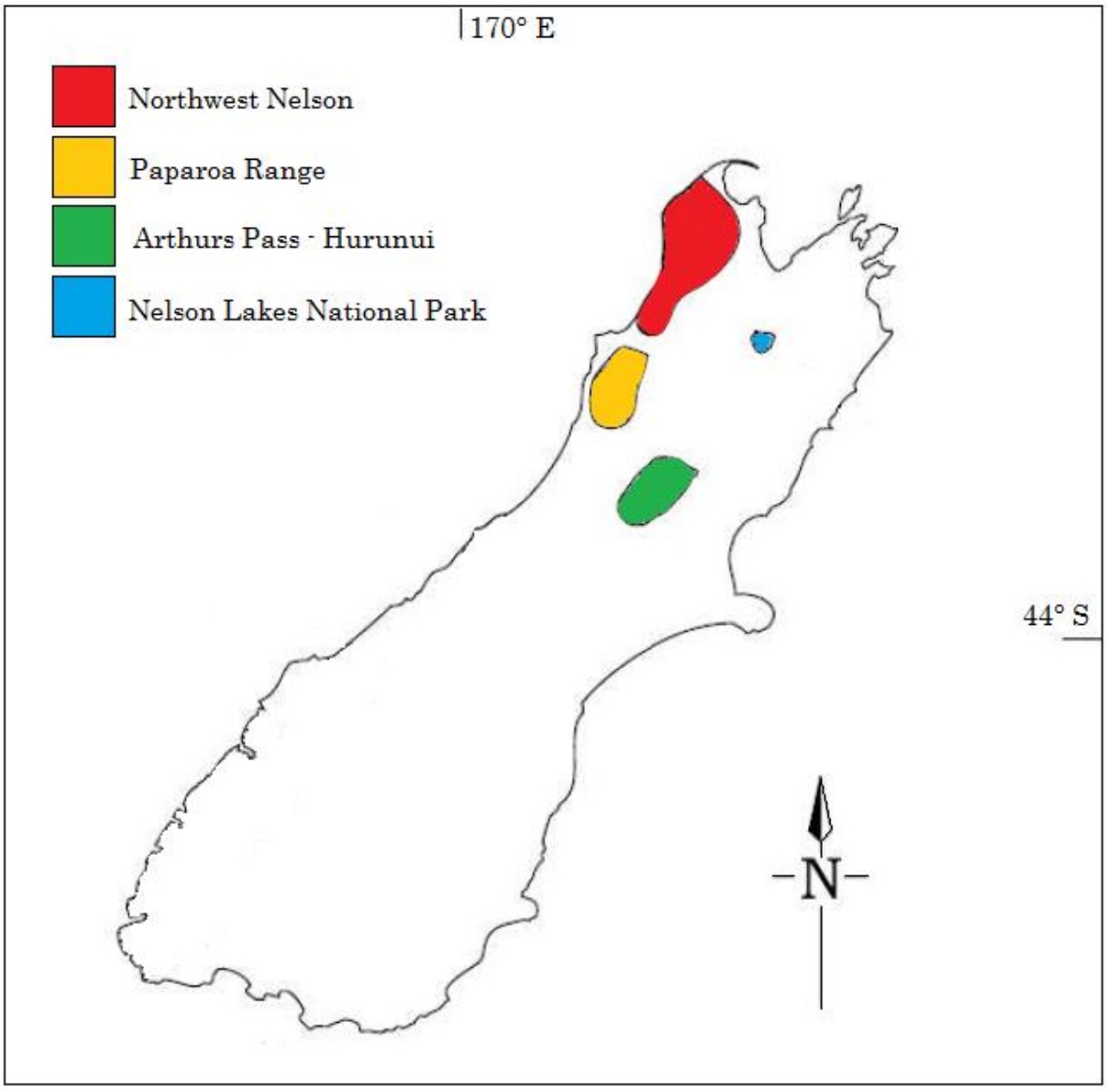


Figure 1.2: The known populations of great spotted Kiwi in the South Island, New Zealand (modified from Holzapfel et al. 2008)

Great spotted kiwi reproduce once per year. The main egg laying period occurs between July and December (peaking in October) (Cockrem et al. 1992; Burbridge et al. 2003). During this time, female great spotted kiwi produce a single, large egg (20% body weight) (Cockrem et al. 1992). Unlike other kiwi species, if this egg fails it will seldom be replaced (Butler & McLennan 1991). In total the incubation period lasts approximately 78 days (Burbridge et al. 2003) and both the male and female birds partake in incubation duties (McLennan & McCann 1989). Males are responsible for the majority of the incubation; however females will take over for 3-8 hrs per night (McLennan & McCann 1989). Although females do not develop a brood patch, they are able to heat the egg to sufficient temperature to sustain embryotic growth (McLennan & McCann 1991). Great spotted kiwi eggs generally have a very low hatching success rate (Sales 2005). McLennan et al. (1996) found that

only 37% of eggs successfully hatched in the wild, predominantly due to desertion and embryonic failure.

1.3 Species Status

The great spotted kiwi is classified as a Category 5 (gradual decline) chronically threatened species (Gasson 2005). In 1996, the total population was estimated at 22,000; unfortunately, given the current rate of decline (c. 2% annual decline for unmanaged populations) current projections for 2018 see this figure dropping below 13,000 (Robertson 2003; Holzapfel et al. 2008). In addition to the population decline, the range of this species has contracted by at least 30% since European settlement (McLennan & McCann 2002). Though now restricted to the high rainfall, mountainous regions of the West Coast, fossil evidence suggests that the range of this species used to extend as far as coastal Canterbury prior to Polynesian settlement (Reid & Williams 1975). The principle agent of this population decline and range restriction is thought to be predation (McLennan et al. 1996, McLennan & McCann 2002).

1.3.1 Causes of Decline

Historically, kiwi population decline was attributed to a combination of habitat loss and predation. As the rate of habitat loss has slowed dramatically in recent times, predation is now perceived as the greatest threat to kiwi on the New Zealand mainland (Miller & Pierce 1995; McLennan et al. 1996). McLennan et al. (1996) examined the role of predation in the population decline of great spotted kiwi. They demonstrated that predation pressure differentially affects different life stages. Kiwi are most vulnerable in their juvenile stage, and are thought to have a juvenile mortality rate of up to 94%, 60% of which is attributed to predation (McLennan & McCann 1996). Meanwhile predation accounts for just 10% of egg losses and 3% of adult mortality (McLennan & McCann 1996). Such a reprieve is probably due to the large size of the adult birds which enables them to deter predators and protect the egg (McLennan & McCann 1996). While dogs (*Canis lupus familiaris*) and ferrets (*Mustela erminea*) are the primary predators of adult birds, the greatest predation threat to juvenile birds comes from stoats (*Mustela ermine*) and feral cats (*Felis catus*) (McLennan & McCann 1996; Sales 2005). Though predation is deemed to be the dominant force limiting populations, other agents of decline have also been noted including: inbreeding, loss of genetic diversity, competition and disease (Holzapfel 2008).

The vulnerability of kiwi to predation owes to the fact that they evolved in an environment free of terrestrial predators; however, they now coexist with up to seven species of obligate mammalian predators (Fuller 1990; Sales 2005). As a result they did not evolve appropriate defensive and/or avoidance behaviours. Kiwi forage independently from their parents from a young age, often in

dense foliage; this dramatically increases their chances of being preyed upon (McLennan et al. 1996). Furthermore, kiwi respond to predators by "freezing" rather than "fleeing" which proves to be an ineffective technique when dealing with predators which hunt by smell (McLennan et al. 1996).

1.4 Conservation Effort

Today a lot of emphasis is placed on kiwi conservation; however, prior to the 1990's there was no coordinated management plan in place at all. The publication of the first Kiwi Recovery Plan in 1991 initiated the Kiwi Recovery Programme that continues to this day (Butler & McLennan 1991). Since 1991, although the long term goal of the programme – "*to restore and, wherever possible, enhance the abundance, distribution and genetic diversity of all Kiwi taxa*" – has remained relatively unchanged, the focus of the programme is in a state of flux (Holzapfel et al. 2008). The initial phase of kiwi recovery (1991-1996) focused on the profiling the five species in terms of distribution, demographic trends, numerical status and taxonomy (Robertson 2003; Holzapfel et al. 2008). The second phase of recovery (1996-2008) focused on the development and refinement of population management techniques including Operation Nest Egg (ONE) and landscape-scale stoat trapping (Robertson 2003). The third stage of recovery, as outlined by the 2008-2018 Kiwi Recovery Plan, will endeavour to build upon the information gained in the earlier phases, refining the current management and monitoring techniques (Holzapfel et al. 2008).

1.4.1 Management

As predators are thought to be the main cause of kiwi population decline, predator control is the primary focus of most management programmes (Sales 2005; Pierce & Westbrooke 2003). Complimentary approaches include the establishment of kiwi 'sanctuaries' and captive breeding programmes (Robertson 2003; Sales 2005).

Relative to other kiwi species, great spotted kiwi receive little active management (Robertson 2003; Holzapfel et al. 2008). The Department of Conservation has traditionally focussed their resources on more critically endangered species such as the rapidly declining North Island brown kiwi (Sales 2005). An emergence of commercial and community led initiatives in recent times may help to turn the tide on this issue (e.g. BNZ save the Kiwi trust, New Zealand Conservation Trust, Paparoa Wildlife Trust & Kiwis for Kiwi) (Holzapfel et al. 2008).

Predator Control

Predator control throughout the great spotted kiwi range is patchy (Holzapfel et al. 2008). Several community groups conduct localised predator control operations. For example, the Arthur's Pass Community Roroa Recovery Project works to trap stoats around the Arthur's Pass township and

wider Bealey Valley area. The Department of Conservation carries out more extensive predator control via projects such as Operation Ark and the Hurunui Mainland Island (Gasson 2005).

Operation Nest Egg

In 1994, the Bank of New Zealand Kiwi Restoration Group set up Operation Nest Egg (ONE) to help address the issues of predation and low chick survival (Colbourne et al. 2005). This programme facilitates the artificial incubation and/or rearing of wild-born kiwi chicks. Most chicks are hatched at captive rearing facilities (e.g. Willowbank Wildlife Reserve) and then transferred to predator-free 'crèches' until they are big enough to safely return to the wild (Robertson et al. 2011). Great spotted kiwi were introduced to the ONE programme in 2007 (BNZ Save the Kiwi Trust 2010). Prior to this only one great spotted kiwi reintroduction event had been documented. Gasson (2005) transferred nine wild, adult great spotted kiwi from Gouland Downs (North West Nelson) to the Rotoiti Nature Recovery Project Area (Nelson Lakes National Park) as part of a trial reintroduction. The reintroduction was highly successful – all nine birds persisted in the area for over a year following release. This success does not appear to extend to the ONE programme. Metzler (2011) monitored sub-adult success following a ONE reintroduction, which was only partially successful: 3 of 5 sub-adults died shortly after release. One death was due to predation and the others were disease-based (avian malaria and fungal pneumonia) (Metzler 2011). Thus refinements still need to be made to the captive rearing process and research is currently investigating reasons for the difference in ONE success between different kiwi species.

1.4.2 Monitoring

One of the biggest hindrances to kiwi conservation is our inability to effectively monitor populations through time (Pierce & Westbrooke 2003; Robertson & Colbourne 2003; Holzapfel et al. 2008). The cryptic, nocturnal habit of kiwi makes them notoriously difficult to study; however, this information is critical if we are to determine the success or failure of management programmes. Current kiwi monitoring procedures can be classified as direct or indirect approaches.

Direct

Direct kiwi monitoring techniques typically involve radio tracking and/or the use of trained dogs (Robertson et al. 1999). Radio telemetry is the arguably the most informative tool for assessing the survival and movement of individual kiwi. Adult kiwi are fitted with transmitters which allow for future relocation via radio telemetry (Robertson & Colbourne 2003). If a large number of birds are fitted with transmitters (20+) this form of monitoring can be used to assess population/survivorship trends. Alternatively, in situations where just a few birds are radio tracked, valuable information about behaviour, breeding success etc. can still be derived (Robertson & Colbourne 2003). A recently

developed alternative is the use of specially trained kiwi dogs. These dogs can be used to locate kiwi in order to estimate the age structure of the population. The proportion of juveniles in the population can be used to infer the health of the population. For example, a high proportion of juveniles (30% +) indicates that predator control is effectively protecting the most vulnerable life stage (Robertson & Fraser 2009). Such a technique works best in high density populations (Robertson & Colbourne 2003; Craig et al. 2011). Though these direct monitoring techniques are very informative, they are not widely used because they are expensive and very time consuming.

Indirect

Indirect techniques involve monitoring indices: indications of the animals' presence rather than the individuals themselves (footprints, calls etc.). Kiwi are difficult to count directly due to their cryptic and nocturnal nature, thus these indirect methods are often favoured. As kiwi produce loud, frequent and sexually dimorphic vocalisations, acoustic monitoring has proven extremely useful.

Acoustic Monitoring

Colbourne & Kleinpaste (1984) were the first to suggest using call rates to monitor populations on a large scale. In the 1990's this was developed further into a nationwide National Call-count Monitoring Scheme (Robertson & Colbourne 2003). In 1993, 20 sites were selected throughout the country that covered all populations of kiwi known or thought to be genetically distinct and 3-6 listening stations established at each (additional stations have since been added). Call-counts take place during the first 2 hours of darkness, 4-8 nights a year, typically from mid-May to June (Pierce & Westbrooke 2003; Robertson & Colbourne 2003). During each survey listeners complete a standard Kiwi Call Scheme card which notes the frequency, timing, gender and location of the calls (Figure 1.3; Robertson & Colbourne 2003). This procedure is then repeated for three consecutive years to establish a baseline level of calling; following this, call-counts are repeated every 5 years to detect changes (Robertson & Colbourne 2003). Information from these surveys is then used to infer site-specific density changes over time (Craig et al. 2011). The call-count method can also be used to assess the effectiveness of specific management activities (Robertson 2004). For example, Pierce & Westbrooke (2003) found a close correlation between the level of management (predator control) and call-counts for North Island brown kiwi in Northland. In the well-managed sites, call-counts remained more or less consistent whereas in unmanaged sites calling decreased over an 8 year period.

While this method of monitoring has proven useful in some contexts (Miller & Pierce 1995; Pierce & Westbrooke 2003), it does have some limitations. Call-count data can only be used to monitor population trends in a specific area over time; it cannot reliably be used to estimate abundance or to compare sites due to site-specific variability (e.g. forest types, topography) and individual variation in

calling rates (Gibb 1996; Pierce & Westbrooke 2003). Furthermore, call-count data is known to be heavily influenced by a suite of factors including observer bias, weather conditions, season and moon phase (Pierce & Westbrooke 2003; Craig et al. 2011). We therefore need to develop alternate indirect tools for assessing kiwi abundance. In the latest Kiwi Recovery Plan, the identification of individuals was identified as a key step towards achieving this goal (Holzapfel et al. 2008). One potential avenue to achieve this individual level identification is through acoustic monitoring (Holzapfel et al. 2008).

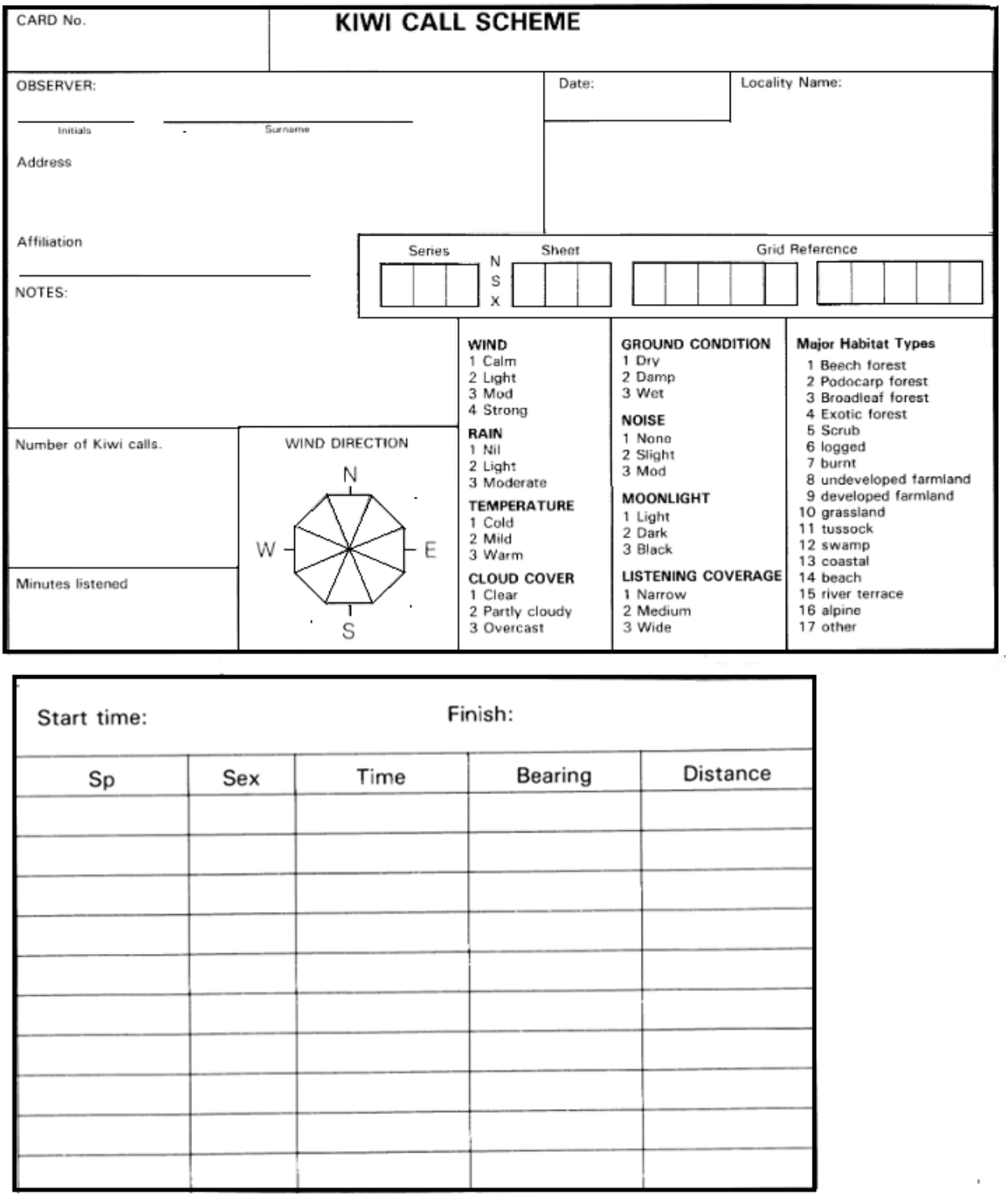


Figure 1.3: Kiwi Call-count Reporting Card (front and back) (Robertson & Colbourne 2003)

1.5 Vocal Individuality

Individually distinctive vocalisations have been described for many avian species (Terry et al. 2005). This phenomenon has been observed in both passerine (e.g. Acadian flycatcher (*Empidonax virescens*) (Wiley 2005), Jackson's weaver (*Ploceus jacksoni*)(Reers & Jacot 2011), long tailed tit (*Aegithalos caudatus*) (Sharp & Hatchwell 2005), brown-flanked bush warbler (*Cettia fortipes*) (Xia et al. 2010) and rufous bristlebird (*Dasyornis broadbenti*) (Rogers & Paton 2005) and non-passerine species (e.g. marbled frogmouth (*Podargus ocellatus*) (Jones & Smith 1997), great bitterns (*Botaurus*

stellaris) (Puglisi & Adamo 2004), black headed gull (*Chroicocephalus ridibundus*)(Mathevon et al. 2003), slender billed gull (*Chroicocephalus genei*) (Mathevon et al. 2003), black throated diver (*Gavia arctica*) (Gilbert et al. 1994), eagle owls (*Bubo bubo*) (Grava at al. 2008), western screech owls (*Megascops kennicottii*) (Tripp & Otter 2006), Visayan hornbill (*Penelopides panini*) (Policht et al. 2009), greater flamingo(*Phoenicopterus roseus*) (Mathevon 1997), great grey owls (*Strix nebulosa*) (Rognan et al. 2009) and pygmy owls (*Strix woodfordii*) (Galeotti et al. 1993)). In reality, individually distinctive vocalisations are thought to be a feature of almost all vocally active species to some degree (Terry et al. 2005). Vocalisations may vary with regard to spectral and/or temporal elements (Jones & Smith 1997; Peake et al. 1998; Grava et al. 2008; Koren & Geffen 2011).

- Spectral variation between individuals tends to be associated with morphological and/or genetic variation.
  Morphological: Sound production in birds is thought to be analogous to the source-filter model proposed for humans (Beckers et al. 2003; Ohms et al. 2010). Sounds are produced when air passes from the lungs and vibrates membranes in the syrinx (Ohms et al. 2010). These sounds are then filtered by elements of the vocal tract (Ohms et al. 2010). As no two individuals have identical morphologies, the source filter model would predict that every individual would have its own unique spectral characteristics (Ohms et al. 2010). In some species, source variability is key with Ballintijin et al. (1995) reporting that individual variation in the structure or size of the syrinx was the primary cause of spectral variation for the collared dove (*Streptopelia decaocto*). In other species, the filtering process has been highlighted as important with Suthers (1994) demonstrating that individual variation in the degree of vocal tract asymmetry in oilbirds (*Steatornis caripensis*) led to the development of individually distinct vocalisations.
  Genetic: Intra-individual spectral variation may also be genetically determined (Levréro et al. 2009). Numerous studies have suggested that this is the case for the signature calls of young colonially breeding birds (Medvin et al. 1993; Levréro et al. 2009).

- Intraspecific temporal variation can be attributed to respiratory pattern (Riede & Goller 2010), environmental variation (Ripmeester et al. 2010) and motivational state (Ręk & Osiejuk 2010). These factors tend to be less consistent over time than morphological and/or genetically determined factors.

1.5.1 Assessing Vocal Individuality

The ability to acoustically identify individual birds relies on low within-individual variation and high between-individual variation in vocalisations (Terry et al. 2005; Grava et al. 2008). In early studies, vocally individuality was assessed qualitatively; discrimination was based upon visual inspection of

individual spectrograms (Terry et al. 2005). Vocal individuality is now more commonly assessed in a quantitative manner. Spectral and temporal elements of calls are measured from spectrograms and used to assess the extent of individuality (Peake et al. 1998; Rebbeck et al. 2001; Rogers & Paton 2005). Quantitative approaches usually employ multivariate statistical techniques; the most widely used is discriminant function analysis (Terry et al. 2005). This analysis determines which of the variables best discriminates between two or more groups of individuals (Terry et al. 2005). The resulting discriminant functions are then validated using reclassification techniques. A high reclassification success (>80%) is considered a good indication that vocalisations are individually distinctive (Terry et al. 2005).

In most cases, the final discrimination between individuals is reliant on a range of both spectral and temporal elements. The relative importance of these elements varies on a case to case basis. Typically spectral variables tend to be more important than temporal. For example, Mathevon (1997) investigated vocal individuality in greater flamingos (*Phoenicopterus roseus*). His analysis revealed that the most individualised call parameters were initial frequency and peak frequency. He suggested that spectral variables may be more rigorous indicators of identity as they are physiologically constrained (Mathevon 1997). Although spectral variables tend to be favoured, other studies have reported that temporal variables are more important. For example, Puglisi & Adamo (2004) studied the vocalisations of male great bitterns (*Botaurus stellaris*). Their analysis found that the interval between booms was the most important discerning factor. Interestingly, in this situation where temporal variables were dominant, male great bitterns could not be re-identified over time as the calls were not stable. Potentially this supports the earlier statement that spectral variables are more rigorous indicators of vocal identity.

Individually distinct vocalisations may be adaptive in many species as they provide a means of individual recognition. The three main reported functions of individually distinctive vocalisations are the recognition of mates, kin and territorial neighbours (Tibbetts & Dale 2007). Accordingly, vocal individuality can also be applied in a conservation setting.

1.5.2 Conservation Applications

As previously stated, almost all vocally active species have some degree of individual distinctiveness (Terry et al. 2005). The degree of this individuality is variable, but in many species, vocalisations may be distinctive enough to allow for use in monitoring. Individual identification is a key step forward for acoustic monitoring as it allows for the calibration of other monitoring techniques (e.g. assessment of census error), provides a means of estimating key population parameters (migration, survival) and allows for the detection of individual behavioural differences (Peake & McGregor 1998).

Monitoring based on vocal individuality has a further advantage over most other individual monitoring techniques (e.g. radio tagging, mark recapture) as it is non-invasive (Terry et al. 2005). While vocal individually is not currently employed as a mainstream monitoring tool, it has proven extremely effective in the contexts in which it has been used (see Case Study examples)

Case Studies

Owls

Owls are an example of a group which is hard to monitor by traditional means due to their low density, secretive nature and nocturnal habits (Puglisi & Adamo 2004: Terry et al. 2005; Tripp & Otter 2006). They produce long range vocalisations which have been shown to be individually distinctive in many species, including eagle owls (*Bubo bubo*) (Grava at al. 2008), western screech owls (*Megascops kennicottii*) (Tripp & Otter 2006), great grey owls (*Strix nebulosa*) (Rognan et al. 2009) and pygmy owls (*Strix woodfordii*) (Galeotti et al. 1993). Vocal individuality in owls has primarily been employed to examine site fidelity, territory turnover and habitat usage. Galeotti and Sacchi (2001) employed vocal individuality techniques to assess territory turnover in the European scops owl (*Otus scops*). Using vocal identification of male owls they were able to show that turnover rate is very high for this species (55-78%). Tripp and Otter (2006) conducted a similar study on western screech owls and found very low turnover rates (28-50%).

Great Bitterns

The European great bittern is an elusive, wetland species known for its 'booming' vocalisation (Puglisi & Adamo 2004). The bittern is one of the few species to have been routinely counted and monitored using vocal individuality (Terry et al. 2005). British populations of great bitterns have been censused in this manner since 1990 (Gilbert et al. 2002). Gilbert et al. (2002) used vocal individuality to assess male survival over a 9 year period. This information has been used to assess local mortality rates and allocate conservation efforts.

Woodcock & Corncrake

Vocal individuality can also be used to validate other monitoring techniques. The woodcock (*Scolopax rusticola*) is a widespread European species; however, population estimates are poor due to the difficulty in monitoring this species (Hoodless et al. 2008). Traditionally, population sizes and trends had been estimated from sightings made during general bird surveys (Hoodless et al. 2008). A new approach was adopted whereby the number of male 'roding' displays (conspicuous display flight performed during breeding season) are used to infer abundance and population trends (Hoodless et al. 2008). This method was initially flawed because the mathematical relationship between the number of 'roding' displays and abundance was unknown. Hoodless et al. (2008) addressed this issue by using vocal individuality to determine the actual population of birds at 43 sites. They were thus

able to quantify the relationship between the number of males and the number of displays and it was deemed to be a suitable index method. A similar clarification of survey methods was used to validate census techniques in corncrakes (*Crex crex*). The corncrake is an endangered land-rail that is difficult to monitor as it occupies areas of dense vegetation. The original census technique involved mapping the location of calling males. This technique was developed following radio tracking studies which suggested that corncrakes rarely moved more than 250m between nights and 75% of males would call on any particular night (Peake & McGregor 2001). The accuracy of this census technique was assessed using vocal individuality (Peake & McGregor 2001). The results of this study indicate that the mapping approach had been underestimating population sizes by 20-30% (Peake & McGregor 2001).

1.5.3 Limitations

As with any monitoring technique, vocal individuality has limitations which could interfere with its use in conservation.

1. Like other forms of acoustic monitoring, vocal individuality is biased towards the most vocally active sections of the population. This may be affected by a variety of factors including gender, breeding status, territorial status, ages or time of year (Terry et al. 2005)

2. Vocal individuality is typically better suited to monitoring male birds. Females of most temperate avian species are quiet and do not have long range vocalisations; as a result, it is often difficult to monitor female birds using vocal individuality (Terry et al. 2005).

3. In order to be an effective tool for long term monitoring, individual vocalisations must remain stable over time (Gilbert & McGregor 1994). This aspect of vocal individuality is often overlooked due to the complexity associated with measurement over time (Lengagne 2001; Terry et al. 2005). While many studies confirm long term stability (Lengagne 2001; Tripp & Otter 2006) others have found evidence for temporal variation in call structure (Puglisi & Adamo 2004).

1.6 Kiwi Vocal Behaviour

1.6.1 Kiwi Vocalisations

Kiwi are the most vocal of the ratite species worldwide (Davies 2002). They produce a variety of different sounds, the most prevalent being the 'whistle' call which has a distinctive repetitive structure (Fuller 1990; Castro 2011). This vocalisation is produced by both sexes and is thought to primarily function in territory defence and pair communication (Colbourne & Kleinpaste 1984; Digby et al. 2013a). Male birds tend to call more often than female birds (Digby et al. 2013a), Taborsky and

Taborsky (1992) determined that male North Island brown kiwi called at a rate of 0.85 calls/hour while females called at a rate of 0.35 calls/hour. Aside from differences in calling rates male and female calls are also acoustically distinct; males produce shrill calls while female calls tend to be more guttural (Fuller 1990; Castro 2011). Surprisingly, despite the reliance on call-count monitoring and the apparent complexity of kiwi vocal behaviour, very few studies have examined kiwi vocalisations in any real depth. Of the five recognized species of kiwi only two have been subject to detailed acoustical study.

North Island Brown Kiwi (Corfield et al. 2008)

Corfield et al. (2008) conducted a detailed examination of vocal behaviour in North Island brown kiwi. The whistle calls in this study consisted of 13- 36 multi-harmonic notes separated by periods of silence. The note duration and inter-gap duration increased throughout the call (note: 0.17-1.28 sec; gap: 0.12 -3.5 sec). The notes produced by males had a clear harmonic structure and contained high frequency components (fundamental frequency of c. 1.5 kHz, overtones c. 13 kHz). Notes in male calls could be grouped into three distinct phrases, defined as groups of notes similar in structure and degree of frequency modulation. Conversely, the female notes were dominated by broadband, low frequency components (fundamental frequency c. 0.1 kHz, overtones <7 kHz). The female calls were thought to contain formant structures. Additionally, this study was the first to highlight duetting amongst kiwi pairs.

Little Spotted Kiwi (Digby et al. 2013a)

Digby et al. (2013) examined the whistle vocalisation of little spotted kiwi. Male birds produced high frequency notes with a clear harmonic structure (minimum frequency ca. 2500 Hz; maximum frequency ca. 3000 Hz). 74% of male calls also had a 'hook' – a descending frequency component at the end of each note. Female calls had less distinct harmonics and the energy was more broadband (minimum frequency ca. 1500Hz; maximum frequency ca. 2000Hz). 63% of female calls contained the formant structure previously noted by Corfield et al. (2008). Unlike North Island brown kiwi, notes in little spotted kiwi were uniform in terms of structure.

1.6.2 Potential for Vocal Individuality

Kiwi are nocturnal, cryptic and found at low densities, making them a perfect candidate for vocal individuality monitoring. While there have been no peer-reviewed accounts of vocal individuality in *Apteryx* species to date, this phenomenon has been investigated in two species. Corfield (2004) evaluated the individuality of North Island brown kiwi vocalisations. Calls from seven male and four female kiwi were recorded from Rarewarewa, Whangerei over the period of a year. A range of

temporal and spectral variables were measured from 62 calls (48 male, 14 female). Discriminant function analysis was able to correctly classify 87.5% of male and 85.7% of female calls. Thus there is preliminary evidence to suggest that the calls of North Island brown kiwi may be individually distinctive (Corfield 2004).

Vocal individuality has also been assessed in the little spotted kiwi (*Apteryx mantelli*). Digby (2013) recorded calls from a population of single little spotted kiwi in Zealandia, a fenced reserve in Wellington. 81 calls from 10 individuals (seven male, three female) were measured for individual analysis. Unlike the earlier findings of Corfield (2004), little spotted kiwi demonstrated low levels of vocal individuality. Discriminant function analysis successfully classified just 57% of the male calls and 28% of female calls. This suggests that the phenomenon of vocal individuality may be highly variable within the A*pteryx* genus. The vocalisations of great spotted kiwi have not previously been subject to detailed acoustical study. Therefore, the potential use of their vocalisations to identify individuals remains unexplored.

1.7 Research Objectives

Aim: The aim of this research is to examine the vocal behaviour of great spotted kiwi and provide a preliminary assessment of whether their vocalisations could be used to identify individuals in monitoring operations.

Objectives:

1. to provide the first quantitative assessment of great spotted kiwi calls.
2. to examine the call rate of individual birds; this will allow estimation of the appropriate length of acoustic recorder field deployment.
3. to determine the degree to which the vocalisations of male and female great spotted kiwi are individually distinctive; this will provide insight in whether great spotted kiwi could be monitored via vocal individuality techniques.
4. to identify the call parameters which best distinguish between great spotted kiwi vocalisations.

Chapter 2

Methods and Materials

2.1 Study Area – Hawdon Valley

This study examined vocal individuality in a population of great spotted kiwi (*Apteryx haastii*) residing in Hawdon Valley, Canterbury, New Zealand (NZ260: K33 08250). The Hawdon Valley is a tributary to the Waimakariri River located within Arthurs Pass National Park (Figure 2.1; Elliot & Suggate 2007). It is approximately 12 kilometres long and less than a kilometre wide (5750 ha). The topography of the surrounding landscape is steep; the valley is bordered by the Polar Range on the right (max. height 2035m) and the Savannah Range on the left (max. height 1847m). The valley floor itself rises from 600m at the base to 1120m at the headwaters (DOC 2004). This high altitude environment receives an annual rainfall of approximately 4500mm (DOC 2007). The forest consists mainly of mixed beech forest. Red beech (*Nothofagus fusca*) is dominant at low altitudes (valley floor) while silver beech (*N. menziesii*) and mountain beech (*N. solandri var. cliffortioides*) are more prevalent elsewhere (DOC 2004).

Hawdon Valley is home to many rare bird species including möhua (*Mohoua ochrocephala*), orange-fronted parakeet (*Cyanoramphus malherbi*) and great spotted kiwi (Elliot & Suggate 2007). The population of great spotted kiwi in the Hawdon Valley is part of the wider Arthur's Pass – Hurunui grouping which inhabit an narrow region of the Southern Alps, approximately 60km long and 18-23 km wide (McLennan & McCann 2002). The density of birds in this region is relatively low, about 2-3 per square kilometre (c. 3000 individuals total) (McLennan & McCann 2002). The Hawdon Valley has approximately 20-25 transmittered birds with known territories (S. Yong, pers. comm. 2013)

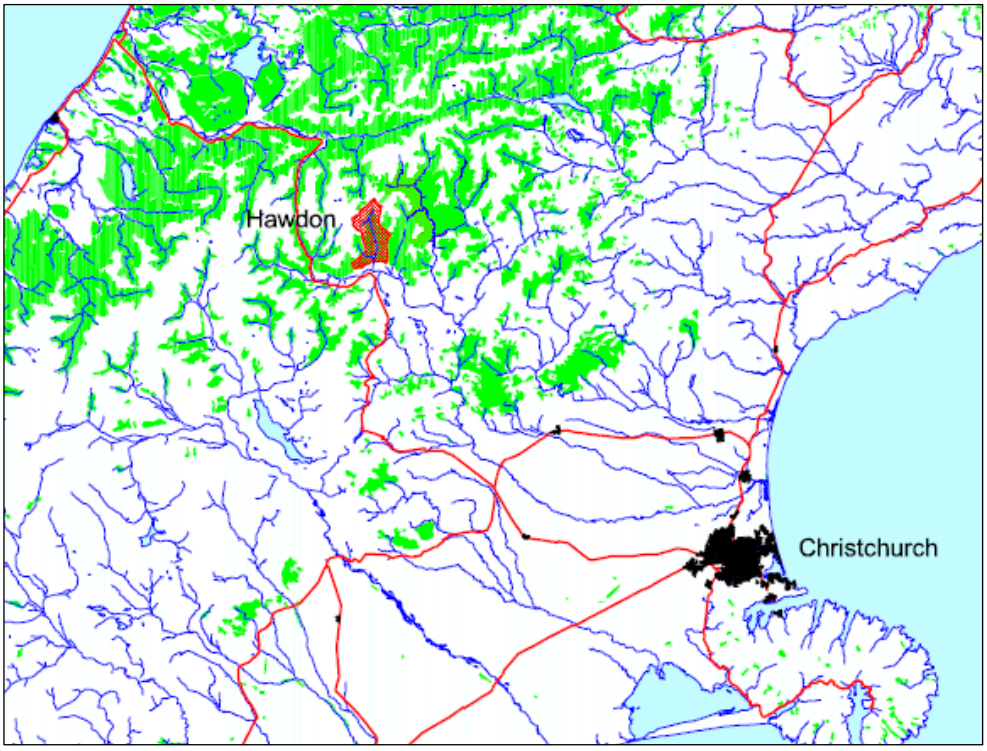


Figure 2.1: Location of Hawdon Valley (Modified from Elliot & Suggate 2007)

2.2 Call Recording

Acoustic recorders were installed near (<20m) the known breeding den sites of seven great spotted kiwi pairs between November 2012 and March 2013 (Table 2.1; Figure 2.2). Recorders were installed during the incubation period or shortly after hatch (78 days) (Table 2.1). In order to locate the nest sites, kiwi were fitted with 'Diagnostic' Transmitters specifically designed for great spotted kiwi. The output of these transmitters indicates the individuals' daily activity levels over a 14 day period. A marked drop in activity was presumed to indicate the initiation of incubation. The nest sites could then be located via radio-tracking the individuals. Department of Conservation recording devices were employed at five of the sites; these devices are single channel (mono) and detect frequencies in the range of 0-4000Hz. SoundCache recording units (Cornell Laboratory of Ornithology, Ithaca, NY, USA) were employed at the remaining two sites; these devices record across two channels (stereo) and were configured to detect frequencies in the range of 0-11000Hz. All recorders were programmed to operate on a predetermined schedule. Recording began at 8pm every night and concluded at 6.15am the following morning (10 hours and 15 minutes worth of recordings per night). All recordings were digitised at 16-bit precision with a sampling rate of 8 kHz (Department of Conservation recorders) or 22 kHz (SoundCache recorders). The recorders were expected to have enough battery life to last approximately two weeks in the field. The number of recording nights per site was inconsistent because three of the recorders were reserviced with new batteries to allow for further collection (Clyde/Bonnie, Bazza/Shazza, Ebb/Flo; Table 2.1)

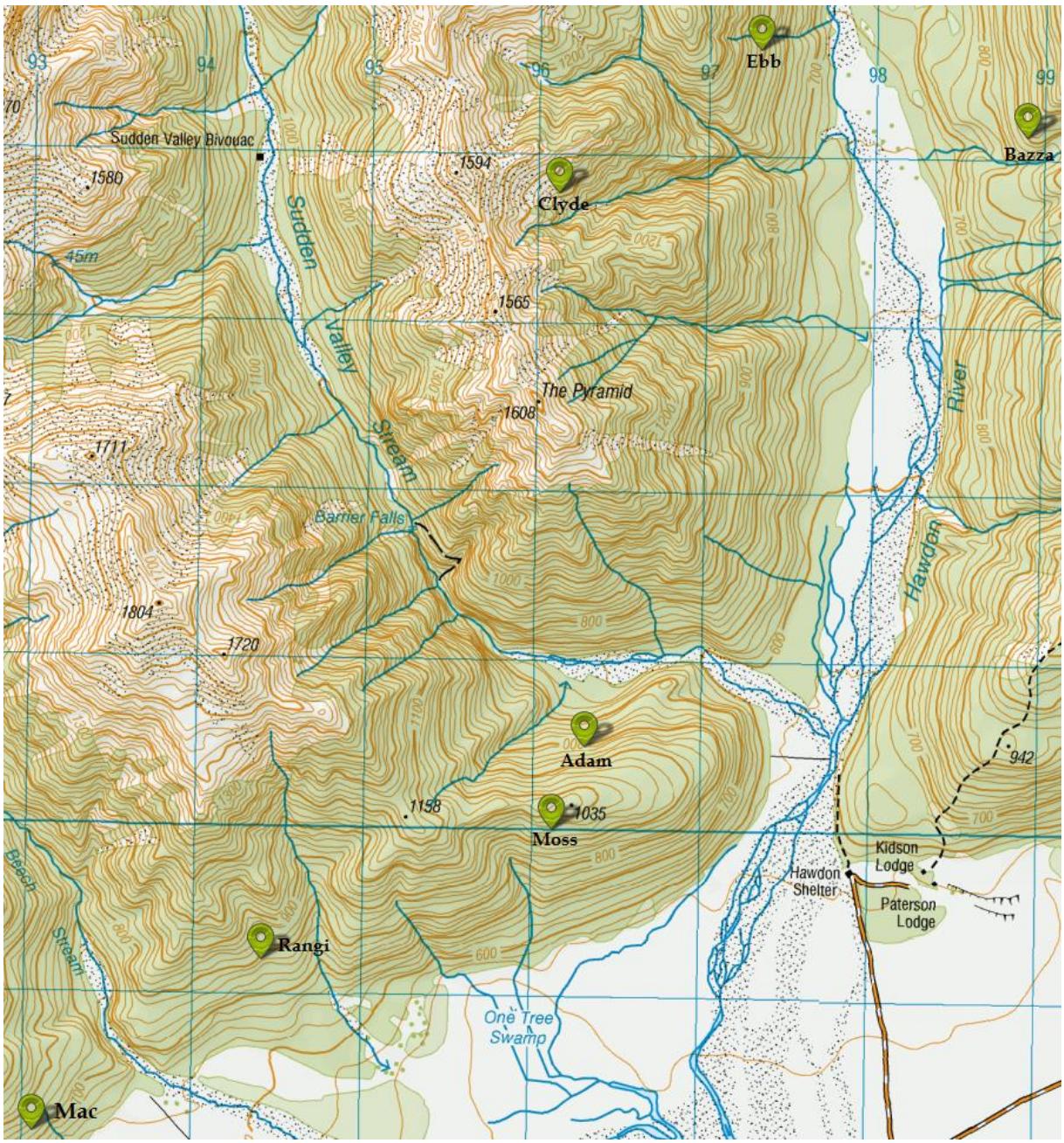


Figure 2.2: Location of acoustic recorders. Acoustic recorders were installed at the breeding den sites of seven great spotted kiwi pairs. The pins on this map indicate the location of these recorders. (Retrieved from http://www.topomap.co.nz 16/10/2013)

Table 2.1: Details of acoustic recorder placement and field duration

Pair	Latitude	Longitude	Altitude (m)	Recorder type	Distance from burrow (m)	Total Nights	Instalment (days after laying)
Adam	-42.98125	171.72834	853	DoC recorder	20	13	16
Eve							
Clyde	-42.95101	171.72668	855	Soundcache	4	24	80
Bonnie							
Rangi	-42.99251	171.70479	798	DoC recorder	5	13	83
Pongo							
Ebb	-42.94403	171.74134	910	DoC recorder	10	26	60
Flo							
Moss	-42.98561	171.72596	945	DoC recorder	10	14	14
Punga							
Bazza	-42.94877	171.76073	905	Soundcache	15	29	83
Shazza							
Mac	-43.00172	171.68811	730	DoC recorder	20	11	unknown
Beth							

2.3 Processing Recordings

2.3.1 Extraction

Raw recordings were visualised as spectrograms in Raven Pro v. 1.5 (Bioacoustics Research Program 2012). These spectrograms were visually and aurally scanned for whistle vocalisations. As whistle vocalisations have a distinctive structure they were easily detected. It was assumed that because great spotted kiwi are territorial and found at low densities in this area, the location of the recorder was indicative of the adjacent territorial pair. This allowed the individual identity of the caller to be determined as kiwi vocalisations are sexually dimorphic (Appendix B.1; Appendix B.2). Each time a call was detected; the call was saved as a separate file and the date and time of calling was noted. In total 303 whistle vocalisations were detected (262 individual calls and 41 duets), however, not all of these vocalisations were suitable for individual analysis (Table 2.2). Calls were discarded for a number of reasons:

Duetting: Duetting occurs when a male or female call is followed by a response call from a mate. Two types of duet were noted in this study: call and reply duets and overlapping duets. Corfield et al. (2008) noted that duetting altered the temporal characteristics of calls. Duetting calls were therefore excluded from the analysis.

Clipping: High amplitude signals (>90dB) can result in audio clipping which distorts spectrogram output. Clipping interferes with the measurement of spectral parameters as all frequencies are assigned equal amplitude (Figure 2.3). Calls with clipping were also excluded from further analysis.

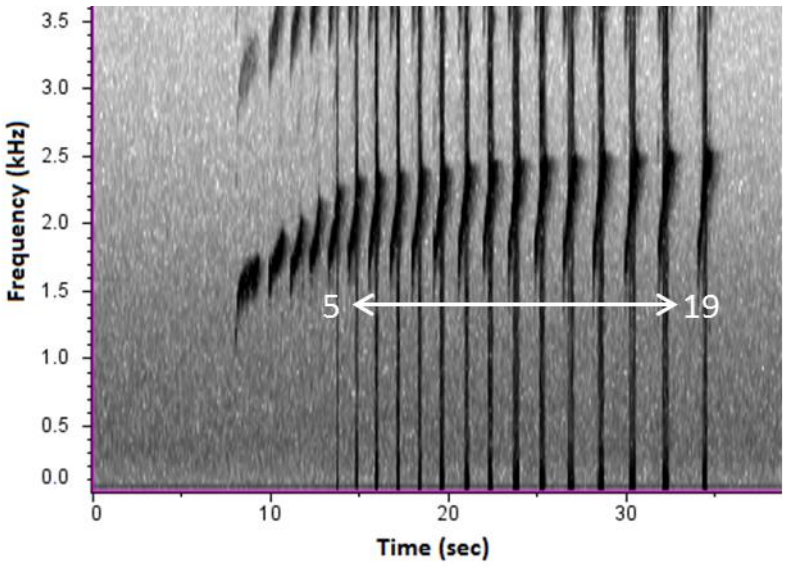


Figure 2.3: High amplitude input results in clipping. This male call spectrogram depicts clipping on syllables 5 to 19

Poor Quality: The amplitude of calls was highly variable due to variation in calling distance, topography, weather and vegetation characteristics. Only calls which had a minimum 20 dB distinction against background noise were included. Call distinction was evaluated using power spectra generated in Raven Pro 1.5. Power spectra describe how the power of a signal is distributed over different frequencies. The difference between the maximum call amplitude and the amplitude of adjacent background noise was derived to estimate overall distinction (Figure 2.4)

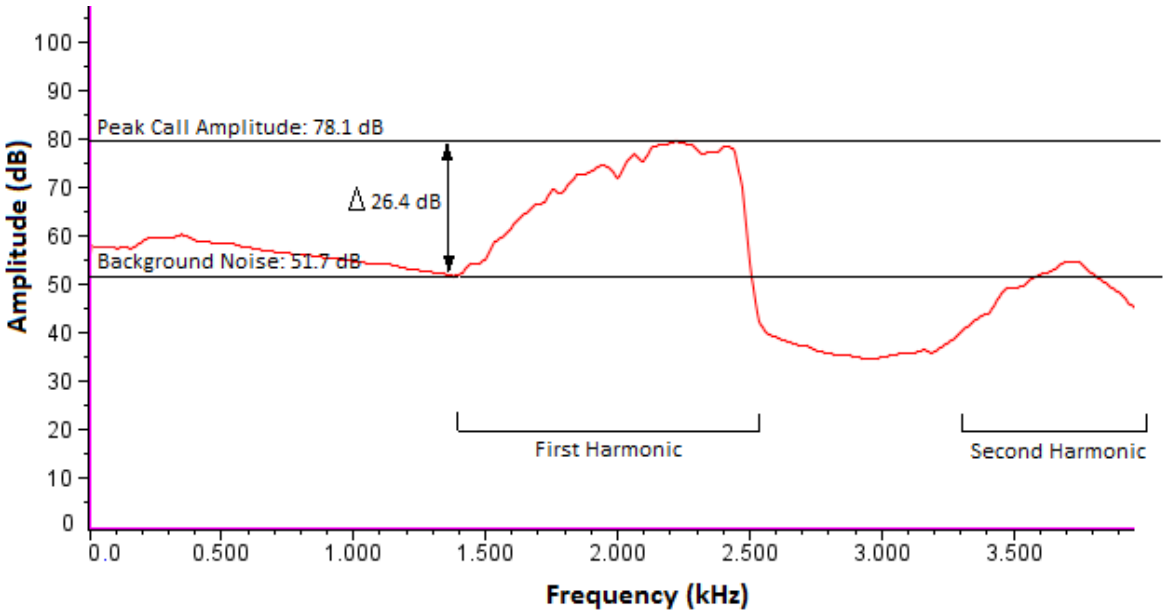


Figure 2.4: Calculation of call distinction from background noise. In this male call, the fundamental harmonic has a maximum distinction of 26.4 dB.

Overlapping: In some cases, calls were partially obscured by heterospecific calls (e.g. morepork (*Ninox novaeseelandiae*)). Whether the call was discarded or not was dependant on the degree and position of the interference.

This left a total of 133 calls that fit the criteria for call measurement (Table 2.2). Two females, Shazza & Bonnie, were excluded from further analysis as they had insufficient calls to allow for replication ($n \leq 1$).

Table 2.2: The number of vocalisations recorded for each bird.

Bird	Total number of calls	Number of calls that met criteria	Number of duets
Adam	43	19	10
Eve	17	14	
Clyde	10	9	1
Bonnie	3	1	
Rangi	24	15	14
Pongo	20	14	
Ebb	49	21	5
Flo	15	9	
Moss	8	4	4
Punga	14	7	
Bazza	31	8	2
Shazza	2	0	
Mac	10	5	5
Beth	16	7	

2.3.2 Filtering

Following extraction, calls collected by SoundCache recorders were downsampled to 8 kHz in SoundStudio 3.5.2 (Kwok 2007) for consistency with sampling rates of Department of Conservation recorders. All calls were subject to background noise removal using Audacity v. 2.0.3 (Audacity Team 2013). A five second segment of background noise adjacent to the call was used to generate a noise profile. This noise profile was then used to subtract background noise from the rest of the call. The amount of volume reduction that was applied to the background noise was 24 dB. Frequency smoothing was used to eliminate artefacts of noise reduction by blurring the noise profile. The amount of smoothing was set at 150 Hz; this value was low enough to avoid distortion of the actual signal while still avoiding artefacts. In order to test whether this noise reduction procedure was appropriate, it was tested on 15 random calls. Frequency parameters (maximum, minimum, peak frequency) were measured before and after noise reduction. No change was detected so the procedure was applied to all calls. In addition to background noise removal, frequencies below 500 Hz and above 4000 Hz were filtered out of all calls prior to measurement.

2.4 Call Measurement

The temporal and spectral parameters of calls were measured from spectrograms and power spectra produced by Raven Pro 1.5 (Bioacoustics Research Program 2012). Both the spectrograms and power spectra were generated using a 512-sample Hann window with a 50% overlap and a frequency resolution of 15.6 Hz. Measurements were taken at a whole call and individual syllable level (Table 2.3). Digby et al. (2013) noted that syllables at the start and end of whistle calls show temporal and spectral fluctuation. This could be interpreted in one of two ways; either these syllables are unsuitable for individual analysis as they lack intra-individual stability, or alternatively, these syllables may be key distinguishing features. In order to capture this variation, three syllables were measured from the start, middle and end of each call (nine syllables per call in total). Once the calls had all been measured, 10% (13) were randomly selected to be remeasured to check for consistency.

Temporal Variables

The temporal variables that were measured were; total duration of call, the number of syllables per call, syllable rate and syllable duration (Table 2.3). Call and syllable duration were derived from the signal energy distribution which is calculated by Raven from the spectrogram selection (Table 2.3; Bioacoustics Research Program 2012). This provided a consistent measure of duration despite substantial variation in background noise and amplitude. Syllable rate was defined as the call duration divided by the total number of syllables (Table 2.3).

Spectral Variables

Zollinger et al. (2012) suggested that un-calibrated spectrograms were unsuitable for making accurate and repeatable measurements of frequency. They noted that variation in background noise and amplitude could dramatically affect the sensitivity of spectral measurement. They suggest an alternative methodology whereby maximum and minimum frequencies (and therefore bandwidth) are measured from a power spectrum at a set number of decibels below the peak amplitude. This approach was used in this study to examine maximum frequency, minimum frequency and bandwidth. Maximum and minimum frequencies were measured at 20 dB below the maximum amplitude on a power spectrum (Figure 2.5; Table 2.3). Bandwidth (delta frequency) was calculated based on this selection (Table 2.3). Peak amplitude and peak frequency were calculated automatically based on the spectrogram selection (Table 2.3; Figure 2.5). It should be noted that all spectral variables were derived from the fundamental harmonic only; this was easily identified on the power spectrum as it corresponds to the first peak in the sound profile (Figure 2.4)

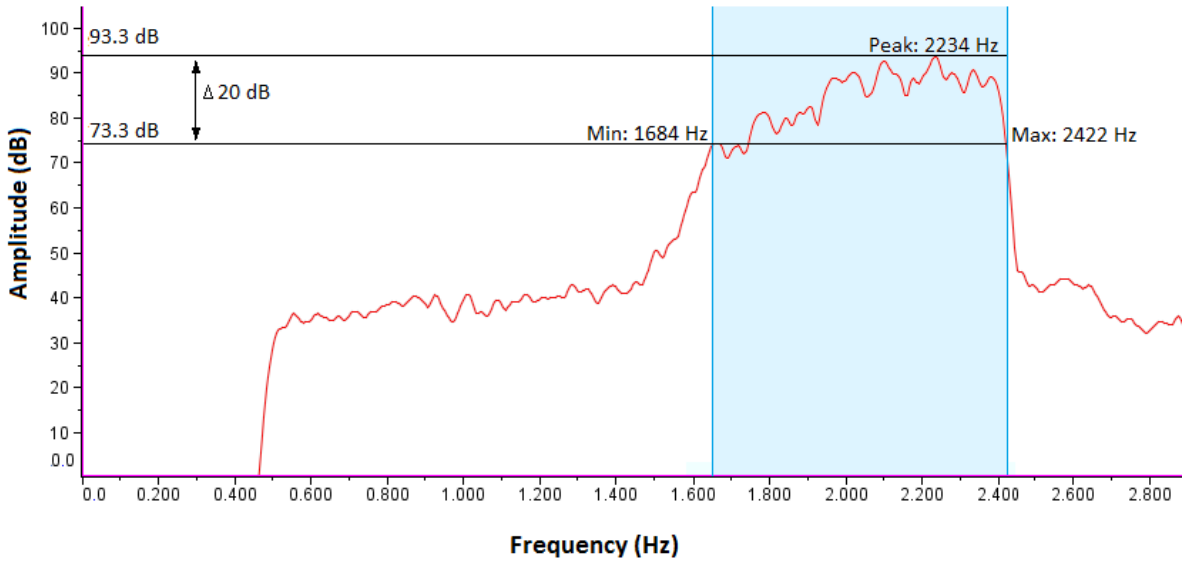


Figure 2.5: The calculation process for minimum frequency, maximum frequency and peak frequency. The spectrum selection defines the region 20 dB below peak amplitude which was used to infer the frequency range.

Table 2.3: The temporal and spectral parameters that were measured.

Variables	Description	Units	Level of Measurement
Time 95%	The point in time that divides the selection (call or syllable) into two time intervals containing 95% and 5% of the energy of the selection.	Seconds	Call and Syllable
Time 5%	The point in time that divides the selection (call or syllable) into two time intervals containing 5% and 95% of the energy of the selection	Seconds	Call and Syllable
Duration 90%	The difference between the 5% and 95% times	Seconds	Call and Syllable
Number of syllables	The number of syllables in the call		Call
Syllable rate	The overall call duration divided by the total number of syllables.	Syllables/Sec	Call
Maximum Frequency	The upper frequency bound of the 20 dB spectrum selection (call or syllable)	Hz	Syllable
Minimum Frequency	The lower frequency bound of the 20 dB spectrum selection (call or syllable)	Hz	Syllable
Delta Frequency	The difference between the upper and lower frequency limits of the 20 dB spectrum selection (bandwidth)	Hz	Syllable
Peak Frequency	The frequency at which peak power occurs within the selection (call or syllable)	Hz	Syllable
Peak Power	The maximum power in the selection (call or syllable)	dB	Call and Syllable

2.5 Statistical Analysis

Prior to analysis, syllable parameters were averaged according to their position within the call (beginning, middle, and end). This formed three variants of each parameter e.g. duration (beginning), duration (middle) and duration (end). Unless otherwise stated all analyses treat males and females separately.

2.5.1 Descriptive Statistics

R v. 2.15.3 (R Development Core Team 2013) was used to calculate descriptive statistics for each variable, including mean, standard error and range. These analyses were conducted at both an overall variable and individual bird level. Graphs were produced to examine within-call trends. The correlation between peak power and temporal measurement was assessed to determine whether amplitude was affecting the sensitivity of analysis.

2.5.2 Analysis of Variance

All ANOVA tests were performed using SPSS v 22.0 (IBM corp. 2013).

Sex Differences

One-way ANOVAs were conducted for all call and syllable parameters to examine the extent to which male and female vocalisations differ (alpha level 0.05). As sample sizes were unequal a Welch's correction was applied. Welch ANOVA tests do not assume homogeneity of variance.

Within-Call Variation

One way repeated measures ANOVAs were used to examine intra-call variation in both spectral and temporal parameters. In cases where the initial ANOVA was significant (alpha level 0.05), a Fisher's Least Significant Difference (LSD) post hoc test was used to examine which measures were significantly different from one another.

ANOVA Assumptions

1. Normality

For ANOVA it is assumed that residuals are normally distributed. This was examined using normal Q-Q plots. If the residuals are normally distributed they will form a straight line on the Q-Q plot.

2. Outliers

Data should not contain significant outliers. Potential outliers were also detected in Q-Q plots. Repeated measures ANOVA and Welch ANOVA tests were run with and without potential outliers. If an outlier removal did not affect the overall test results it was retained in the analysis.

3. Sphericity – repeated measures ANOVA ONLY

In repeated measures ANOVAs data sphericity is also assumed. Sphericity requires that the repeated measures demonstrate homogeneity of variance and covariance. This was examined using Mauchly's Test of Sphericity. Mauchly's Test of Sphericity tests the null hypothesis that the variances are equal. A significant result ($p < 0.05$) indicates that the assumption of sphericity has been violated. In these cases a Greenhouse-Geisser correction was applied to normalise the variances.

2.5.3 Variable Assesment

Potential for Individuality Coding

The potential for individuality coding (PIC) was assessed for each variable in order to provide an initial indication of discriminatory potential (Trimble & Charrier 2011; Nagy & Rockwell 2013). PIC is expressed as the ratio between the amount of inter-individual variation (CVb) and the amount of intra-individual variation (CVi) (Charrier et al. 2001). The intra-individual coefficient of variation (CVi) was calculated using the formula $CVi = \frac{SDi \times 100}{Xi} \times (1 + \frac{1}{4n})$ (Xi = mean value of each individual, SDi = standard deviation of each individual, n = number of calls) (Sokal & Rohlf 2012). This formula has been corrected for small sample size bias $\left(1 + \frac{1}{4n}\right)$ (Sokal & Rohlf 2012). Inter-individual coefficients of variation (CVb) were also calculated for each variable. The formula for this coefficient is slightly different as there is no need for a small sample size correction, $CVb = \frac{SDb \times 100}{Xb}$ (Xb = mean values of all calls, SDb= standard deviation of all calls) (Sokal & Rohlf 2012). The resulting CVi & CVb values were used to determine the PIC for each variable using the formula $PIC = CVb/meanCVi$ (mean CVi = average of each intra-individual CVi) (Charrier et al. 2001). For each variable, a PIC value greater than 1 indicates that the variable is individualized (intra-individual variability less than inter-individual variability) (Charrier et al. 2001). PIC values greater than 2 indicate that a parameter is highly stereotyped within an individual and therefore could be utilised for individual discrimination (Charrier et al. 2001).

Parameter Stability

A similar logic was applied to test the assumption that syllables could be combined to produce subset averages (beginning, middle and end). The within-call coefficient of variation (CVs) was calculated from individual syllables, $CVs = \frac{SDs \times 100}{Xs} \times (1 + \frac{1}{4n})$ (X*s* = syllable mean, SD*s* = syllable standard deviation, n = number of syllables = 3). The between-call coefficient of variation (CVc) was calculated in the same way, $CVc = \frac{SDc \times 100}{Xc} \times (1 + \frac{1}{4b})$ (X*c*= call mean for each bird, SD*c* = call standard deviation for each bird, n = number of calls per bird). The ratio of CVc to CVs ($CVc/meanCVs$) indicates the degree of parameter stability within calls. Values (>1) suggest that there is more variation between calls than within them, thus supporting the averaging of syllables. This ratio was averaged across all birds to determine whether certain variables were more unstable than others. Values < 1 indicated that variables should be excluded from further analysis.

Redundant Variables

One issue with having three sets of variables for each call (beginning, middle, end) is that there is a tendency for variables to be highly correlated and thus redundant for discriminatory purposes. In order to evaluate potential redundancy, a correlation matrix was generated for all measured variables. High correlations (> 0.8) were deemed to be problematic. In these situations, the variable with the highest PIC score was retained and the correlated partner variable was excluded from further analysis.

2.5.4 Discriminant Function Analysis

SPSS v 22.0 (IBM corp. 2013) was used to conduct stepwise Discriminant Function Analysis (DFA). DFA is a multivariate method that is used to evaluate which explanatory variables best discriminate between two or more naturally occurring groups (Terry et al. 2005). It is a two stage process;

1. *Analysis*: Discriminant functions are derived. Discriminant functions represent linear combinations of predictor variables that best differentiate between groups.
2. *Classification*: The discriminant functions are utilized to predict group membership.

Analysis

Stepwise discriminant function analysis progressively adds independent variables to the model based on Wilk's Lambda scores. Wilks' lambda statistic is the proportion of total variability not explained by the model. At each step, the variable that minimises the overall Wilks' lambda is entered into the equation.

Output: ***Wilks' Lambda*** is interpreted at both a variable and discriminant function level.

Variables - The smaller the lambda for an independent variable, the more that variable contributed to the discriminant function. The F test of Wilks' lambda indicates which of the variables made significant contributions (alpha level $p < 0.05$).

Discriminant function - Wilks' lambda is also used to indicate the contribution of each discriminant function to group differentiation. In this case significance is derived from a Chi Square test (alpha level $p < 0.05$).

Eigenvalues indicate how well each discriminant function differentiates between the groups in the analysis (individuals). The larger the eigenvalue, the better the function differentiates between individuals. The eigenvalue table also indicates the 'percentage of variance' explained by each discriminant function. This is the proportion of discriminating ability each discriminant function contributes.

Classification

A cross validation technique known as jack-knifing was used to test the reclassification success of the resultant discriminant functions. One by one, individual calls are removed from the data set. Each time, the remaining cases are used to develop discriminant functions and classify the excluded call. This process is repeated for all cases. If group membership is known this process allows calculation of reclassification success.

Output : ***Classification success*** is presented in SPSS as the percentage of cases successfully categorised.

DFA Model Assumptions

1. Sample Size

Although unequal sample sizes are acceptable in DFA, there must be a sufficiently high ratio between the number of cases and number of predictor variables. Tabachnick & Fidell (2007) suggest that unless the number of cases in the smallest group exceeds the number of predictor variables, over-fitting of results may occur. In situations where the stepwise model had more predictor variables than cases in the smallest group, the model was either recalibrated with less variables or the individual with the smallest sample size was removed.

2. Multivariate Normality

It is assumed that each predictor variable is normally distributed. This was examined using normal Q-Q plots. If the residuals are normally distributed they will form a straight line on the Q-Q plot.

3. Outliers

Discriminant function analysis is extremely sensitive to the inclusion of outliers. Mahalanobis distances were used to detect multivariate outliers. High mahalanobis distances indicate problematic cases.

4. Homogeneity of Variance/Covariance Matrices

It is assumed that the variance/covariance matrices of variables are homogeneous across groups. Discriminant function analysis is fairly robust to violations of this assumption provided the data do not contain significant outliers. Box's M tests were used to test this assumption. When M is non-significant, the null hypothesis (homoscedasticity) can be accepted (alpha level 0.001). Box's M has been criticized for being overly sensitive; therefore discriminant function analysis may still be robust despite test failure (Tabachnick & Fidell 2007).

5. Non-Multicollinearity

Multicollinearity refers to the situation where there are high inter-correlations between predictor variables. Discriminate function analysis assumes that predictor variables are fairly independent of one another; therefore highly correlated variables are of concern. Prior to analysis redundant variables were identified from a correlation matrix. Variable tolerance was also used to examine multicollinearity. Tolerance refers to the proportion of variance not accounted for by other variables in the equation. Tolerance values greater than 0.2 indicate multicollinearity (O'Brian 2007).

Chapter 3

Results

3.1 Descriptive Statistics (Objectives 1 & 2)

There was no significant difference between male and female calls in terms of total length ($F_{1, 112}$ = 1.16, p = 0.283), syllable rate ($F_{1, 72}$ = 1.45, p = 0.232), and syllable count ($F_{1, 115}$ = 3.4, p = 0.068). However, male and female calls differed significantly across all measured syllable parameters (Appendix A.1). Male syllables are longer and contained higher frequency elements (minimum frequency, maximum frequency, peak frequency) than their female counterparts. Female syllables contained lower frequency elements and had greater bandwidth than male syllables (Figure 3.1; Figure 3.2; Figure 3.3; Figure 3.4; Figure 3.5, Appendix A.1)

3.1.1 Male

Male great spotted kiwi called at an average rate of 1.8 (SE ± 0.5) calls per night (Table 3.1). Individual call rate was variable; the least vocal bird (Clyde) called at a rate of 0.5 calls per night while the most vocal bird (Adam) called at a rate of 4.1 calls per night. Each call was composed of a series of repetitive notes (syllables) with a distinctive harmonic structure (Appendix B.1)

Table 3.1: Average number of calls recorded each night.

Bird	Calling Rate (calls/night)
Adam	4.1
Clyde	0.5
Rangi	2.9
Ebb	2.1
Moss	0.9
Bazza	1.1
Mac	1.4
Male Average	1.8
Eve	2.1
Bonnie	0.2
Pongo	2.6
Flo	0.8
Punga	1.3
Shazza	0.1
Beth	1.9
Female Average	1.3

Temporal

On average, male calls contained 18.1 syllables (SE ± 0.3) and lasted for 25.5 seconds (SE ± 0.4; Table 3.2). This is equivalent to a rate of 0.71 syllables per second (SE ± 0.01). The repeated measures ANOVA for syllable duration confirmed that there was a significant degree of intra-call variation in this parameter ($F_{1.19, 92.93} = 113.19$, $p < 0.001$, Figure 3.2; Appendix A.2). Syllables at the start of calls were significantly longer than all other syllables ($p < 0.001$; Table 3.2; Figure 3.1). There was no significant difference between middle syllable duration and end syllable duration ($p = 0.334$; Table 3.2; Figure 3.1; Appendix A.2).

Table 3.2: Temporal parameters of male great spotted kiwi calls. Values are reported as averages and displayed alongside the standard error of the mean.

				Syllable Duration (sec)		
	Number of Syllables	Call Duration (sec)	Syllable Rate (syllables/sec)	Beginning	Middle	End
Adam (19)	20.3 ± 0.5	29.2 ± 0.8	0.70 ± 0.01	0.58 ± 0.01	0.52 ± 0.01	0.54 ± 0.01
Clyde (9)	14.4 ± 0.4	22.3 ± 0.5	0.65 ± 0.01	0.76 ± 0.02	0.52 ± 0.02	0.48 ± 0.01
Rangi (15)	16.5 ± 0.4	22.4 ± 0.6	0.73 ± 0.01	0.71 ± 0.02	0.46 ± 0.01	0.45 ± 0.01
Ebb (21)	19.2 ± 0.3	26.8 ± 0.6	0.72 ± 0.01	0.57 ± 0.03	0.42 ± 0.01	0.46 ± 0.01
Moss (4)	18.3 ± 0.8	26.3 ± 1.3	0.70 ± 0.01	0.93 ± 0.04	0.5 ± 0.04	0.5 ± 0.04
Bazza (8)	14.9 ± 0.8	22.9 ± 0.9	0.65 ± 0.02	0.65 ± 0.03	0.54 ± 0.03	0.50 0.02
Mac (5)	21.6 ± 0.4	24.9 ± 0.8	0.87 ± 0.01	0.7 ± 0.05	0.52 ± 0.01	0.55 ± 0.03
Overall Male	18.1 ± 0.3	25.5 ± 0.4	0.71 ± 0.01	0.65 ± 0.01	0.48 ± 0.01	0.49 ± 0.01
Range	(12 - 23)	(18.2 – 33.0)	(0.59-0.89)	(0.37-1.03)	(0.37-0.60)	(0.4-0.6)

Spectral

The repeated measures ANOVAs indicated that all spectral parameters had a significant degree of intra-call variation (minimum frequency: $F_{2, 156} = 300.09$, $p < 0.001$, maximum frequency: $F_{1.52, 118.2} = 773.56$, $p < 0.001$, peak frequency: $F_{1.70, 132.4} = 840.1$, $p < 0.001$, bandwidth: $F_{1.67, 230.15} = 242.13$, $p < 0.001$; Appendix A.2). Three spectral parameters; maximum frequency, bandwidth, and peak frequency had a similar intra-call trend (Figure 3.3; Figure 3.4; Figure 3.5; Appendix A.2). Syllables at the beginning of calls had lower values of maximum frequency, peak frequency, and bandwidth than middle syllables (maximum frequency: $p < 0.001$, peak frequency: $p < 0.001$, bandwidth: $p < 0.001$;

Table 3.3; Appendix A.2). Middle syllables in turn had lower maximum frequency, peak frequency and bandwidth than end syllables (maximum frequency: $p < 0.001$, peak frequency: $p < 0.001$, bandwidth: $p < 0.001$; Table 3.3; Appendix A.2). Although these parameters increased significantly throughout the call, the change was most pronounced between the beginning and middle call parts (Figure 3.3; Figure 3.4; Figure 3.5; Appendix A.2). Minimum syllable frequency had a slightly different intra-call trend (Figure 3.2). Middle and end syllables had higher minimum frequencies than syllables at the beginning of calls ($p < 0.001$) but were not significantly different from one another ($p = 0.471$; Table 3.3; Appendix A.2).

All repeated measures ANOVAs adhered to the condition of normality. However, all analyses violated the assumption of sphericity; therefore a Greenhouse-Geisser correction was applied to normalise the variances (Appendix A.2). The removal of potential outliers did not affect the overall test.

Table 3.3: Spectral parameters of male great spotted kiwi calls. Values are reported as averages and displayed alongside the standard error of the mean.

	Beginning				Middle				End			
	Minimum Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Peak Frequency (Hz)	Minimum Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Peak Frequency (Hz)	Minimum Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Peak Frequency (Hz)
Adam (19)	1697 ± 16	2056 ± 28	359 ± 17	1891 ± 20	1831 ± 10	2544 ± 7	714 ± 10	2431 ± 22	1789 ± 15	2642 ± 6	852 ± 15	2542 ± 16
Clyde (9)	1332 ± 20	1676 ± 11	344 ± 14	1514 ± 14	1583 ± 12	2001 ± 13	419 ± 14	1923 ± 14	1616 ± 12	2156 ± 32	541 ± 40	2027 ± 25
Rangi (15)	1582 ± 23	1992 ± 28	411 ± 12	1814 ± 27	1884 ± 26	2592 ± 12	708 ± 20	2338 ± 24	1848 ± 29	2695 ± 24	847 ± 48	2461 ± 25
Ebb (21)	1620 ± 25	2052 ± 31	432 ± 12	1888 ± 28	1781 ± 26	2425 ± 5	644 ± 22	2229 ± 13	1854 ± 25	2500 ± 5	646 ± 22	2335 ± 12
Moss (4)	1397 ± 23	1754 ± 30	357 ± 19	1591 ± 21	1668 ± 18	2159 ± 12	490 ± 13	2053 ± 19	1658 ± 16	2548 ± 89	890 ± 93	2329 ± 60
Bazza (8)	1348 ± 35	1684 ± 45	336 ± 19	1543 ± 51	1526 ± 29	2149 ± 66	622 ± 43	1910 ± 38	1556 ± 33	2333 ± 36	777 ± 23	2087 ± 63
Mac (5)	1722 ± 21	2265 ± 52	544 ± 38	2048 ± 40	1895 ± 20	2756 ± 49	861 ± 62	2511 ± 30	1950 ± 9	2977 ± 39	1027 ± 36	2590 ± 58
Overall Male	1565 ± 18	1960 ± 23	395 ± 9	1792 ± 21	1766 ± 16	2417 ± 25	651 ± 15	2240 ± 24	1778 ± 16	2546 ± 24	782 ± 20	2364 ± 23
Range	1158-1822	1462-2444	278-689	1226-2143	1429-2005	1895-2882	348-982	1755-2594	1460-2065	2069-3069	399-1107	1849-2810

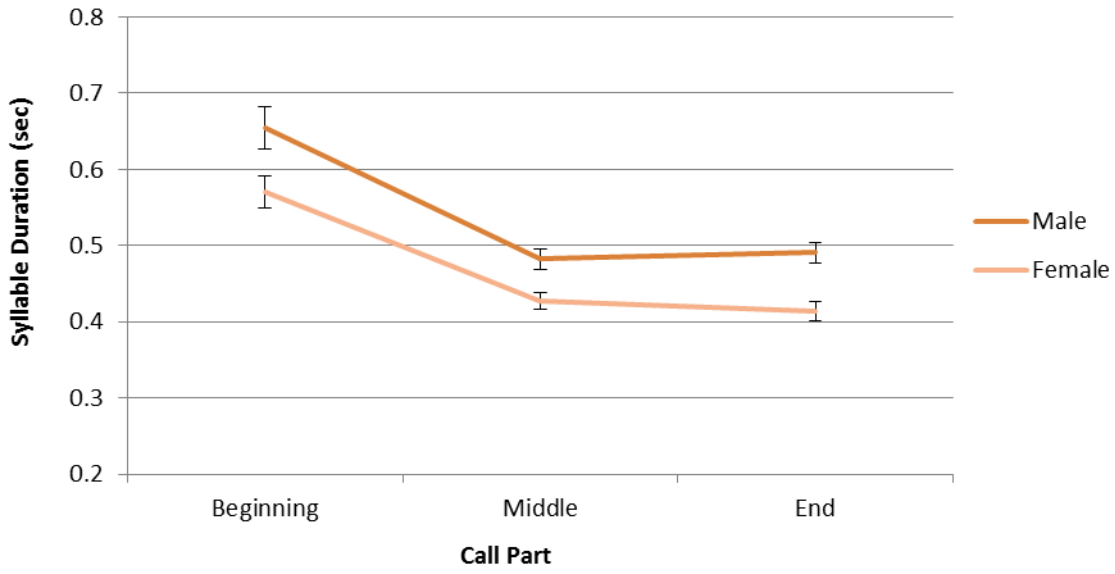


Figure 3.1: Intra-call variation in syllable duration (sec) for male and female great spotted kiwi. Error bars are indicative of the 95% confidence intervals

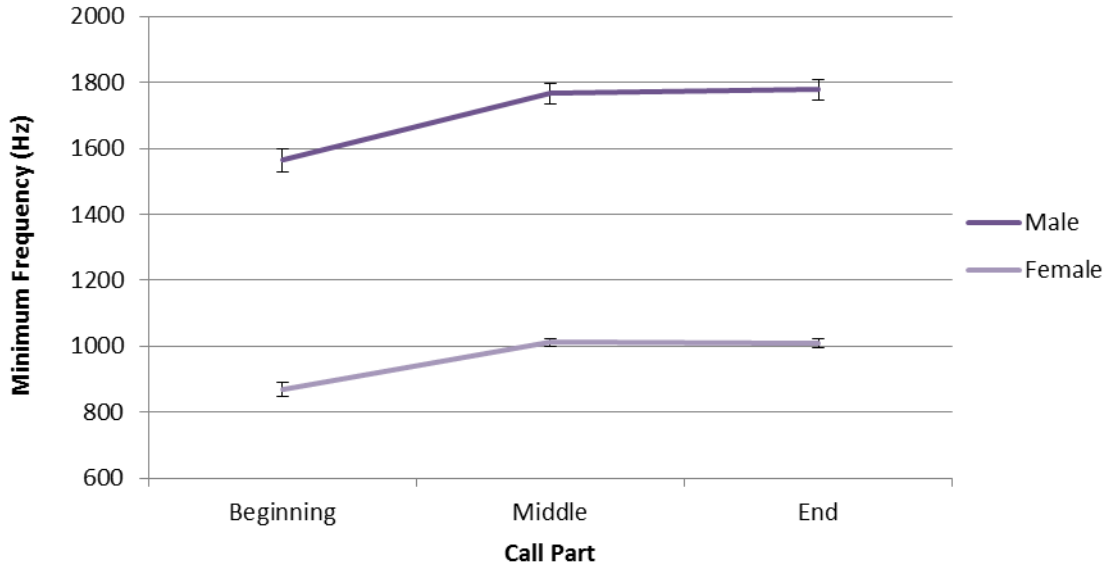


Figure 3.2: Intra-call variation in minimum syllable frequency (Hz) for male and female great spotted kiwi. Error bars are indicative of the 95% confidence intervals.

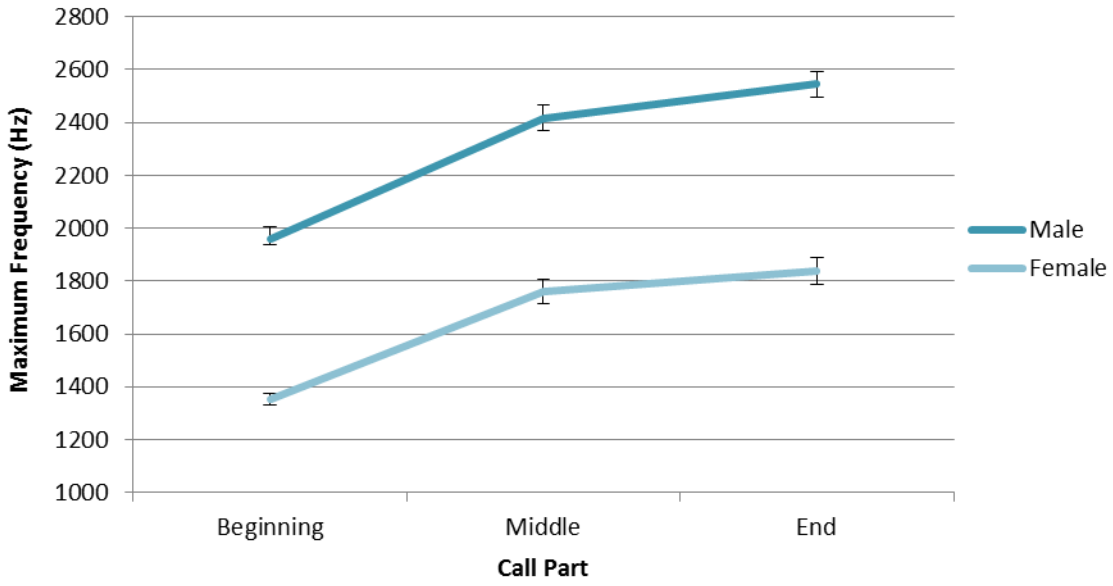


Figure 3.3: Intra-call variation in maximum syllable frequency (Hz) for male and female great spotted kiwi. Error bars are indicative of the 95% confidence intervals.

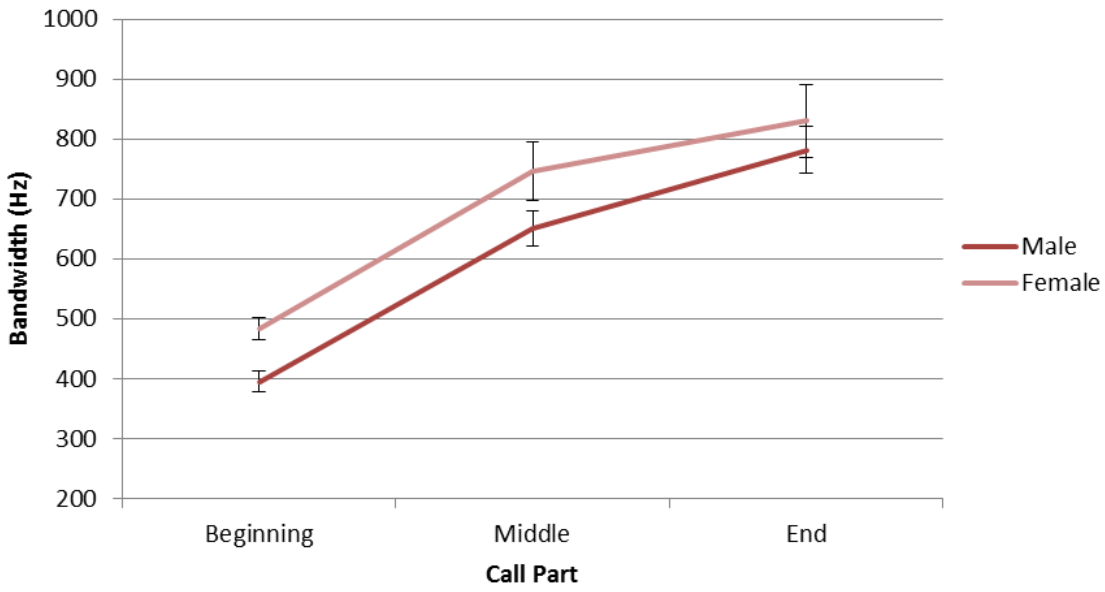


Figure 3.4: Intra-call variation in syllable bandwidth (Hz) for male and female great spotted kiwi. Error bars indicate 95% confidence intervals.

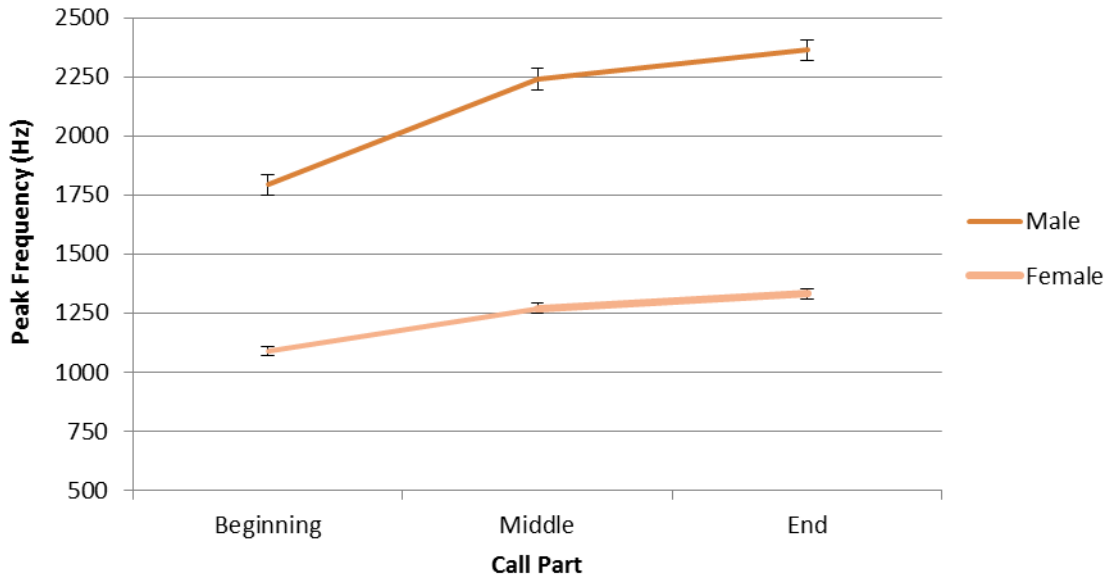


Figure 3.5: Intra-call variation in peak syllable frequency (Hz) for male and female great spotted kiwi. Error bars are indicative of the 95% confidence interval.

3.1.2 Female

Female great spotted Kiwi called at a lower rate than males (1.3 ± SE 0.4 calls per night) (Table 3.1). The least vocal female (Shazza) called at a rate of 0.1 calls per night while the most vocal female (Pongo) called at a rate of 2.6 calls per night (Table 3.1). Like the male call, the female call is composed of a series of repetitive syllables; unlike the male call these syllables are distinctly broadband in nature (Appendix B.2)

Temporal

The average length of the female call is 26.2 seconds (± 0.5) and each call contains an average of 18.8 syllables (SE ± 0.3) (Table 3.4). As for male calls, the repeated measures ANOVA indicated that there was a significant degree of intra call variation in syllable duration ($F_{1.48, 73.89} = 202.75$, $p < 0.001$; Appendix A.3). Syllables at the beginning of calls were the longest ($p < 0.001$), while the duration of middle and end syllables were not significantly different ($p = 0.22$) (Table 3.5, Appendix A.3)

Table 3.4: Temporal parameters of female great spotted kiwi calls. . Values are reported as averages and displayed alongside standard error of the mean.

				Syllable Duration (sec)		
	Number of Syllables	Call Duration (sec)	Syllable Rate (syllable/sec)	Beginning	Middle	End
Eve (14)	17.6 ± 0.3	27.8 ± 0.5	0.63 ± 0.00	0.63 ± 0.02	0.46 ± 0.01	0.46 ± 0.02
Pongo (14)	18.0 ± 0.4	23.1 ± 0.6	0.78 ± 0.01	0.52 ± 0.02	0.43 ± 0.01	0.41 ± 0.01
Flo (9)	19.6 ± 0.8	27.1 ± 1.3	0.72 ± 0.01	0.52 ± 0.02	0.41 ± 0.01	0.38 ± 0.01
Punga (7)	18.4 ± 1.3	24.8 ± 0.5	0.76 ± 0.07	0.56 ± 0.02	0.41 ± 0.01	0.40 ± 0.00
Beth (7)	22.1 ± 0.5	29.5 ± 0.9	0.75 ± 0.01	0.61 ± 0.02	0.40 ± 0.00	0.40 ± 0.00
Overall Female	18.8 ± 0.3	26.2 ± 0.5	0.72 ± 0.01	0.57 ± 0.01	0.42 ± 0.01	0.41 ± 0.01
Range	(14 - 24)	(18.8 - 32.2)	(0.60-1.00)	(0.4 - 0.733)	(0.4 - 0.53)	(0.33-0.53)

Spectral

The repeated measures ANOVAs indicated that there was a significant degree of intra-call variation for all spectral parameters (minimum frequency: $F_{1.55, 77.57} = 253.94$, $p < 0.001$, maximum frequency: $F_{1.65, 82.64} = 252.13$, $p < 0.001$, peak frequency: $F_{1.65, 82.64} = 175.69$, $p < 0.001$, bandwidth: $F_{1.66, 83.01} = 133.52$, $p < 0.001$) (Appendix A.3). Although male and female calls are spectrally distinct, the intra-call trends tended to be consistent. Maximum frequency, peak frequency and bandwidth all increased throughout the duration of the female call (Figure 3.3; Figure 3.4; Figure 3.5). Beginning syllables had lower values of maximum frequency, peak frequency and bandwidth than middle syllables (maximum frequency: $p < 0.001$, peak frequency: $p < 0.001$, bandwidth: $p < 0.001$; Table 3.5; Appendix A.3). In turn, middle syllables had lower maximum frequency, peak frequency, and bandwidth than end syllables (maximum frequency: $p < 0.001$, peak frequency: $p < 0.001$, bandwidth: $p < 0.001$; Table 3.5; Appendix A.3). As in males, beginning syllable minimum frequency was lower than all other syllables ($p < 0.001$) but did not vary between the middle and end of calls ($p = 0.19$; Figure 3.2; Table 3.5; Appendix A.3).

All repeated measure ANOVAs adhered to the condition of variable normality. All analyses violated the assumption of sphericity; therefore the Greenhouse-Geisser correction was applied (Appendix A.3). The removal of potential outliers did not affect the overall test results.

Table 3.5: Spectral parameters of female great spotted kiwi calls. Values are reported as averages and are displayed with standard error of the mean.

	Beginning				Middle				End			
	Minimum Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Peak Frequency (Hz)	Minimum Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Peak Frequency (Hz)	Minimum Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Peak Frequency (Hz)
Eve (14)	765 ± 14	1310 ± 11	545 ± 12	1002 ± 14	965 ± 6	1855 ± 31	890 ± 35	1350 ± 7	975 ± 10	1932 ± 58	957 ± 65	1448 ± 7
Pongo (14)	809 ± 7	1298 ± 11	490 ± 11	1073 ± 20	989 ± 8	1660 ± 17	671 ± 14	1260 ± 17	975 ± 10	1848 ± 12	925 ± 14	1261 ± 17
Flo (9)	928 ± 12	1362 ± 21	434 ± 15	1126 ± 16	1043 ± 10	1627 ± 39	584 ± 34	1241 ± 14	1065 ± 13	1630 ± 47	565 ± 38	1333 ± 25
Punga (7)	960 ± 13	1411 ± 21	451 ± 19	1094 ± 15	1036 ± 12	1827 ± 24	791 ± 19	1199 ± 21	1017 ± 7	1886 ± 19	869 ± 13	1310 ± 21
Beth (7)	860 ± 25	1416 ± 40	556 ± 28	1119 ± 26	1014 ± 17	2031 ± 40	1017 ± 44	1358 ± 30	986 ± 9	2045 ± 52	1059 ± 53	1379 ± 19
Overall Female	1565 ± 18	1960 ± 23	395 ± 9	1792 ± 21	1766 ± 16	2417 ± 25	651 ± 15	2240 ± 24	1778 ± 16	2546 ± 24	782 ± 20	2364 ± 23
Range	714-1021	1207-1598	375-663	966-1258	903-1115	1386-2160	345-1188	1130-1521	910-1140	1423-2328	379-1388	1164-1544

3.2 Variable Assessment

3.2.1 Potential for Individuality coding

Potential for individuality coding (PIC) scores indicated that all male variables were individualised (all PIC ≥ 1) (Table 3.6). Parameters were more variable between calls of different individuals than calls of the same individual. The most individualised parameters were; maximum frequency (middle) (PIC = 3.22) and peak frequency (middle) (PIC = 2.80). Syllable duration (end) (PIC = 1.14) was least individualised. Female call parameters were also all individualised (all PIC ≥ 1) (Table 3.6). The variables with greatest potential for individuality coding were bandwidth (end) (PIC = 2.04) and bandwidth (middle) (PIC = 1.97). The least individualised parameter for female calls was maximum frequency (beginning) (PIC = 1.20).

Table 3.6: The potential for individuality coding (PIC) scores for all temporal and spectral parameters. Larger PIC scores indicate a more highly individualised parameter.

		Male PIC	Female PIC
Whole	Syllables	1.65	1.21
	Call Length	1.47	1.41
	Syllable Rate	1.76	1.51
Beginning	Duration	1.51	1.31
	Minimum	2.04	1.81
	Maximum	1.97	1.20
	Bandwidth	1.35	1.31
	Peak Frequency	2.01	1.21
Middle	Duration	1.33	1.54
	Minimum	2.13	1.25
	Maximum	3.22	1.81
	Bandwidth	1.68	1.97
	Peak Frequency	2.80	1.41
End	Duration	1.14	1.81
	Minimum	2.04	1.57
	Maximum	2.33	1.29
	Bandwidth	1.55	2.04
	Peak Frequency	1.85	1.45

3.2.2 Intra-call Variability

The temporal and spectral parameters of male calls were more variable between calls (CVc) than within calls (CVs) (average CVc/Cvs ≥ 1) (Table 3.7). This supported the combination of variables into three groups (beginning, middle, and end). One female call parameter, syllable duration (beginning), was more variable within calls than between calls (average CVc/Cvs = 0.81) (Table 3.7). This indicates that the combination of beginning syllables to determine average syllable duration may be unjustified. Accordingly, syllable duration (beginning) was excluded from further analysis.

Table 3.7: The ratio of inter-call variation to intra-call variation. Variables with an average score > 1 have less variation within calls than between calls.

		Male	Female
Beginning	Duration	1.07	0.81
	Minimum	1.54	1.09
	Maximum	1.05	1.01
	Bandwidth	1.00	1.58
	Peak Frequency	1.44	2.55
Middle	Duration	2.39	4.10
	Minimum	2.53	1.85
	Maximum	1.26	1.92
	Bandwidth	1.56	1.92
	Peak Frequency	1.21	1.68
End	Duration	1.61	7.90
	Minimum	1.72	4.21
	Maximum	2.26	1.88
	Bandwidth	2.25	2.04
	Peak Frequency	1.04	1.03

3.2.3 Redundant Variables

The repeated measures ANOVA results indicate that some of the measured parameters are redundant. In both male and female calls, middle / end syllable duration, and middle / end minimum syllable frequency were not significantly different from one another. In males, PIC comparison led to the removal of end syllable duration and end syllable minimum frequency. In females, the opposite

was true; middle syllable duration and middle syllable minimum frequency had lower PIC values so were excluded from further analyses.

The correlation matrix of male call parameters identified five pairs of highly correlated parameters (Appendix A.4): syllables and call duration (0.906), maximum frequency (beginning) and minimum frequency (beginning) (0.866), minimum frequency (beginning) and peak frequency (beginning) (0.871), maximum frequency (beginning) and peak frequency (beginning) (0.914), and minimum frequency (middle) and minimum frequency (end) (0.834). PIC comparisons led to the further exclusion of call duration, maximum frequency (beginning) and peak frequency (beginning). Fewer variables were correlated in female calls (Appendix A.5). Only two pairs of parameters had high correlations: bandwidth (end) and maximum frequency (end) (0.975), and bandwidth (middle) and maximum frequency (middle) (0.946). PIC comparisons led to the exclusion of maximum frequency (middle) and maximum frequency (end). Temporal variables were not found to be highly correlated with peak amplitude; this allowed these parameters to be used without standardisation (Appendix A.6).

3.3 Discriminant Function Analysis (Objectives 3 & 4)

3.3.1 Male

Moss (n= 4) and Mac (n=5) were not included in the discriminant function analysis on account of small sample size. The stepwise discriminant function model was thus constructed using 72 calls from five birds. The resulting model incorporated eight predictor variables (Appendix A.7). The contribution of all predictor variables to the model was shown to be significant (Table 3.8). In order of decreasing importance the predictor variables were; maximum frequency (middle), peak frequency (middle), minimum frequency (beginning), bandwidth (end), number of syllables, syllable duration (middle), bandwidth (middle), and syllable duration (beginning) (Table 3.8).

Table 3.8: The relative importance of the predictor variables in the male discriminant function analysis. Variables are listed in the order they were incorporated into the model. Low values of Wilks' Lambda and high F –values indicate more important variables. The significance of the variables contribution to the model is indicated by the P-value.

	Wilks' Lambda	F (*df*)	P-value	Importance
Maximum Frequency (middle)	0.083	177.6 (4, 64)	< 0.001*	**1**
Syllables	0.337	31.465 (4, 64)	< 0.001*	**5**
Syllable Duration (middle)	0.388	25.238 (4, 64)	< 0.001*	**6**
Peak Frequency (middle)	0.145	94.342 (4, 64)	< 0.001*	**2**
Syllable Duration (beginning)	0.562	12.462 (4, 64)	< 0.001*	**8**
Bandwidth (end)	0.33	32.45 (4, 64)	< 0.001*	**4**
Bandwidth (middle)	0.399	24.083 (4, 64)	< 0.001*	**7**
Minimum Frequency (beginning)	0.305	36.467 (4, 64)	< 0.001*	**3**

* denotes significant results

The eight predictor variables were combined to form four discriminant functions (Appendix A.7).The overall Wilks' Lambda of the model (0.002) was significant ($\chi^2_{32} = 385.20$, $p < 0.001$), indicating that there are significant individual differences across these four discriminant functions (Table 3.9). Nearly all of the discriminatory power of the model derives from the first three discriminant functions (96.1%; Table 3.10). The first discriminant function alone accounts for 65.7% of the discriminatory power (Table 3.10). This model had a total reclassification success of 94.2%. Three birds; Clyde, Rangi and Ebb, had a reclassification success of 100% (Table 3.11). Bazza the lowest rates of reclassification (57.1%) due to incorrect assignment as Clyde and Ebb (Table 3.11).

Table 3.9: Test of male discriminant functions. Chi-square test of Wilks Lambda statistic indicates significant discriminant functions.

	Initial Model				Modified Model			
Test of Function(s)	Wilks' Lambda	Chi-square	df	p - value	Wilks' Lambda	Chi-square	df	p - value
1 through 4	0.002	385.197	32	< 0.001*	0.002	396.455	32	< 0.001*
2 through 4	0.026	217.515	21	< 0.001*	0.027	222.716	21	< 0.001*
3 through 4	0.151	112.605	12	< 0.001*	0.162	111.888	12	< 0.001*
4	0.52	38.921	5	< 0.001*	0.551	36.682	5	< 0.001*

* denotes significant results

Table 3.10: The weighting of discriminant functions used in male discriminant function analysis. Eigenvalues indicate the relative importance of discriminant functions.

	Initial Model		Modified Model	
Discriminant Function	Eigenvalue	% of Variance	Eigenvalue	% of Variance
1	15.75	65.7	15.69	67.3
2	4.83	20.2	4.73	20.3
3	2.45	10.2	2.36	10.1
4	0.923	3.9	0.54	2.3

One assumption of discriminant function analysis is that the number of cases (calls) in the smallest group exceeds the number of predictor variables. The smallest group size in the initial discriminant function model was eight (Bazza), this is equal to the number of predictor variables. Rather than remove another individual from the analysis, the model was recalibrated with seven predictor variables only. Syllable duration (beginning) was discarded as it was the least important predictor variable in the initial model (Table 3.8). The significance and importance of the seven predictor variables was unaffected by the model modification (Table 3.8). The overall Wilks' Lambda of the modified model was significant (Wilks lambda = 0.002, $\chi^2_{32} = 396.46$, $p < 0.0001$), indicating that the modified discriminant functions were effective in differentiating between individuals (Table 3.9). As in the initial model, most of the models discriminatory power derives from the first three

discriminant functions (97.7%; Table 3.10). The weighting of the first discriminant function increased to 67.3% (Table 3.10).

Reduction in the number of predictor variables actually increased the overall reclassification success of the model to 95.7% (Figure 3.6). The individual reclassification success rates of Clyde, Rangi, Ebb and Adam were unaffected by the removal of the eighth predictor variable; however, the reclassification success of Bazza increased from 57.1% to 71.4% (Table 3.11). This increase arises due to a greater distinction between Bazza and Clyde (Table 3.11).

Table 3.11: Summary of male reclassification success. Rows are actual identity; columns are the bird the call was assigned to by the analysis. Success rates (%) of individual birds are highlighted.

	Initial Model					Modified Model				
	Clyde	**Bazza**	**Adam**	**Rangi**	**Ebb**	**Clyde**	**Bazza**	**Adam**	**Rangi**	**Ebb**
Clyde	100	0	0	0	0	100	0	0	0	0
Bazza	28.6	57.1	0	0	14.3	14.3	71.4*	0	0	14.3
Adam	0	0	94.4	5.6	0	0	0	94.4	5.6	0
Rangi	0	0	0	100	0	0	0	0	100	0
Ebb	0	0	0	0	100	0	0	0	0	100

* denotes a change in reclassification success

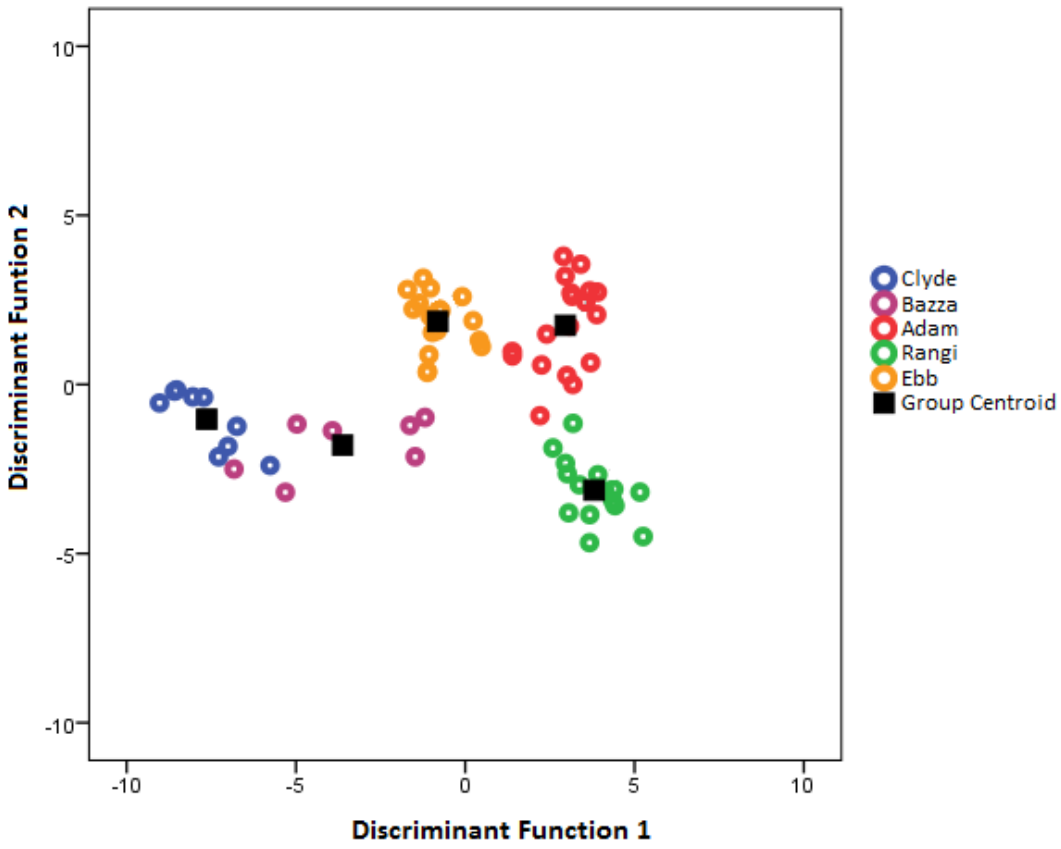


Figure 3.6: The separation of individual male great spotted kiwi by the first two discriminant functions of the modified model. Group centroids represent the mean values of the discriminant functions for each group.

Assumptions

The Box's M statistic of the modified model was significant ($F_{84, 3697} = 2.675$, $p < 0.001$). This indicates that homogeneity could not be assumed. As all of the mahalanobis distance scores were small, no further actions were taken to account for the lack of homogeneity. The variable Q-Q plots suggest that all univariate data was normally distributed, this implies multivariate normality. Tolerance values were suitably high for all predictor variables, thus non-multicollinearity was assumed (Appendix A.7).

3.3.2 Female

51 calls from five female birds were used to perform the stepwise discriminant function analysis. The resulting model incorporated five predictor variables (Table 3.12; Appendix A.8). All five predictor variables were significant in discriminating between groups (Table 3.12). In order of most importance the variables were: minimum frequency (beginning), bandwidth (middle), syllable rate, peak frequency (middle) and syllable duration (end) (Table 3.12). These variables were used to formulate four discriminant functions (Table 3.13; Appendix A.8). The ability of these functions to discriminate

between groups was shown to be significant (Wilks lambda = 0.01, $\chi^2_{20} = 204.37$, $p < 0.001$; Table 3.13).

Table 3.12: The relative importance of the predictor variables utilised by the female discriminant function model. Variables are listed in the order they were incorporated into the model. Variables with low Wilks' Lambda and high F –values are highly important. The significance of the variables contribution to the model is indicated by the P-value.

	Wilks' Lambda	F (df)	P-value	Importance
Minimum Frequency (beginning)	.272	30.09 (4, 45)	< 0.001*	1
Bandwidth (middle)	.285	28.17 (4, 45)	< 0.001*	2
Syllable Rate	.408	16.30 (4, 45)	< 0.001*	3
Peak Frequency (middle)	.454	13.53 (4, 45)	< 0.001*	4
Syllable Duration (end)	.607	7.29 (4, 45)	< 0.001*	5

* denotes significant results

Table 3.13: Test of female discriminant functions. Chi-square test of Wilks Lambda indicates significant discriminant functions.

Test of Function(s)	Wilks' Lambda	Chi-square	df	p - value
1 through 4	.010	204.370	20	< 0.001*
2 through 4	.079	111.588	12	< 0.001*
3 through 4	.399	40.412	6	< 0.001*
4	.926	3.396	2	.183

* denotes significant results

The first three discriminant functions accounted for 99.4% of the models discriminatory power (Table 3.14). The first discriminant function alone accounted for 57.1% (Table 3.14). The contributions of the first, second and third discriminant functions were significant; however, the fourth discriminant function did not significantly contribute to individual discrimination ($X^2_2 = 3.40$, $p = 0.183$; Table 3.14). Despite only having three significant discriminant functions, the female discriminant function model had an overall reclassification success of 90% (Figure 3.7). Only Beth was classified with 100%

accuracy (Table 3.15). Punga had the lowest reclassification success rate (66.7%) due to insufficient separation from Beth (Table 3.15; Figure 3.7).

Table 3.14: The weighting of the female discriminant functions. Eigenvalues indicate the relative importance of discriminant functions.

Discriminant Function	Eigenvalue	% of Variance
1	7.24	57.1
2	4.04	31.9
3	1.32	10.4
4	0.08	0.6

Table 3.15: Summary of female reclassification success. Rows are actual identity; columns are the bird the call was assigned to by the analysis. Success rates (%) of individual birds are highlighted.

	Punga	Eve	Pongo	Flo	Beth
Punga	**66.7**	0	0	0	33.3
Eve	0	**92.9**	7.1	0	0
Pongo	0	0	**92.9**	7.1	0
Flo	0	0	11.1	**88.9**	0
Beth	0	0	0	0	**100**

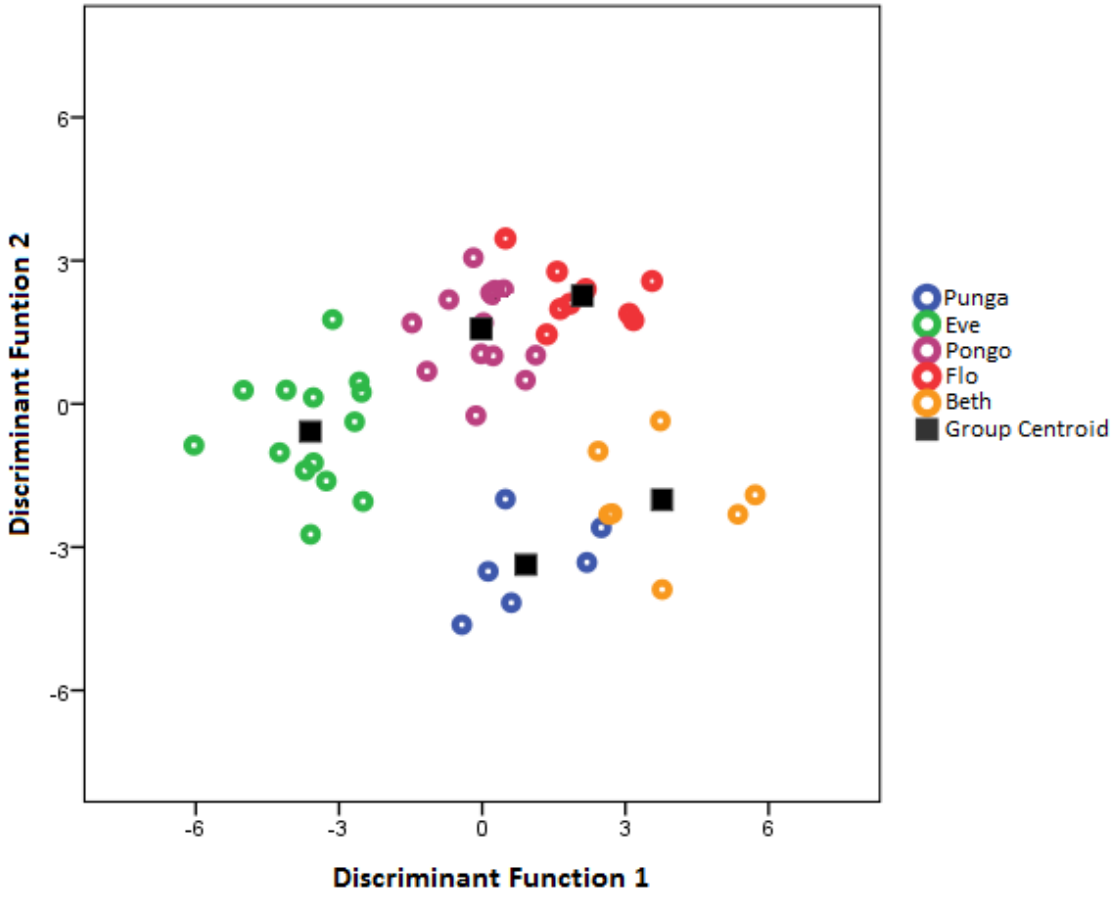


Figure 3.7: The separation of individual female great spotted kiwi by discriminant function 1 and discriminant function 2. Group centroids represent the mean values of the discriminant functions for each group.

Assumptions

The Box's M statistic was significant ($F_{60, 1834} = 3.57$, $p < 0.001$) indicating that homogeneity could not be assumed. Again all of the mahalanobis distance scores were low, thus the model is likely robust despite heterogeneity of variance/covariance matrices. The variable Q-Q plots indicated that the univariate data was normality distributed; this implies multivariate normality. Tolerance values were high for all predictor variables, thus non-multicollinearity was assumed (Appendix A.8).

Chapter 4

Discussion

4.1 Call Description (Objective 1)

Male and female 'whistle' vocalisations are the same length and contain a similar number of syllables. The syllables themselves appear to be sexually dimorphic. Male syllables were longer and more highly pitched than their female counterparts. Female syllables were characterised by lower spectral elements and had greater bandwidth than male syllables. Sexual dimorphism in calling has also been noted in little spotted kiwi and North Island brown kiwi (Corfield et al. 2008; Digby et al. 2013a). Ballintijin et al. (1997) suggested that sexually dimorphic vocalisations could arise in one of three ways, either males and females have similar vocal structures but use them differently, males and females have different vocal anatomy, or males and females differ in both anatomy and production. It remains to be determined what drives dimorphism in *Apteryx* species. Digby et al. (2013a) suggested the difference was likely due to vocal tract morphology.

Despite their differences, temporal and spectral intra-call trends were consistent between sexes. Syllable duration and minimum frequency showed least intra-call variation; variation in these parameters was restricted to the beginning of the call. On the other hand, maximum frequency, bandwidth and peak frequency all increased throughout the duration of the call. Intra-call variation has also been noted in the calls of North Island brown kiwi (Corfield et al. 2008). Great spotted kiwi and North Island brown kiwi had equivalent patterns of intra-call syllable duration; however, patterns of intra-call spectral variation were quite distinct (Corfield et al. 2008). Unlike the great spotted kiwi, North Island brown kiwi calls underwent mid-call depressions in maximum frequency and peak frequency; in addition, minimum frequencies were elevated at the end of calls (Corfield 2004). These differences could be due, in part, to disparities in the scale of trend measurement (syllable versus call part). Intra-call variation in little spotted kiwi could not be compared as only middle syllables were measured (Digby 2013).

Due to the use of syllable subsets in this study, it is unknown whether great spotted kiwi syllables vary continuously within calls or exist in distinct structural phases. Corfield et al. (2008) noted that syllables in male North Island brown kiwi calls could be grouped into three distinct phases on the basis of their structure. On the other hand, Digby et al. (2013a) noted that syllables in little spotted kiwi calls were uniform and did not show significant structural variation. Quantitative comparisons of syllable structure have not been conducted for *Apteryx* species, however, visual inspection of spectrograms suggests that great spotted kiwi syllables may be more comparable to the syllables of

little spotted kiwi. More investigation is required to test this observation (Appendix B.3; Appendix B.4).

4.2 Call Rate (Objective 2)

Male great spotted kiwi called at an average rate of 1.8 calls/night. Females called slightly less frequently with an average rate of 1.3 calls/per night. These rates are very low relative to other studies of great spotted kiwi. McLennan & McCann (2002) examined the average calling rates of great spotted kiwi populations; sites in northern Northwest Nelson had the highest call rates (average of 3.3/hour with some sites exceeding 15/hour), while southern Northwest Nelson sites had the lowest average calling rate (0.9/hour). Populations in the Arthurs Pass-Hurunui region were reported to have calling rates of 1.1/hour. The rate of calling noted in this study is much lower than anticipated by these findings. McLennan & McCann (2002) suggested that inter-site variation in calling rate was primarily due to variation in bird density.

It appears that density alone cannot account for the low rate of calling observed in the Hawdon Valley. The Department of Conservation has collected long term listening data for great spotted kiwi from two nearby valleys; the Hurunui North Branch and South Branch. Listening surveys are conducted annually in each valley (K. Morrison pers. comm. 2013). Each survey consists of 3-4 nights of listening (for 2 hours) at three different sites in each valley (K. Morrison pers. comm. 2013). In addition to the listening surveys, acoustic recorders were deployed during the period from December 2012 to January 2013 (K. Morrison pers. comm. 2013). The North Branch population (unmanaged) had an average calling rate of 2.58 calls per two hours of listening (K. Morrison pers. comm. 2013) while the South Branch population (managed) had an average calling rate of 6.64 calls per 2 hours of listening (K. Morrison pers. comm. 2013). These results are noteworthy as the North Branch population is thought to be of similar density to the Hawdon Valley population (S. Yong pers. comm. 2013).

One factor that could account for the low calling rate in the Hawdon Valley is the time of year when the recordings were made. Colbourne (2002) noted that the calling rate of North Island brown kiwi dropped from 8 calls/ hour prior to the breeding season to 1 call/hour during the incubation period. As the recordings in this study were largely made during the incubation period, this may partly explain the low rates of calling. Again this explanation does not fully account for the Hawdon call rate as acoustic recorders were also deployed in the South Branch and North Branch during this time and the call rates were consistently higher.

The difference between the valleys may also stem from recorder placement. In the Hawdon, the acoustic recorders were deployed in close proximity to nests. The Hurunui acoustic recorders were

not deployed at nest sites; instead they were deployed at established listening stations. The low calling rate of kiwi in this study may reflect a difference in calling behaviour between the nests and other parts of the birds' territory (L. Molles pers. comm. 2013). Although intra-territory variation in calling rates has not been examined in kiwi, it has been noted in other bird species. Krams (2000) examined the frequency of vocalisation in the crested tit (*Lophophanes cristatus*). He noted that male birds called more frequently at the periphery of their territory. This is thought to be more effective in territorial defence. It is not known where the nest sites were located in relation to the territorial boundary, but if nests are located deep within the territory; this may explain the low rate of calling observed.

Calling rate may also be a reflection of the stability of the population. As whistle vocalisations are thought to function in territorial defence, the rate of calling may reflect territory stability. Martinez & Zuberogoitia (2003) found that the vocalisation rate of male eagle owls (*Bubo bubo*) was higher in areas with larger numbers of floating individuals. Though the density of birds is similar between sites, there may be site specific differences in the level of territorial competition.

The disparity in call rate may have been exaggerated due to inconsistency in call detection methodology. The call rate in this study is derived from ten hours of recordings; however, the call rate in most other valleys is formulated from two hours of vocal activity. Kiwi calling rate is known to be highest during the first hour of darkness (Colbourne 2002). Rates calculated from this time window will therefore be higher than expected over an entire night. Conversely, the inclusion of long silent periods into calculation of the overall call rate would have pulled down the average. This disparity between measures could indicate that the low Hawdon calling rate is not as dramatic as it initially appears.

4.3 Vocal Individuality (Objective 3)

My analyses revealed that great spotted kiwi individuals in the Hawdon Valley could be identified on the basis of their vocalisations. Male great spotted kiwi calls were classified with an accuracy of 95.7% while female calls were classified with an accuracy of 90%. The level of discrimination noted in and is comparable with that of other species which have been reported to have high degrees of vocal individuality (Table 4.1).

Table 4.1: Classification success of other species which have reported high degrees of vocal individuality. Classification success in all situations is based of discriminant function analysis.

Common Name	Scientific Name	Classification Success	Citation
Rufous Headed Hornbill	*Aceros waldeni*	89%	Policht et al. 2009
Visayan Hornbill	*Penelopides panini*	90%	Policht et al. 2009
Pygmy Owl	*Glaucidium passerinum*	84%	Galeotti et al. 1993
Corncrake	*Crex crex*	100%	Peake et al. 1998
European Nightjar	*Caprimulgus europaeus*	99%	Rebbeck et al. 2001
European Eagle Owl	*Bubo bubo*	98%	Grava et al. 2008
Great Gray Owl	*Strix nebulosa*	92.8%	Rognan et al. 2009
Woodcock	*Scolopax rusticola*	95%	Hoodless et al. 2008
Eastern Phoebe	*Sayornis phoebe*	85.3%	Foote et al. 2013
Steere's Liocichla	*Liocichla steerii*	86%	Mays et al. 2006
Rufous Bristlebirds	*Dasyornis broadbenti*	87%	Rogers & Paton 2005
Western Screech Owls	*Megascops kennicottii*	92.3%	Tripp & Otter 2006

Vocal individuality has also been assessed in two other *Apteryx* species; the North Island brown kiwi (Corfield 2004) and the little spotted kiwi (Digby 2013). It appears that the degree of vocal individuality is highly variable within the *Apteryx* genus. Corfield (2004) determined that North Island brown kiwi had a high degree vocal individuality; males were reclassified with 87.5% accuracy while females were reclassified with 85.7% accuracy. In contrast, little spotted kiwi vocalisations do not appear to be individualised; a similar analysis by Digby (2013) yielded a reclassification rate of 56.8% for males and just 28.1% for females. The results of this study indicate that the great spotted kiwi is more individually distinctive than either species (male: 95.7% and female: 90%). The low degree of vocal individuality in little spotted kiwi relative to other species could be due to genetic diversity (Digby 2013). Little spotted kiwi have lower genetic diversity than other species (Ramstad et al. 2010). As genetic diversity is often associated with variation in call structure (Seddon et al. 2004) this could explain the low level of individual distinctiveness in little spotted kiwi. Further study should be conducted to determine whether genetic diversity is coupled with the degree of vocal individuality.

The low level of vocal individuality in little spotted kiwi may also be explained by variation in recording quality. Like the calls in this study, little spotted kiwi calls were collected autonomously (Digby 2013). As a result, there was a lot of variation in the amplitude and quality of the calls that were measured (Digby 2013). The parameters used to assess vocal individuality in this study were specifically choosen to be robust against variation in amplitude; spectral parameters were derived from a power spectra rather than the signal energy distribution (Zollinger et al. 2012). On the contrary, Digby (2013) was reliant on the energy distribution for the measurement of most spectral

parameters (5% frequency, 95% frequency, centre frequency, Q1 frequency, Q3 frequency). These measures are sensitive to variation in signal amplitude and thus could partly explain the low reclassification success of little spotted kiwi (Zollinger et al. 2012).

4.3.1 Male vs. Female

All assessments of vocal individuality in *Apteryx* species have noted lower reclassification success of females relative to males. The magnitude of this difference was fairly minimal in North Island brown kiwi (- 1.8%; Corfield 2004) and great spotted kiwi (- 4.2%) but little spotted kiwi females were far less individually distinctive than males (- 28.7%; Digby 2013). The consistency of lower female reclassification success may indicate that the individual qualities of female calls are less stereotyped than those of their male counterparts.

It is often difficult to monitor females using acoustic identification procedures because they tend to have lower calling rates than males (Terry et al. 2005). Indeed this is the case for most kiwi species (Colbourne 2006). Males call more frequently than females in both the North Island brown kiwi and little spotted kiwi (M/F ratio of 2.12 and 2.49 respectively; Colbourne 2006). As a result, female analyses were weak relative to males in these species (NIBK – 14 calls for four females; LSK – 15 calls for three females) (Corfield 2004; Digby 2013). Such low replication could have compromised the accuracy of female identification. Colbourne (2006) noted that great spotted kiwi were the only species of kiwi in which the call rate of females matched that of males (M/F ratio 1). Accordingly, the discrepancy between male and female calling rate was less prominent in this study; 51 calls were used to discriminate between five females. This indicates that, in great spotted kiwi, both sexes could be viably monitored using vocal individuality.

4.4 Key Parameters (Objective 4)

In this study, vocal individuality is the product of a combination of both spectral and temporal parameters (Peake et al. 1998, Terry et al. 2005). Male individual discrimination was conducted on the basis of seven call parameters; maximum frequency (middle), peak frequency (middle), minimum frequency (beginning), bandwidth (end), number of syllables, syllable duration (middle), bandwidth (middle). Female discrimination was centred on five predictor variables; minimum frequency (beginning), bandwidth (middle), syllable rate, peak frequency (middle) and syllable duration (end). The fact that the most important measures were different for males and females could be indicative of sexual dimorphism in vocal structures or differential call production (Ballintijin et al. 1997).

In both male and female analyses spectral parameters had greater discriminatory power. This is a finding reflected in many other studies (Galeotti et al. 1993; Sharp & Hatchwell 2005, Fernandez-Juricic et al. 2009; Foote et al. 2013). All assessments of vocal individuality in *Apteryx* species to date

have found spectral variables to be most individually distinctive, despite different parameters being assessed in each case. In this study the most important predictor variables were maximum frequency (beginning) (male) and minimum frequency (beginning) (female). Corfield (2004) determined that the most important parameters for discrimination of North Island brown kiwi were syllable start frequency (male) and syllable peak frequency (female). Although Digby (2013) did not find strong evidence of vocal individuality, potential for individuality coding (PIC) scores indicated that spectral variables were the most highly individualised in little spotted kiwi as well (syllable bandwidth (males) and centre frequency (females)). It would be interesting to examine whether the use of consistent parameters would have resulted in consistent parameter ranking.

4.4.1 Basis of Individuality

The significant parameters in this study represent the following parameter classes: maximum frequency, minimum frequency, bandwidth, peak frequency, syllable duration, syllable rate and the total number of syllables. Call production mechanisms are poorly understood in *Apteryx* species; however, these parameters have been extensively studied in a suite of other species which gives us some insight into how vocal individuality could have arisen in great spotted kiwi. Potential explanations for intraspecific variation in these parameters are discussed below.

Spectral Range (Minimum Frequency, Maximum Frequency, Bandwidth)

Male and female analyses both indicated that aspects of an individual's spectral range were most important in discerning identity (maximum frequency and minimum frequency respectively). In this study, measures of maximum frequency, minimum frequency and bandwidth were derived from the fundamental harmonic (also known as the fundamental frequency). According to the source-filter model, the fundamental frequency of a syllable is determined by the source (syrinx) (Riede et al. 2010; Goller & Riede 2013). Fundamental frequencies tend to pass relatively unimpeded from the source through the vocal tract (Podos et al. 2004). Therefore, the measures of maximum frequency, minimum frequency and bandwidth are likely to be a reflection of the range of acoustic energies produced at the syrinx.

There are many possible reasons for the observed intraspecific variation in source frequency:

- Syrinx size: larger syrinxes are known to produce lower frequency sounds (Podos et al. 2004). Syrinx size is often shown to be coupled with body size (Bradbury & Vahrencamp 1998). Intraspecific variation in body size did not correlate with lower frequency vocalisations in little spotted kiwi (Digby et al. 2013aa). Thus, if syrinx size is important in

determining intraspecific variation in source frequency, it probably does not scale allometrically with body size (Digby et al. 2013aa).

- Viscoelastic properties of the oscillating structure (Goller & Riede 2013): mechanical properties of the connective tissue in the syrinx can contribute to vocal differences between birds (Fee 2002; Goller & Riede 2013).
- Neuromuscular control of syringeal movements (Goller & Riede 2013): muscles of the vocal organ allow direct neural control of fundamental frequency by affecting the position and tension of the labia (Goller & Riede 2013). This could contribute to both intraspecific and intra-call variation.
- Air sac pressure: airflow is essential for tissue oscillation therefore variation in air pressure can affect the frequencies produced (Goller & Riede 2013). High fundamental frequencies tend to be associated with higher pressures (Gaunt et al. 1973). As with muscular control, air sac pressure could also contribute to the intra-call variation in fundamental frequency (Goller & Riede 2013).
- Genetic differences: source frequency cannot always be explained by morphological variation. Seddon et al. (2004) demonstrated a negative correlation between heterozygosity and maximum frequency in the trills of the sub-desert mesite (*Monias benschi*)

Consistent intraspecific variation in any/multiple of these parameters could have contributed to vocal individuality in great spotted kiwi.

Frequency Amplification (Peak Frequency)

According to the source-filter model, once fundamental frequencies have been produced in the syrinx, components of the vocal tract (trachea, larynx, and beak) modify the spectral properties of the call (Podos et al. 2004; Beckers et al. 2003). Part of this filtering process involves selective frequency amplification and dampening (Podos et al. 2004). Therefore, the frequency of peak amplitude is likely to be the result of vocal tract filtering.

Intraspecific variation in peak frequency could arise in a number of ways including:

- Variation in tracheal length (Podos et al. 2004): longer tracheas emphasise lower frequency sounds (Daley & Goller 2003)
- Positioning of the larynx, glottis or tongue (Podos et al. 2004)
- Calling posture (Podos et al. 2004). Variation in posture during calling could also contribute to intra-call variation in peak frequency.

- Beak length: longer beaks tend to produce lower peak frequencies (Palacios & Tubaro 2000; Huber & Podos 2006; Derryberry 2009). Digby et al. (2013a) demonstrated beak length did not correlate with peak frequency in little spotted kiwi. Thus this is unlikely to be a candidate for individual variation in peak frequency for great spotted kiwi.
- Beak gape: Wider gapes typically amplify higher frequencies (Hausberger et al. 1991; Westneat et al. 1993, Hoese et al. 2000). Variation in gape throughout the call could also have contributed to intra-call variation in peak frequency (Nelson et al. 2005)

Consistent intraspecific variation in any of these vocal tract features could have allowed peak frequency encode information about the identity of the caller.

Temporal Pattern (Syllable Rate, Syllable Duration, Number of Syllables)

The three significant temporal parameters, syllable duration, syllable rate and the number of syllables, are likely to be constrained by similar processes. Intraspecific variation in syllable rate and syllable duration (and therefore overall call duration) is ultimately a reflection of the individuals' respiratory pattern (Wohlgemuth et al. 2010). Respiratory pattern is under neural control and can be affected by social context and level of arousal (Glaze & Troyer 2006; Wohlgemuth et al. 2010). Syllable duration can also be genetically determined, for instance Seddon et al. (2004) reported that male heterozygosity corresponded with syllable duration in the sub-desert mesite.

4.4.2 Intra-Call Variation

Temporal and spectral parameters were measured from three syllable subsets at the beginning, middle and end of calls. Individually distinctive features were dispersed throughout the call but the majority of significant parameters were derived from the middle syllables (4 out of 6 syllable parameters in males, 2 out of 4 syllable parameters in females). This reflects the findings of Corfield (2004) who noted that middle syllables had the greatest discriminatory power. This emphasis on middle syllables may be due to greater syllable stability. Digby et al. (2013a) and Corfield (2004) both reported that syllables at the start and end of whistle calls were more variable. This is a fairly widespread phenomenon in birds with repetitive vocalisations; it is thought to occur due to priming of the vocal apparatus (Jones & Smith 1997). The inclusion of beginning and end syllable parameters in this study was justified as they were shown to have more variation between calls than within calls.

This methodology of dealing with intra-call variability is different than had been used previously. Corfield (2004) dealt with intra-call variability by averaging syllables across calls while Digby (2013) choose to exclude the variability altogether, measuring only between the 15th and 35th syllables. Intra call variability is not necessarily a bad thing; variability may actually represent a point of difference between individuals, it just needs to be dealt with in an appropriate way. For instance, the most important parameter in female discrimination was the minimum frequency of beginning syllables. The benefit of using a stepwise model of discriminant function analysis is that it is able to separate out the useful variability from the noise.

4.4.3 Other Features

In addition to the call features measured in this study, the harmonic structure of the male call and the formant structure in the female call have been identified as potential cues for individual discrimination (Corfield et al. 2008). In particular formants, which are frequency peaks resulting from vocal tract resonances, have been shown to encode identity in many other species (Goller & Riede 2013). Identification of formants in great spotted kiwi calls and inclusion of higher harmonics could increase the accuracy of identification in this species.

4.5 Individual Recognition

My analyses demonstrated that great spotted kiwi could be reliably identified by their vocalisations. It is possible that great spotted kiwi utilise this variation in call structure to recognise individuals within a population (Foote et al. 2013). Such individual voice recognition is thought to have been selected for in nocturnal and territorial bird species (Beer 1970, McGregor 1993). The whistle vocalisation is thought to primarily function in territorial defence and pair communication (Colbourne & Kleinpaste 1984). Digby et al. (2013a) suggested that male and female whistle calls in little spotted kiwi have divergent functions; the male vocalisation is better suited to territory defence while the female call is better suited to pair contact calling. Individual recognition would aid in both of these call functions.

Individual recognition has been shown to be particularly useful in a territorial context as it allows individuals to assess the relative threat that a caller presents and respond accordingly. Territorial birds that are able to discriminate between neighbours and strangers benefit as they conserve energy and avoid unnecessary conflict (Lovell & Lein 2005). This differential treatment of neighbours and strangers has been termed the “dear enemy” effect and it is fairly widespread (Temeles 1994). Most examples of this effect only examine the ability of an individual to discriminate between familiar (neighbour) and unfamiliar (stranger) stimuli (Budka & Osiejuk 2013). Individual recognition is a much more complex form of discrimination (Lovell & Lein 2005). For example, Lovell & Lein

(2005) investigated individual recognition in the songs of the alder flycatcher (*Empidonax alnorum*). They found that subjects responded to songs of a neighbour played from the opposite territorial boundary with a similar level of aggression to songs of strangers. This indicates that males associate a particular song with a given location (territory) and thus recognise individuals. Miles et al. (1997) reported that broadcasting the calls of strangers to North Island brown kiwi elicited an aggressive response. While this does not necessarily confirm individual recognition, it adds to the argument that kiwi are able to utilise vocalisations for individual recognition of competitors.

Individual recognition could also be pivotal to pair communication. Recognition of mates is important for the maintenance of complex cooperative behaviours (Beletsky 1983). In nocturnal birds, vocal recognition is a good candidate for this. For example: Cure et al. (2011) determined that nocturnal female Yelkouan shearwaters (*Puffinus yelkouan*) only responded to playback of their partners' calls. Mate recognition has not been directly examined in *Apteryx* species; however, the widespread occurrence of pair duetting strongly suggests that individuals recognise their mates from their vocalisations (Corfield 2004; Hall 2004; Digby et al. 2013aa). When duets are performed by fixed pairs, as they are in monogamous *Apteryx* species, individuals must recognise the vocalisations of their mate in order to respond appropriately (Hall 2004). Thus the vocal distinctiveness identified by this study is likely to have at least one functional role, and possibly several.

4.6 Future Study and Limitations

4.6.1 Future Study

Although this study provides strong evidence for within-season vocal individuality, it cannot predict long term stability. Many studies have determined that the individually distinct features of songs and calls are stable between seasons (Legagne 2001; Tripp & Otter 2006). Exceptions to this have been noted in several species; for example Puglisi & Adamo (2001) found significant variation in all measured parameters (duration, maximum frequency, and minimum frequency) in male great bitterns over time. Even in parameters which are largely consistent, some variation is expected due to variation in age, health, size etc. (Tripp & Otter 2006). Certain systems may be more complex than others, for example, Walcott et al. (1999) observed that the call structure of common loons (*Gavia immer*) changed when males switched territories, while males that remained on the same territory retained a constant call structure. Further study must be conducted to determine the extent of vocal stability in great spotted kiwi.

Another possible area of further study is duetting. Duetting was excluded from this analysis on the basis that it altered the temporal characteristics of calls (Corfield et al. 2008). However, there is potential that duetting could also be utilised in an identification context. Pair-distinctive duets have been reported in a variety of species (Klenova et al. 2009; Budde 2001). Klenova et al. (2009) determined that pair specific duets were stable over a five year period in the red crowned crane (*Grus japonensis*), allowing them to be utilised in long term monitoring. In this study, some individuals had a very low individual call rate and predominantly called as part of a duet (Shazza, Bonnie). Due to the monogamous nature of kiwi, pair distinctive duets could be used as a complementary tool to individually distinctive vocalisations. This would increase the detection probabilities of individuals with low call rates. Alternatively, acoustic investigation of duets may indicate that certain duet parameters could be still be useful in individual analysis, provided the deviation between duets and individual calls is still less than between birds. Further study is required to evaluate the role that duets may play in acoustic identification.

4.6.2 Data Limitations

The biggest limitation in this study was the small sample size. In both the male and female analyses, the individual with the smallest sample size had the lowest reclassification success (Bazza – 8, Punga – 7). In addition, four birds were not included in the analyses owing to low sample size (Ebb, Mac, Bonnie, Shazza). Even though the minimum sample size in discriminant function analysis is one more than the number of predictor variables, in an ideal situation, each group should have at least 20 cases to ensure robust analyses (Tabachnik & Fidell 2007). In this study, calling rate was low and many calls had to be discarded; as a result very few individuals met this recommendation. A minimum of 20 calls may be unrealistic due to the difficulty of call collection, but it appears that approximately 10-15 calls/bird is sufficient to ensure accurate reclassification. In most cases two deployments of the acoustic recorders should be sufficient to achieve this. Even though sample size was small in this study, it was the most extensive assessment of vocal individuality in an *Apteryx* species to date. Corfield (2004) used 48 calls to examine seven males and 14 calls for four females, Digby (2013) used 66 calls for seven males and 15 calls to for three females. In this study 72 calls were used to discriminate between five males and 51 calls were used to discriminate between five females.

The other major limitation of this study was the degree of variability in recording quality. 50.7% of calls were discarded due to poor quality (predominantly due to insufficient amplitude). Given current technology, there is little that can be done to remedy this situation. Autonomous recorders offer a trade-off between recording quality and detection (Digby et al. 2013b). Manually recorded calls tend to be higher quality but autonomous recorders are a more efficient. For instance, Corfield (2004)

collected individual kiwi calls by means of manual recording (within 20m of bird). Although the quality of recordings was much higher, his analyses dealt with a very limited sample size. In this study, we did not observe any correlation between call amplitude and parameter measurement, therefore, despite the variability in quality, autonomous recorders were preferable. The high rates of call detection mean that low quality recordings can be discarded without crippling the analyses.

4.7 Potential Applications and Limitations of Acoustic Identification

The 2008-2018 Kiwi Recovery Plan outlined individual identification as a key area in need of development (Holzapfel et al. 2008). This study found strong evidence for vocal individuality in great spotted kiwi (90-95.7% reclassification success). This finding is an important first step towards the development of an acoustic identification system. Several factors have been identified which could limit the success of vocal individuality as a management tool (see literature review). The majority of these limitations were also addressed in this study:

***Limitation 1**: **Bias towards more vocally active members of the population**:* this study did note some individual variation in call rate; however, we expect that even low-calling individuals would be detected given adequate replication of sampling and/or the inclusion of duets as identification tools. Further investigation into the effect of age or territorial status on calling rate is required.
***Limitation 2: Poor female reclassification success**:* Great spotted kiwi females had a high reclassification success and called at a similar rate to males. This indicates that vocal individuality could be a viable monitoring option for both sexes in this species.
***Limitation 3: Temporal stability**.* If vocalisations are not temporally stable, their application will be limited to short term monitoring. This limitation was not examined in this study. Further work should be conducted to determine if individually distinctive vocalisations are stable between seasons.

Therefore, provided temporal stability can be addressed in further studies, the great spotted kiwi appears to be a good candidate for vocal individuality monitoring. Acoustic identification of kiwi has potential to vastly improve the quality and extent of monitoring data. Although the techniques used in this study discriminated between known individuals, with sufficient data, a classification system could be developed that allows for the identification of unknown individuals (Terry et al. 2005). This would allow refinement of the current call-count monitoring scheme and permit calculation of actual population size. If individually distinctive vocalisations are confirmed to be stable over time, they could also be used to re-identify individuals between seasons and thus infer territory stability, survival, pair-bond stability etc.

4.8 Conclusion

This study has produced the first quantitative description of male and female great spotted kiwi calls to date. As in other *Apteryx* species, vocalisations were shown to be sexually dimorphic and had a significant degree of temporal and spectral variation within calls. Calling rate in this study was lower than expected based on previous assessments of vocal behaviour in great spotted kiwi. Based on the rates observed in this study, acoustic recorders would need to be deployed twice to acquire sufficient replication for robust analysis. Both male and female birds could be accurately identified by spectral and temporal features of their call. The level of individuality noted in this study was actually very high (90 - 95% reclassification success). As is often the case, this individuality was primarily defined by spectral parameters. Findings from this study suggest that great spotted kiwi vocalisations could be used in acoustic identification. This has the potential to revolutionise the management of this species.

References

Audacity Team (2013). *Audacity 2.0.3*. Carnegie Mellon University, Pittsburgh.

Ballintijn, M. R., & tenCate, C. (1997). Sex differences in the vocalizations and syrinx of the Collared Dove (*Streptopelia decaocto*). *Auk, 114*(1), 22-39.

Ballintijn, M. R., tenCate, C., Nuijens, F. W., & Berkhoudt, H. (1995). The syrinx of the collared dove (*Streptopelia decaocto*): structure, inter-individual variation and development. *Netherlands Journal of Zoology, 45*(3-4), 455-479.

Beckers, G. J. L., Suthers, R. A., & ten Cate, C. (2003). Mechanisms of frequency and amplitude modulation in ring dove song. *Journal of Experimental Biology, 206*(11), 1833-1843.

Beer, C. G. (1970). Individual recognition of voice in the social behaviour of birds. *Advances in the Study of Behaviour, 3*, 27-74.

Beletsky, L. D. (1983). Vocal mate recognition in male red-winged blackbirds, *Agelaius phoeniceus*. *Behaviour, 84*, 124-134.

Bioacoustics Research Programme (2012) *Raven Pro 1.5*. Cornell Lab of Ornithology, New York.

BNZ Save the Kiwi Trust. (2010). BNZ save the Kiwi: Great spotted Kiwi. *BNZ Save The Kiwi Trust*.

Bradbury, J., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland: Sinauer Associates.

Budde, C. (2001). Individual features in the calls of the Grey Crowned Crane, *Balearica regulorum gibbericeps*. *Ostrich, 72*(3-4), 134-139.

Budka, M., & Osiejuk, T. S. (2013). Neighbour-stranger call discrimination in a nocturnal rail species, the Corncrake Crex crex. *Journal of Ornithology, 154*(3), 685-694.

Burbridge, M. L., Colbourne, R. M., Robertson, H. A., & Baker, A. J. (2003). Molecular and other biological evidence supports the recognition of at least three species of Brown Kiwi. *Conservation Genetics, 4*, 167-177.

Butler, D., & McLennan, J. (1991) Kiwi recovery plan. *Threatened Species Recovery Plan Series, 2*. Wellington: Department of Conservation.

Castro, I. (2011). *Kiwi: a natural history*. Auckland: New Holland.

Charrier, I., Jouventin, P., Mathevon, N., & Aubin, T. (2001). Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*. *Polar Biology, 24*(5), 378-382.

Cockrem, J. F., Goudswaard, R., Fox, E. K., Sibley, M., Johnson, T. M., & Bell, M. J. (1992). The breeding season of three species of Kiwi (*Apteryx*) in captivity as determined from egg-laying dates. *Journal of Zoology, 226*, 95-107.

Colbourne, R. (2002). Incubation behaviour and egg physiology of Kiwi (*Apteryx* spp.) in natural habitats. *New Zealand Journal of Ecology, 26*(2), 129-138.

Colbourne, R., Bassett, S., Billing, T., McCormack, H., McLennan, J., Nelson, A., & Robertson, H. (2005) The development of Operation Nest Egg as a tool in the conservation management of Kiwi. *Science for Conservation, 24*. Wellington: Department of Conservation.

Colbourne, R., & Kleinpaste, R. (1984). North Island brown Kiwi vocalisations and their use in censuring populations. *Notornis, 31*(3), 191-201.

Colbourne, R. M. (2006). Technical report S5020/129. Wellington: Department of Conservation.

Corfield, J. (2004). *Description, dueting, seasonal variations, and individual identification of the vocalisations of the Brown Kiwi (Apteryx mantelli).* Master of Applied Science, Auckland University of Technology, Auckland.

Corfield, J., Gillman, L., & Parsons, S. (2008). Vocalizations of the North Island brown Kiwi (*Apteryx mantelli*). *Auk, 125*(2), 326-335.

Craig, E., Gardiner, C., Renwick, N., & Sporle, W. (2011). *Taxon plan for Northland Brown Kiwi (Apteryx mantelli): strategic plan for Northland Brown Kiwi 2010–2019 and beyond.* Whangarei: Department of Conservation.

Cure, C., Aubin, T., & Mathevon, N. (2011). Sex discrimination and mate recognition by voice in the Yelkouan Shearwater *Puffinus yelkouan*. *Bioacoustics-the International Journal of Animal Sound and Its Recording, 20*(3), 235-249.

Daley, M., & Goller, F. (2004). Tracheal length changes during zebra finch song and their possible role in upper vocal tract filtering. *Journal of Neurobiology*, *59*(3), 319-330.

Davies, S. J. (2002). *Ratites and tinamous*. Oxford: Oxford University Press.

Derryberry, E. P. (2009). Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in White-Crowned Sparrow song. *American Naturalist, 174*(1), 24-33.

Digby, A. (2013). *Whistling in the dark: an acoustic study of little spotted Kiwi.* Victoria University, Wellington.

Digby, A., Bell, B. D., & Teal, P. D. (2013a). Vocal cooperation between the sexes in little spotted Kiwi Apteryx owenii. *Ibis, 155*(2), 229-245.

Digby, A., Towsey, M., Bell, B. D., & Teal, P. D. (2013b). A practical comparison of manual and autonomous methods for acoustic monitoring. *Methods in Ecology and Evolution 4*, 675–683.

DOC. (2004). *Operation ark - operation plan for predator control in the Hawdon and Poulter valleys*. Christchurch: Canterbury Conservancy.

DOC. (2007) Arthur's Pass National Park Management Plan 2007. *Vol. 14. Canterbury Conservancy Management Planning*. Christchurch: Department of Conservation.

Elliot, G., & Suggate, R. (2007). *Operation ark: three year progess report*. Christchurch: Department of Conservation.

Fee, M. S. (2002). Measurement of the linear and nonlinear mechanical properties of the oscine syrinx: Implications for function. *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology, 188*(11-2), 829-839.

Fernandez-Juricic, E., del Nevo, A. J., & Poston, R. (2009). Identification of individual and population level variation in vocalisations of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*). *Auk, 126*(1), 89-99.

Foote, J. R., Palazzi, E., & Mennill, D. J. (2013). Songs of the Eastern Phoebe, a suboscine songbird, are individually distinctive but do not vary geographically. *Bioacoustics-the International Journal of Animal Sound and Its Recording, 22*, 137-151.

Fuller, E. (1990). *Kiwi*. Auckland: Seto Publishing.

Galeotti, P., Paladin, M., & Pavan, G. (1993). Individually distinct hooting in male pygmy owls *Glaucidium passerinum* - a multivariate approach. *Ornis Scandinavica, 24*(1), 15-20.

Galeotti, P., & Sacchi, R. (2001). Turnover of territorial Scops Owls *Otus scops* as estimated by spectrographic analyses of male hoots. *Journal of Avian Biology, 32*(3), 256-262.

Gasson, P. A. (2005). *Translocation of Great spotted Kiwi/Roa (Apteryx haasti) to Rotoiti nature recovery project*. Nelson: Department of Conservation.

Gaunt, A. S., Stein, R. C., & Gaunt, S. L. L. (1973). Pressure and air flow during distress calls of the starling, *Sturnus vulgaris*. *Journal of Experimental Zoology, 183*, 241–262.

Gibb, J. A. (1996). First seen or first heard? a useful distinction when counting forest birds. *Notornis, 43*, 7-13.

Gilbert, G., McGregor, P. K., & Tyler, G. (1994). Vocal individuality as a census tool - practical considerations illustrated by a study of 2 rare species. *Journal of Field Ornithology, 65*(3), 335-348.

Gilbert, G., Tyler, G. A., & Smith, K. W. (2002). Local annual survival of booming male Great Bittern *Botaurus stellaris* in Britain, in the period 1990-1999. *Ibis, 144*(1), 51-61.

Glaze, C. M., & Troyer, T. W. (2006). Temporal structure in zebra finch song: Implications for motor coding. *Journal of Neuroscience, 26*(3), 991-1005.

Goller, F., & Riede, T. (2013). Integrative physiology of fundamental frequency control in birds. *Journal of Physiology-Paris, 107*(3), 230-242.

Grava, T., Mathevon, N., Place, E., & Balluet, P. (2008). Individual acoustic monitoring of the European Eagle Owl *Bubo bubo*. *Ibis, 150*(2), 279-287.

Hall, M. L. (2004). A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology, 55*(5), 415-430.

Hausberger, M., Black, J. M., & Richard, J. P. (1991). Bill opening and sound spectrum in Barnacle Goose loud call - individuals with wide mouths have higher pitched voices *Animal Behaviour, 42*, 319-322.

Heather, B. D., & Robertson, H. A. (2005). *The field guide to the birds of New Zealand*. Auckland: Penguin.

Hoese, W. J., Podos, J., Boetticher, N. C., & Nowicki, S. (2000). Vocal tract function in birdsong production: experimental manipulation of beak movements. *Journal of Experimental Biology, 203*(12), 1845-1855.

Holzapfel, S., Robertson, H. A., McLennan, J. A., Sporle, W., Hackwell, K., & Impey, M. (2008). *Kiwi (Apteryx spp.) recovery plan: 2008–2018.* Wellington: Department of Conservation.

Hoodless, A. N., Inglis, J. G., Doucet, J. P., & Aebischer, N. J. (2008). Vocal individuality in the roding calls of Woodcock *Scolopax rusticola* and their use to validate a survey method. *Ibis, 150*(1), 80-89.

Huber, S. K., & Podos, J. (2006). Beak morphology and song features covary in a population of Darwin's finches (*Geospiza fortis*). *Biological Journal of the Linnean Society, 88*(3), 489-498.

IBM Corp. (2013). *IBM SPSS statistics for windows: version 22.0*. Armonk, New York.

Jones, D. N., & Smith, G. C. (1997). Vocalisations of the marbled frogmouth: an assessment of vocal individuality as a potential census technique. *Emu, 97*, 296-304.

Keye, C. (2008). *A study of home ranges, movement and activity patterns of great spotted kiwi* (*Apteryx haastii*) *in the Hurunui Region, South Island, New Zealand*. Master of International Nature Conservation, Lincoln University, Lincoln.

Klenova, A. V., Volodin, I. A., & Volodina, E. V. (2009). Examination of pair-duet stability to promote long-term monitoring of the endangered red-crowned crane (Grus japonensis). *Journal of Ethology, 27*(3), 401-406.

Koren, L., & Geffen, E. (2011). Individual identity is communicated through multiple pathways in male rock hyrax (*Procavia capensis*) songs. *Behavioral Ecology and Sociobiology, 65*(4), 675-684.

Krams, I. (2000). Long-range call use in dominance-structured Crested Tit *Parus cristatus* winter groups. *Journal of Avian Biology, 31*(1), 15-19.

Kwok, L. (2007). *Sound studio*. Felt Tip Inc, New York.

Lengagne, T. (2001). Temporal stability in the individual features in the calls of eagle owls (*Bubo bubo*). *Behaviour, 138*, 1407-1419.

Levréro, F., Durand, L., Vignal, C., Blanc, A., & Mathevon, N. (2009). Begging calls support offspring individual identity and recognition by zebra finch parents. *Comptes Rendus Biologies*, *332*(6), 579-589.

Lovell, S. F., & Lein, M. R. (2005). Individual recognition of neighbors by song in a suboscine bird, the alder, flycatcher *Empidonax alnorum*. *Behavioral Ecology and Sociobiology, 57*(6), 623-630.

Martinez, J. A., & Zuberogoitia, I. (2003). Factors afecting the vocal behaviour of Eagle Owls *Bubo bubo*: Effects of season, density and territory quality. *Ardeola, 50*(2), 255-258.

Mathevon, N. (1997). Individuality of contact calls in the Greater Flamingo *Phoenicopterus ruber* and the problem of background noise in a colony. *Ibis, 139*(3), 513-517.

Mathevon, N., Charrier, I., & Jouventin, P. (2003). Potential for individual recognition in acoustic signals: a comparative study of two gulls with different nesting patterns. *Comptes Rendus Biologies, 326*(3), 329-337.

Mays, H. L., Yao, C. T., & Yuan, H. W. (2006). Antiphonal duetting in Steere's liocichla (*Liocichla steerii*): male song individuality and correlation between habitat and duetting behavior. *Ecological Research, 21*(2), 311-314.

McGregor, P. K. (1993). Signalling in territorial systems - a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 340*(1292), 237-244.

McLennan, J., & McCann, T. (2002) Genetic variability, distribution and abundance of Great spotted Kiwi (Apteryx haastii). *Science and Research Internal Report, 191*. Wellington: Department of Conservation

McLennan, J. A. (1988). Breeding of North Island brown Kiwi, *Apteryx australis mantelli*, in Hawke's Bay, New Zealand. *New Zealand Journal of Ecology, 11*, 89-97.

McLennan, J. A., Dew, L., Miles, J., Gillingham, N., & Waiwai, R. (2004). Size matters: predation risk and juvenile growth in North Island brown Kiwi (*Apteryx mantelli*). *New Zealand Journal of Ecology, 28*(2), 241-250.

McLennan, J. A., & McCann, A. J. (1991). Incubation temperatures of Great spotted Kiwi *Apteryx haastii*. *New Zealand Journal of Ecology, 15*, 163-166.

McLennan, J. A., & McCann, T. (1989). Incubation by female Great spotted Kiwi. *Notornis, 36*, 325-326.

McLennan, J. A., Potter, M. A., Robertson, H. A., Wake, G. C., Colbourne, R., Dew, L., . . . Reid, J. (1996). Role of predation in the decline of Kiwi, *Apteryx* spp, in New Zealand. *New Zealand Journal of Ecology, 20*(1), 27-35.

Medvin, M. B., Stoddard, P. K., & Beecher, M. D. (1993). Signals for parent offspring recognition - a comparative analysis of begging calls of cliff swallows and barn swallows. *Animal Behaviour*, *45*(5), 841-850.

Metzler, C. (2011). *Home ranges and dispersal patterns of Great spotted Kiwi (Apteryx haastii) subadults.* Master of Science, University of Natural Resources and Life Sciences, Vienna.

Miles, J., Potter, M. A., & Fordham, R. A. (1997) Northern brown Kiwi (*Apteryx australis mantelli*) in Tongariro National Park and Tongariro Forest: ecology and threats. *Science for Conservation 51*. Wellington: Department of Conservation.

Miller, P. J., & Pierce, R. J. (1995). Distribution and decline of the North Island brown Kiwi (*Apteryx australis mantelli*) in Northland. *Notornis, 42*, 203-211.

Nagy, C. M., & Rockwell, R. F. (2012). Identification of individual Eastern Screech-Owls *Megascops asio* via vocalization analysis. *Bioacoustics-the International Journal of Animal Sound and Its Recording, 21*(2), 127-140.

Nelson, B. S., Beckers, G. J. L., & Suthers, R. A. (2005). Vocal tract filtering and sound radiation in a songbird. *Journal of Experimental Biology, 208*(2), 297-308.

O'Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity, 41*(5), 673-690.

Ohms, V. R., Snelderwaard, P. C., ten Cate, C., & Beckers, G. J. L. (2010). Vocal tract articulation in zebra finches. *Plos One, 5*(7).

Palacios, M. G., & Tubaro, P. L. (2000). Does beak size affect acoustic frequencies in woodcreepers? *Condor, 102*(3), 553-560.

Peake, T. M., McGregor, P. K., Smith, K. W., Tyler, G., Gilbert, G., & Green, R. E. (1998). Individuality in corncrake *Crex crex* vocalizations. *Ibis, 140*(1), 120-127.

Peake, T. M., & McGregor, P. M. (2001). Corncrake *Crex crex* census estimates: a conservation application of vocal individuality. *Animal Biodiversity and Conservation, 24*, 81-90.

Pierce, R., & Westbrooke, I. (2003). Call count responses of North Island brown Kiwi to different levels of predator control in Northland, New Zealand. *Biological Conservation, 109*(2), 175-180.

Podos, J., Huber, S. K., & Taft, B. (2004). Bird song: The interface of evolution and mechanism. *Annual Review of Ecology Evolution and Systematics, 35*, 55-87.

Policht, R., Petru, M., Lastimoza, L., & Suarez, L. (2009). Potential for the use of vocal individuality as a conservation research tool in two threatened Philippine hornbill species, the Visayan Hornbill and the Rufous-headed Hornbill. *Bird Conservation International, 19*(1), 83-97.

Puglisi, L., & Adamo, C. (2004). Discrimination of individual voices in male Great Bitterns (*Botaurus stellaris*) in Italy. *Auk, 121*(2), 541-547.

R Core Development Team (2013). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Ramstad, K. M., Colbourne, R. M., Robertson, H. A., Allendorf, F. W., & Daugherty, C. H. (2013). Genetic consequences of a century of protection: serial founder events and survival of the little spotted Kiwi (*Apteryx owenii*). *Proceedings of the Royal Society B-Biological Sciences, 280*(1762).

Rebbeck, M., Corrick, R., Eaglestone, B., & Stainton, C. (2001). Recognition of individual European Nightjars *Caprimulgus europaeus* from their song. *Ibis, 143*(3), 468-475.

Reers, H., & Jacot, A. (2011). The effect of hunger on the acoustic individuality in begging calls of a colonially breeding weaver bird. *BMC Ecology, 11*(3).

Reid, B., Ordish, R. G., & Harrison, M. (1982). An analysis of the gizzard contents of 50 North Island brown Kiwi (*Apteryx australis mantelli*) and notes on feeding observations. *New Zealand Journal of Ecology, 5*, 76-85.

Reid, B., & Williams, G. R. (1975). The Kiwi. In G. Kuschel (Ed.), *Biogeography and ecology in New Zealand*. Hague: Junk.

Ręk, P., & Osiejuk, T. S. (2010). Sophistication and simplicity: conventional communication in a rudimentary system. *Behavioral Ecology, 21*(6), 1203-1210.

Riede, T., Fisher, J. H., & Goller, F. (2010). Sexual dimorphism of the zebra finch syrinx indicates adaptation for high fundamental frequencies in males. *Plos One, 5*(6).

Riede, T., & Goller, F. (2010). Functional morphology of the sound-generating labia in the syrinx of two songbird species. *Journal of Anatomy, 216*(1), 23-36.

Ripmeester, E. A. P., Kok, J. S., van Rijssel, J. C., & Slabbekoorn, H. (2010). Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European blackbirds. *Behavioral Ecology and Sociobiology, 64*(3), 409-418.

Robertson, H. (2004) Research and monitoring plan for the Kiwi sanctuaries. *Science for Conservation, 241*. Wellington: Department of Conservation.

Robertson, H., & Colbourne, R. (2003). *Kiwi (Apteryx spp.) best practice manual*. Wellington: Department of Conservation.

Robertson, H. A. (2003). *Kiwi (Apteryx Spp.) recovery plan 1996-2006*. Wellington: Department of Conservation.

Robertson, H. A., Colbourne, R. M., Graham, P. J., Miller, P. J., & Pierce, R. J. (1999). Survival of brown Kiwi (Apteryx mantelli) exposed to brodifacoum poison in Northland, New Zealand. *New Zealand Journal of Ecology, 23*(2), 225-231.

Robertson, H. A., Colbourne, R. M., Graham, P. J., Miller, P. J., & Pierce, R. J. (2011). Experimental management of Brown Kiwi *Apteryx mantelli* in central Northland, New Zealand. *Bird Conservation International, 21*(2), 207-220.

Robertson, H. A., & Fraser, J. R. (2009). Use of trained dogs to determine the age structure and conservation status of Kiwi (*Apteryx* spp.) populations. *Bird Conservation International, 19*, 121-129.

Rogers, D. J., & Paton, D. C. (2005). Acoustic identification of individual Rufous Bristlebirds, a threatened species with complex song repertoires. *Emu, 105*(3), 203-210.

Rognan, C. B., Szewczak, J. M., & Morrison, M. L. (2009). Vocal Individuality of Great Gray Owls in the Sierra Nevada. *Journal of Wildlife Management, 73*(5), 755-760.

Sales, J. (2005). The endangered Kiwi: a review. *Folia Zoologica, 54*(1-2), 1-20.

Seddon, N., Amos, W., Mulder, R. A., & Tobias, J. A. (2004). Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird. *Proceedings of the Royal Society B-Biological Sciences, 271*(1550), 1823-1829.

Sharp, S. P., & Hatchwell, B. J. (2005). Individuality in the contact calls of cooperatively breeding long-tailed tits (*Aegithalos caudatus*). *Behaviour, 142*, 1559-1575.

Sokal, R. R., & Rohlf, F. J. (2012). *Biometry: the principles and practice of statistics in biological research: 4th edition*. New York: W. H. Freeman and Company.

Suthers, R. A. (1994). Variable asymmetry and resonance in the avian vocal-tract - a structural basis for individually distinct vocalizations. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 175*(4), 457-466.

Tabachnick, B. G., & Fidell, L. S. (2007). *Using multivariate statistics*. New York: Pearson Education Ltd.

Taborsky, B., & Taborsky, M. (1992). Spatial-organization of the North Island brown Kiwi *Apteryx australis mantelli* : sex, pairing status and territoriality. *Ibis, 134*(1), 1-10.

Taborsky, B., & Taborsky, M. (1999). The mating system and stability of pairs in Kiwi *Apteryx* spp. *Journal of Avian Biology, 30*(2), 143-151.

Temeles, E. J. (1994). The role of neighbours in territorial systems - when are they dear enemies. *Animal Behaviour, 47*(2), 339-350.

Terry, A. M., Peake, T.M. & McGregor, P.K. (2005). The role of vocal individuality in conservation. *Frontiers in Zoology, 2*(10).

Tibbetts, E. A., & Dale, J. (2007). Individual recognition: it is good to be different. *Trends in Ecology & Evolution, 22*(10), 529-537.

Trewick, S. A., & Gibb, G. C. (2010). Vicars, tramps and assembly of the New Zealand avifauna: a review of molecular phylogenetic evidence. *Ibis, 152*(2), 226-253.

Trimble, M., & Charrier, I. (2011). Individuality in South American sea lion (*Otaria flavescens*) mother-pup vocalizations: Implications of ecological constraints and geographical variations? *Mammalian Biology, 76*(2), 208-216.

Tripp, T. M., & Otter, K. A. (2006). Vocal individuality as a potential long-term monitoring tool for Western Screech-owls, *Megascops kennicottii*. *Canadian Journal of Zoology, 84*(5), 744-753.

Walcott, C., Evers, D., Froehler, M., & Krakauer, A. (1999). Individuality in "yodel" calls recorded from a banded population of common loons (*Gavia immer*). *Bioacoustics-the International Journal of Animal Sound and Its Recording, 10*, 101-114.

Westneat, M. W., Long, J. H., Hoese, W., & Nowicki, S. (1993). Kinematics of birdsong - functional correlation of cranial movements and acoustic features in sparrows. *Journal of Experimental Biology, 182*, 147-171.

Wiley, R. H. (2005). Individuality in songs of Acadian flycatchers and recognition of neighbours. *Animal Behaviour, 70*, 237-247.

Wohlgemuth, M. J., Sober, S. J., & Brainard, M. S. (2010). Linked control of syllable sequence and phonology in birdsong. *Journal of Neuroscience, 30*(39), 12936-12949.

Xia, C. W., Xiao, H., & Zhang, Y. Y. (2010). Individual variation in brownish-flanked bush warbler songs. *Condor, 112*(3), 591-595.

Zollinger, S. A., Podos, J., Nemeth, E., Goller, F., & Brumm, H. (2012). On the relationship between, and measurement of, amplitude and frequency in birdsong. *Animal Behaviour, 84*(4), E1-E9.

Appendix A

A.1 One-way ANOVA with Welch correction for comparison of male and female call parameters.

Robust Tests of Equality of Means

		Statistic	df1	df2	Sig.
Syllables	Welch	3.405	1	115.494	.068
Length	Welch	1.163	1	112.242	.283
Tempo	Welch	1.453	1	72.540	.232
DurBeg	Welch	14.113	1	117.693	.000
MinBeg	Welch	1029.754	1	108.908	.000
MaxBeg	Welch	603.811	1	94.343	.000
DeltaBeg	Welch	61.773	1	108.439	.000
PeakBeg	Welch	946.020	1	95.645	.000
DurMid	Welch	30.496	1	117.591	.000
MinMid	Welch	1730.709	1	85.705	.000
MaxMid	Welch	373.072	1	117.625	.000
DeltaMid	Welch	11.789	1	82.349	.001
PeakMid	Welch	1370.864	1	95.418	.000
DurEnd	Welch	62.120	1	119.062	.000
MinEnd	Welch	1930.138	1	95.735	.000
MaxEnd	Welch	382.259	1	106.791	.000
DeltaEnd	Welch	5.902	1	80.167	.017
PeakEnd	Welch	1583.488	1	98.941	.000

A.2 Repeated measures ANOVAs for the male syllable parameters. Significant results are shaded grey.

Measure		Type III Sum of Squares	df	Mean Square	F	Sig.
Minimum	Sphericity Assumed	1832301.750	2	916150.875	234.399	.000
	Greenhouse-Geisser	1832301.750	1.775	1032133.892	234.399	.000
Maximum	Sphericity Assumed	12446811.433	2	6223405.717	774.653	.000
	Greenhouse-Geisser	12446811.433	1.175	10592402.066	774.653	.000
Peak	Sphericity Assumed	12099635.758	2	6049817.879	691.551	.000
	Greenhouse-Geisser	12099635.758	1.638	7385842.919	691.551	.000
Delta	Sphericity Assumed	4843063.611	2	2421531.805	255.047	.000
	Greenhouse-Geisser	4843063.611	1.400	3458511.061	255.047	.000
Duration	Sphericity Assumed	1.053	2	.526	95.359	.000
	Greenhouse-Geisser	1.053	1.238	.850	95.359	.000

Results of Mauchlys Sphericity Test for the syllable parameters used in the male repeated measure ANOVAs.

Mauchly's Test of Sphericity

Within Subjects Effect	Measure	Mauchly's W	Approx. Chi-Square	df	Sig.	Greenhouse-Geisser Epsilon
Call Part	Minimum	.873	9.069	2	.011	.888
	Maximum	.298	81.120	2	.000	.588
	Peak	.779	16.719	2	.000	.819
	Delta	.572	37.455	2	.000	.700
	Duration	.385	64.036	2	.000	.619

Pairwise comparison of the male syllable parameters identified as significantly by the repeated measure ANOVA. Call part is coded as 1 – beginning, 2 - middle, 3 – end. Significant results are shaded grey.

Pairwise Comparisons

Measure	(I) Call Part	(J) Call Part	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Minimum	1	2	-196.350*	10.931	.000	-218.163	-174.537
		3	-202.663*	12.028	.000	-226.665	-178.660
	2	1	196.350*	10.931	.000	174.537	218.163
		3	-6.313	8.700	.471	-23.674	11.048
	3	1	202.663*	12.028	.000	178.660	226.665
		2	6.313	8.700	.471	-11.048	23.674
Maximum	1	2	-456.230*	17.426	.000	-491.004	-421.456
		3	-566.454*	18.839	.000	-604.047	-528.862
	2	1	456.230*	17.426	.000	421.456	491.004
		3	-110.224*	6.325	.000	-122.846	-97.603
	3	1	566.454*	18.839	.000	528.862	604.047
		2	110.224*	6.325	.000	97.603	122.846
Peak	1	2	-444.520*	17.026	.000	-478.494	-410.546
		3	-561.136*	18.268	.000	-597.589	-524.684
	2	1	444.520*	17.026	.000	410.546	478.494
		3	-116.616*	11.710	.000	-139.984	-93.249
	3	1	561.136*	18.268	.000	524.684	597.589
		2	116.616*	11.710	.000	93.249	139.984
Delta	1	2	-259.876*	16.235	.000	-292.273	-227.479
		3	-363.674*	20.896	.000	-405.371	-321.976
	2	1	259.876*	16.235	.000	227.479	292.273
		3	-103.798*	11.197	.000	-126.141	-81.455
	3	1	363.674*	20.896	.000	321.976	405.371
		2	103.798*	11.197	.000	81.455	126.141
Duration	1	2	.154*	.014	.000	.125	.183
		3	.148*	.015	.000	.118	.179
	2	1	-.154*	.014	.000	-.183	-.125
		3	-.006	.006	.334	-.018	.006
	3	1	-.148*	.015	.000	-.179	-.118
		2	.006	.006	.334	-.006	.018

A.3 Repeated measures ANOVAs for the female syllable parameters. Significant results are shaded grey.

Measure		Type III Sum of Squares	df	Mean Square	F	Sig.
Minimum	Sphericity Assumed	665781.812	2	332890.906	253.952	.000
	Greenhouse-Geisser	665781.812	1.474	451678.418	253.952	.000
Maximum	Sphericity Assumed	6910638.326	2	3455319.163	262.430	.000
	Greenhouse-Geisser	6910638.326	1.540	4487332.454	262.430	.000
Peak	Sphericity Assumed	1620529.080	2	810264.540	180.148	.000
	Greenhouse-Geisser	1620529.080	1.588	1020299.533	180.148	.000
Delta	Sphericity Assumed	3366674.197	2	1683337.098	133.477	.000
	Greenhouse-Geisser	3366674.197	1.661	2026703.666	133.477	.000
Duration	Sphericity Assumed	.759	2	.380	202.745	.000
	Greenhouse-Geisser	.759	1.478	.514	202.745	.000

Results of Mauchlys Sphericity Test for the syllable parameters used in the female repeated measure ANOVAs.

Mauchly's Test of Sphericity

Within Subjects Effect	Measure	Mauchly's W	Approx. Chi-Square	df	Sig.	Greenhouse-Geisser Epsilon
Call Part	Minimum	.643	21.626	2	.000	.737
	Maximum	.701	17.384	2	.000	.770
	Peak	.741	14.702	2	.001	.794
	Delta	.796	11.178	2	.004	.831
	Duration	.647	21.367	2	.000	.739

Pairwise comparison of the female syllable parameters identified as significantly by the repeated measure ANOVA. Call part is coded; 1 – beginning, 2 - middle, 3 – end. Significant results are shaded grey.

Measure	(I) Call Part	(J) Call Part	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	95% Confidence Interval
						Lower Bound	Upper Bound
Minimum	1	2	-142.861*	8.087	.000	-159.104	-126.619
		3	-136.812*	8.251	.000	-153.386	-120.239
	2	1	142.861*	8.087	.000	126.619	159.104
		3	6.049	4.554	.190	-3.098	15.196
	3	1	136.812*	8.251	.000	120.239	153.386
		2	-6.049	4.554	.190	-15.196	3.098
Maximum	1	2	-404.816*	22.072	.000	-449.149	-360.483
		3	-485.863*	27.821	.000	-541.743	-429.984
	2	1	404.816*	22.072	.000	360.483	449.149
		3	-81.047*	16.966	.000	-115.125	-46.970
	3	1	485.863*	27.821	.000	429.984	541.743
		2	81.047*	16.966	.000	46.970	115.125
Peak	1	2	-180.126*	14.015	.000	-208.277	-151.975
		3	-242.800*	15.562	.000	-274.057	-211.543
	2	1	180.126*	14.015	.000	151.975	208.277
		3	-62.674*	9.516	.000	-81.787	-43.561
	3	1	242.800*	15.562	.000	211.543	274.057
		2	62.674*	9.516	.000	43.561	81.787
Delta	1	2	-261.950*	20.237	.000	-302.597	-221.302
		3	-349.050*	26.757	.000	-402.793	-295.306
	2	1	261.950*	20.237	.000	221.302	302.597
		3	-87.100*	18.926	.000	-125.114	-49.086
	3	1	349.050*	26.757	.000	295.306	402.793
		2	87.100*	18.926	.000	49.086	125.114
Duration	1	2	.142*	.010	.000	.122	.163
		3	.156*	.009	.000	.137	.174
	2	1	-.142*	.010	.000	-.163	-.122
		3	.013*	.006	.022	.002	.024
	3	1	-.156*	.009	.000	-.174	-.137
		2	-.013*	.006	.022	-.024	-.002

A.4 Correlation matrix of male temporal and spectral parameters. Highly correlated parameters (>0.8) are shaded grey.

	Syllables	Call Duration	Syllable Rate	Duration (Beginning)	Minimum (Beginning)	Maximum (Beginning)	Bandwidth (Beginning)	Peak Frequency (Beg)	Duration (Middle)	Minimum (Duration)	Maximum (Middle)	Bandwidth (Minimum)	Peak Frequency (Mid)	Duration (End)	Minimum (End)	Maximum (End)	Bandwidth (End)	Peak Frequency (End)
Syllables	1.00	.906	-.070	.026	.077	.047	-.022	.059	-.201	.277	.541	.121	.309	.005	.098	.374	.153	.216
Call Duration	.906	1.00	.352	.132	-.025	-.078	-.116	-.073	-.049	.092	.332	.162	.240	.005	-.053	.231	.210	.216
Syllable Rate	-.070	.352	1.00	.263	-.249	-.316	-.254	-.335	.335	-.392	-.461	.071	-.150	.009	-.336	-.325	.122	-.010
Duration (Beginning)	.026	.132	.263	1.00	-.656	-.534	-.080	-.526	-.039	-.497	-.194	.403	-.043	.092	-.464	.034	.497	.141
Minimum (Beginning)	.077	-.025	-.249	-.656	1.00	.871	.234	.866	.023	.719	.301	-.566	.136	-.045	.662	.199	-.543	-.035
Maximum (Beginning)	.047	-.078	-.316	-.534	.871	1.00	.682	.914	.029	.669	.330	-.487	.216	.029	.605	.204	-.481	-.013
Bandwidth (Beginning)	-.022	-.116	-.254	-.080	.234	.682	1.00	.519	.024	.254	.205	-.121	.225	.124	.211	.108	-.142	.027
Peak Frequency (Beg)	.059	-.073	-.335	-.526	.866	.914	.519	1.00	-.070	.690	.358	-.488	.232	-.088	.661	.248	-.508	.022
Duration (Middle)	-.201	-.049	.335	-.039	.023	.029	.024	-.070	1.00	-.251	-.293	.048	-.277	.539	-.125	-.210	-.017	-.104
Minimum (Duration)	.277	.092	-.392	-.497	.719	.669	.254	.690	-.251	1.00	.499	-.723	.400	-.127	.834	.410	-.574	.054
Maximum (Middle)	.541	.332	-.461	-.194	.301	.330	.205	.358	-.293	.499	1.00	.238	.563	-.039	.441	.740	.052	.418
Bandwidth (Minimum)	.121	.162	.071	.403	-.566	-.487	-.121	-.488	.048	-.723	.238	1.00	.001	.111	-.583	.131	.685	.272
Peak Frequency (Mid)	.309	.240	-.150	-.043	.136	.216	.225	.232	-.277	.400	.563	.001	1.00	-.176	.251	.411	.024	.278
Duration (End)	.005	.005	.009	.092	-.045	.029	.124	-.088	.539	-.127	-.039	.111	-.176	1.00	-.096	-.019	.082	.046
Minimum (End)	.098	-.053	-.336	-.464	.662	.605	.211	-.125	.661	.834	.441	-.583	.251	-.096	1.00	.361	-.776	.143
Maximum (End)	.374	.231	-.325	.034	.199	.204	.108	.248	-.210	.410	.740	.131	.411	-.019	.361	1.00	.307	.482
Bandwidth (End)	.153	.210	.122	.497	-.543	-.481	-.142	-.508	-.017	-.574	.052	.685	.024	.082	-.776	.307	1.00	.180
Peak Frequency (End)	.216	.216	-.010	.141	-.035	-.013	.027	.022	-.104	.054	.418	.272	.278	.046	.143	.482	.180	1.00

A.5 Correlation matrix of female temporal and spectral parameters. Highly correlated parameters (>0.8) are shaded grey.

	Syllables	Call Duration	Syllable Rate	Duration (Beginning)	Minimum (Beginning)	Maximum (Beginning)	Bandwidth (Beginning)	Peak Frequency (Beg)	Duration (Middle)	Minimum (Duration)	Maximum (Middle)	Bandwidth (Minimum)	Peak Frequency (Mid)	Duration (End)	Minimum (End)	Maximum (End)	Bandwidth (End)	Peak Frequency (End)
Syllables	1.000	.653	-.477	.074	-.053	.057	.116	-.134	-.089	.103	.182	.146	.090	.106	.129	.176	.136	.185
Call Duration	.653	1.000	.350	.060	.058	.130	.103	.051	-.148	.355	.433	.312	.250	.142	.228	.283	.214	.406
Syllable Rate	-.477	.350	1.000	-0.030	.153	.125	.012	.257	-.044	.289	.268	.170	.400	.024	.125	.104	.068	.237
Duration (Beginning)	.074	.060	-0.030	1.000	-.051	.057	.115	.021	.341	.145	.310	.259	.037	.381	.071	.077	.056	.043
Minimum (Beginning)	-.053	.058	.153	-.051	1.000	.578	-.214	.550	.099	.491	-.123	-.282	.241	.004	.579	-.205	-.324	.127
Maximum (Beginning)	.057	.130	.125	.057	.578	1.000	.674	.713	.234	.305	.181	.080	.424	.029	.372	.050	-.038	.018
Bandwidth (Beginning)	.116	.103	.012	.115	-.214	.674	1.000	.355	.190	-.080	.329	.351	.289	.031	-.079	.246	.248	-.094
Peak Frequency (Beg)	-.134	.051	.257	.021	.550	.713	.355	1.000	.313	.356	-.022	-.138	.394	-.064	.416	-.218	-.299	.114
Duration (Middle)	-.089	-.148	-.044	.341	.099	.234	.190	.313	1.000	.061	.240	.217	.103	.385	.101	.211	.175	.086
Minimum (Duration)	.103	.355	.289	.145	.491	.305	-.080	.356	.061	1.000	0.128	-.199	.537	.071	.567	.120	-.017	.285
Maximum (Middle)	.182	.433	.268	.310	-.123	.181	.329	-.022	.240	.128	1.000	.946	.338	.471	.054	.688	.632	.304
Bandwidth (Minimum)	.146	.312	.170	.259	-.282	.080	.351	-.138	.217	-.199	.946	1.000	.159	.442	-.131	.641	.630	.207
Peak Frequency (Mid)	-.090	.250	.400	.037	.241	.424	.289	.394	.103	.537	.338	.159	1.000	.131	.331	.221	.132	.438
Duration (End)	.106	.142	.024	.381	.004	.029	.031	-.064	.385	.071	.471	.442	.131	1.000	.121	.415	.361	.095
Minimum (End)	.129	.228	.125	.071	.579	.372	-.079	.416	.101	.567	.054	-.131	.331	.121	1.000	-.168	-.385	.213
Maximum (End)	.176	.283	.104	.077	-.205	.050	.246	-.218	.211	.120	.688	.641	.221	.415	-.168	1.000	.975	.234
Bandwidth (End)	.136	.214	.068	.056	-.324	-.038	.248	-.299	.175	-.017	.632	.630	.132	.361	-.385	.975	1.000	.170
Peak Frequency (End)	.185	.406	.237	.043	.127	.018	-.094	.114	.086	.285	.304	.207	.438	.095	.213	.234	.170	1.000

A.6 Correlation between peak call power and temporal variables. Low correlation values indicate that amplitude of the call does not affect sensitivity of temporal measurement.

	Peak Power (dB)
Call Duration (s)	0.036
Syllable duration (beginning) (s)	0.078
Syllable duration (middle) (s)	-0.203
Syllable duration (end) (s)	-0.255

A.7 Stepwise statistics for the initial male discriminant function analysis. At each step the predictor variables that lowered the model Wilks Lambda most was added the model. The initial model had eight steps.

Stepwise Statistics

Step	Number of Variables	Lambda	df1	df2	df3	Exact F				Approximate F			
						Statistic	df1	df2	Sig.	Statistic	df1	df2	Sig.
1	1	.084	1	4	62	169.410	4	62.0	.000				
2	2	.032	2	4	62	70.040	8	122.0	.000				
3	3	.013	3	4	62					55.606	12	159.03	.000
4	4	.007	4	4	62					45.505	16	180.88	.000
5	5	.005	5	4	62					38.772	20	193.31	.000
6	6	.003	6	4	62					35.037	24	200.05	.000
7	7	.002	7	4	62					33.024	28	203.33	.000
8	8	.002	8	4	62					30.576	32	204.42	.000

A structure matrix of the male discriminant functions (initial model with 8 predictor variables). The table shows the correlation of each variable with each discriminant function. * denotes the greatest contribution of each predictor variable.

Structure Matrix

	Function			
	1	2	3	4
MaxMid	.819*	.176	-.297	-.052
PeakMid	.586*	.308	.047	.539
Syllables	.201	.511*	.035	.055
MinBeg	.335	.366*	-.084	.151
DurBeg	-.071	-.361*	.029	.320
DurMid	-.087	-.132	.762*	-.157
DeltaEnd	.305	-.159	.352*	-.340
DeltaMid	.279	.083	.017	-.521*

The modified discriminant function structure matrix with only seven predictor variables

Structure Matrix

	Function			
	1	2	3	4
MaxMid	.828*	.156	-.310	-.071
Syllables	.207	.522*	.034	-.005
MinBeg	.317	.375*	-.083	-.167
DurMid	-.071	-.112	.765*	.334
PeakMid	.571	.332	.094	-.676*
DeltaMid	.286	.052	-.018	.624*
DeltaEnd	.312	-.178	.331	.421*

The Box's M test of homogeneity for the final male discriminant function model (seven variable)

Box's M		301.959
F	Approx.	2.657
	df1	84
	df2	3697.727
	Sig.	.000

Tolerance values for the predictor variables included in the final male discriminant function model (seven variable).

	Tolerance
MaxMid	.312
Syllables	.657
DurMid	.844
PeakMid	.631
DeltaEnd	.443
DeltaMid	.293
MinBeg	.393

A.8 Stepwise statistics for the initial female discriminant function analysis. At each step the predictor variables that lowered the model Wilks Lambda most was added the model. The model had five steps.

Stepwise Statistics

Step	Number of Variables	Lambda	df1	df2	df3	Exact F				Approximate F			
						Statistic	df1	df2	Sig.	Statistic	df1	df2	Sig.
1	1	.272	1	4	45	30.09	4	45	.000				
2	2	.077	2	4	45	28.62	8	88	.000				
3	3	.033	3	4	45					25.087	12	114.06	.000
4	4	.016	4	4	45					23.029	16	128.45	.000
5	5	.010	5	4	45					20.930	20	156.94	.000

The structure matrix of the female discriminant function model. The table shows the correlation of each variable with each discriminant function. * denotes the greatest contribution of each predictor variable.

Structure Matrix

	Function			
	1	2	3	4
MinBeg	.270	.725*	-.076	.477
Tempo	-.337	-.133	.644*	.296
DeltaMid	.393	-.480	.580*	.350
DurationEnd	-.280	-.084	.035	.778*
PeakMid	.096	-.513	-.183	.587*

The Box's M test of homogeneity for the female discriminant function analysis

Box's M		310.345
F	Approx.	3.570
	df1	60
	df2	1834.601
	Sig.	.000

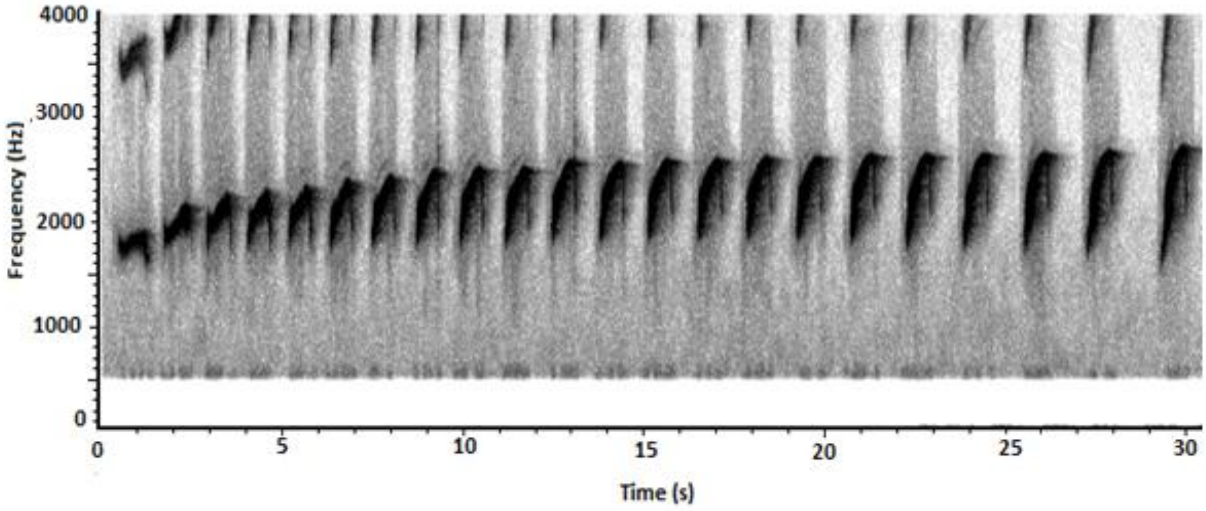
Tolerance values for the predictor variables included in the female discriminant function analysis

	Tolerance
MinBeg	.834
DeltaMid	.678
Tempo	.764
PeakMid	.762
DurationEnd	.773

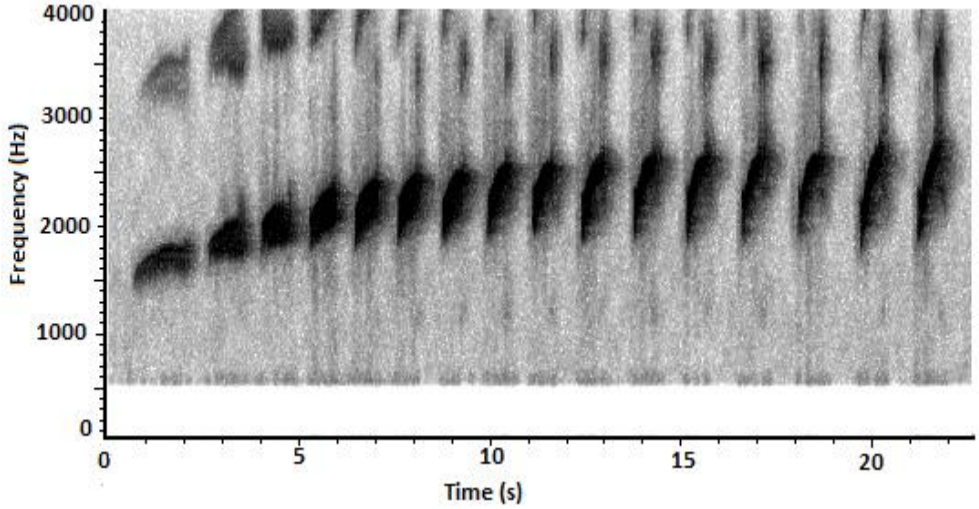
Appendix B

B.1 Representative spectrograms of male individuals in this study

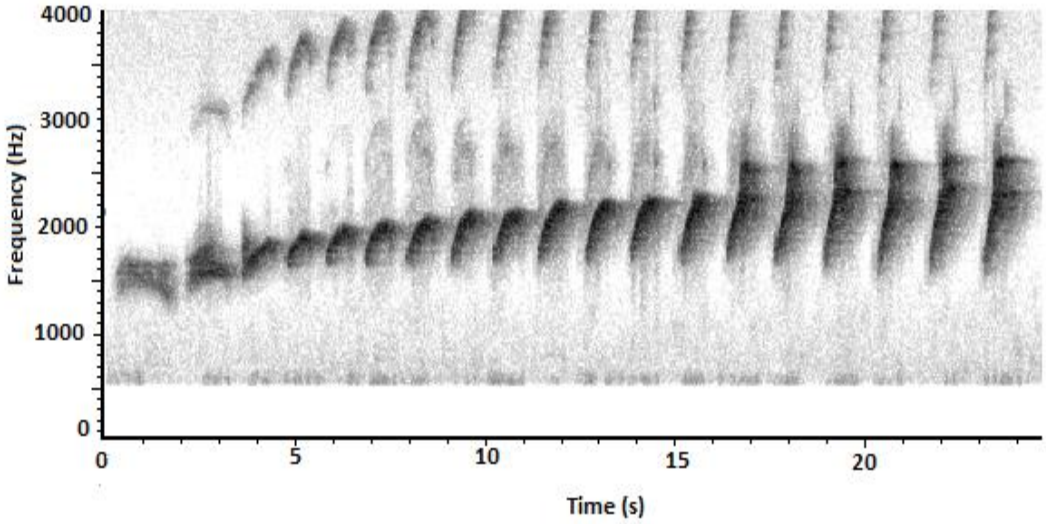
Adam



Rangi



Moss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Frequency (Hz)
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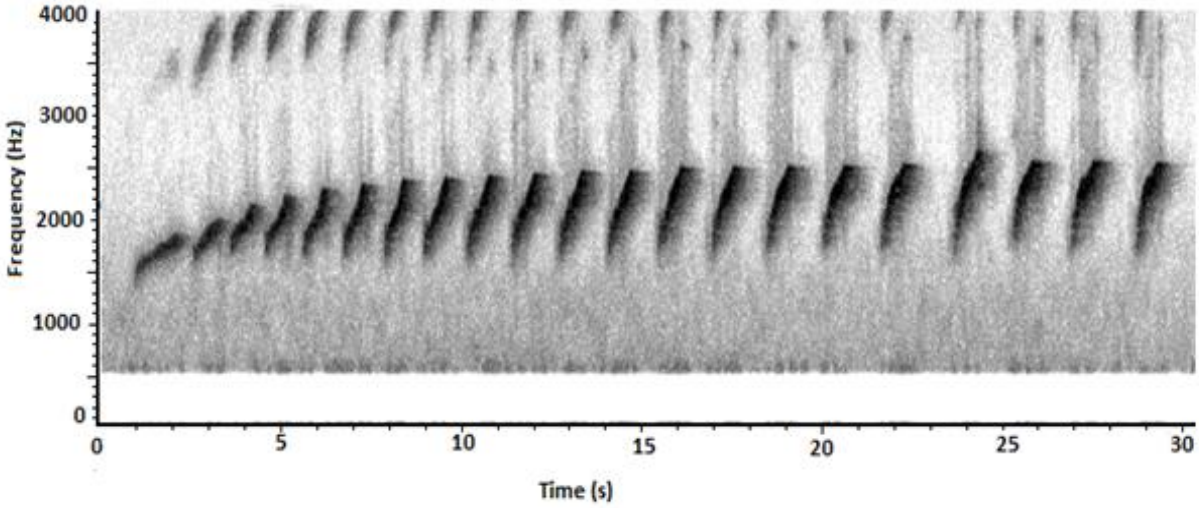
5
10
15
20
Time (s)

Ebb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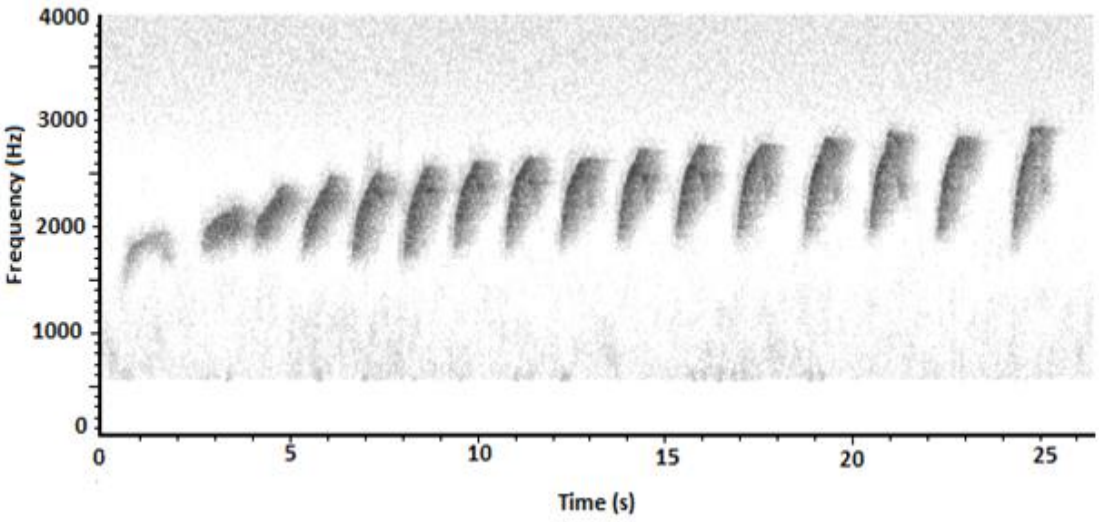
5
10
15
20
25
30
Time (s)

Mac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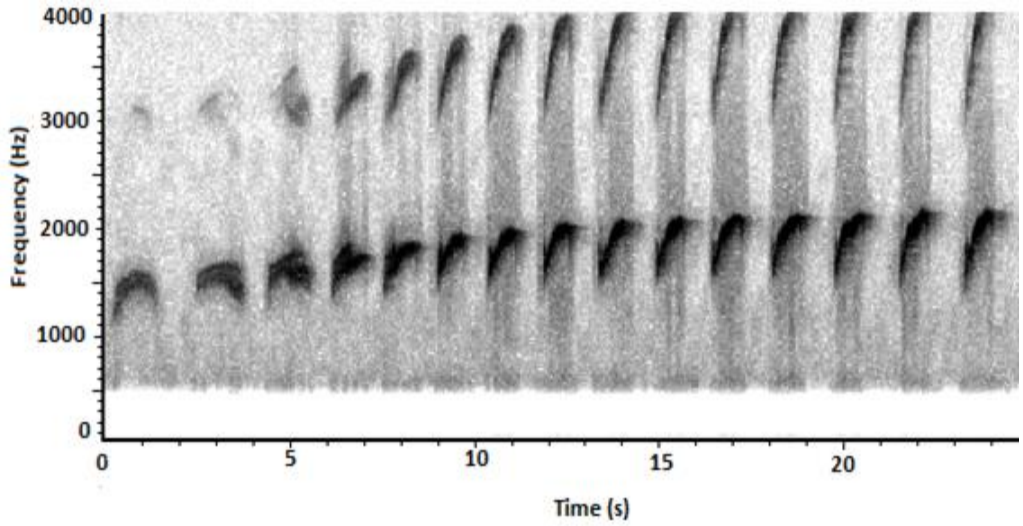
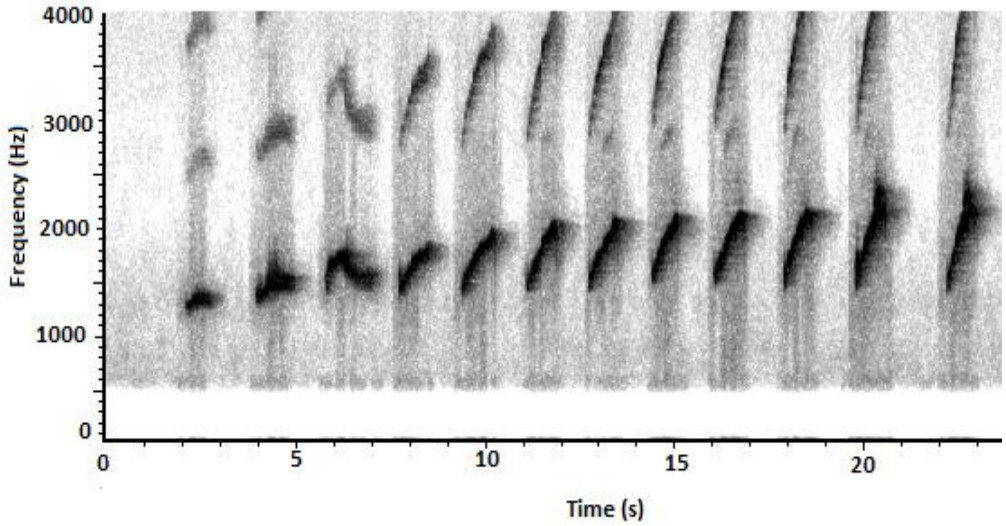
10
15
20
25
Time (s)

Clyde

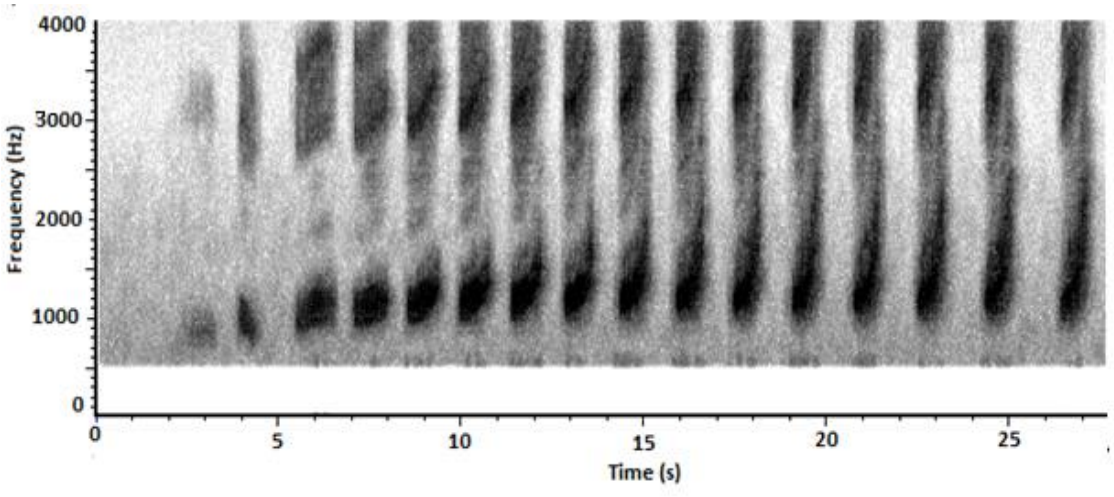


Bazza

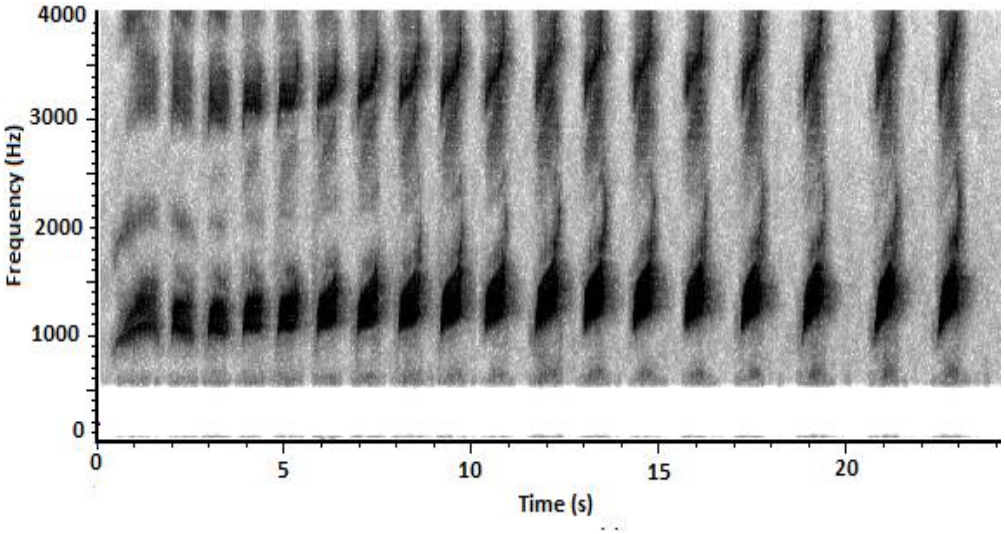


B.2 Representative spectrograms of female individuals in this study

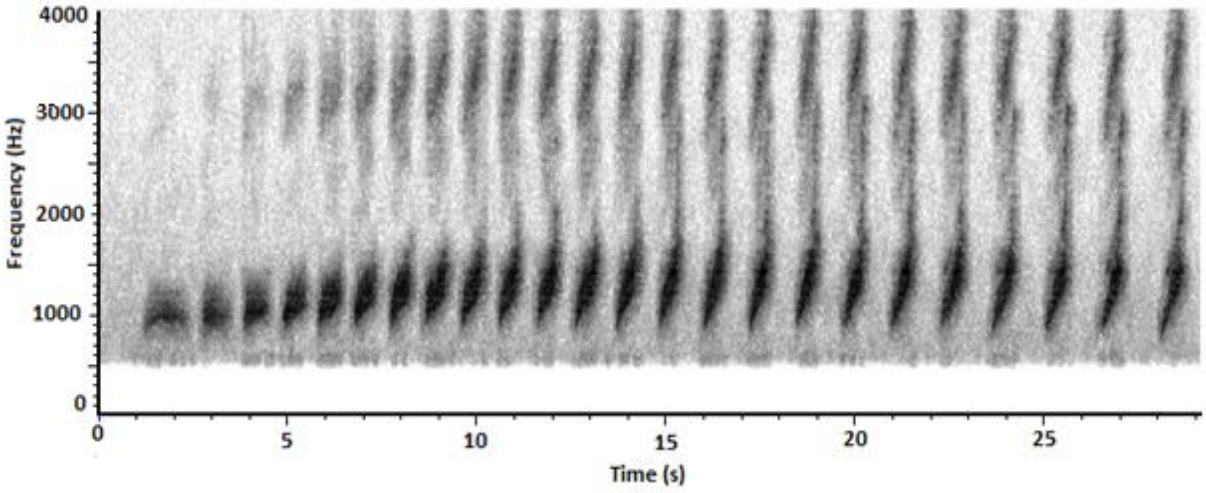
Eve



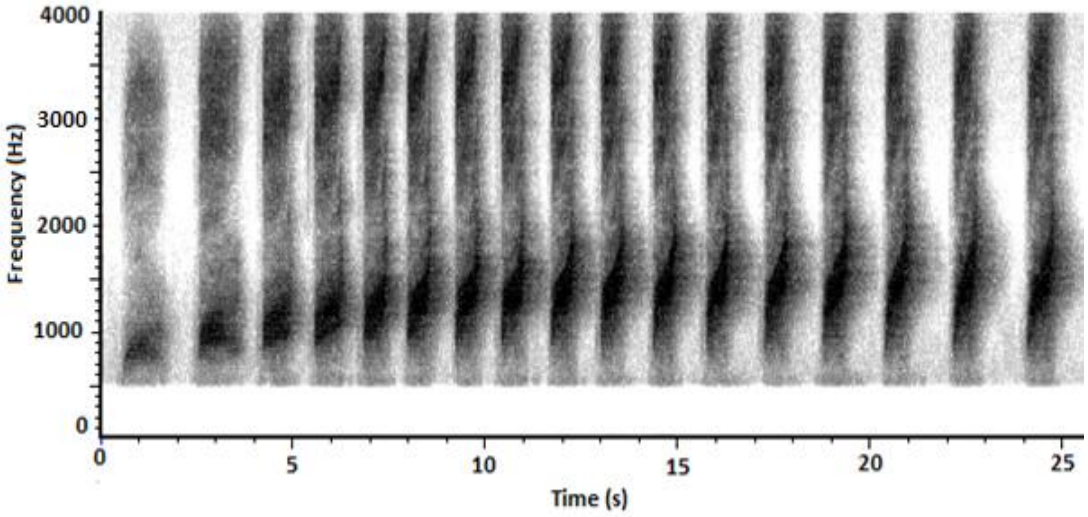
Pongo



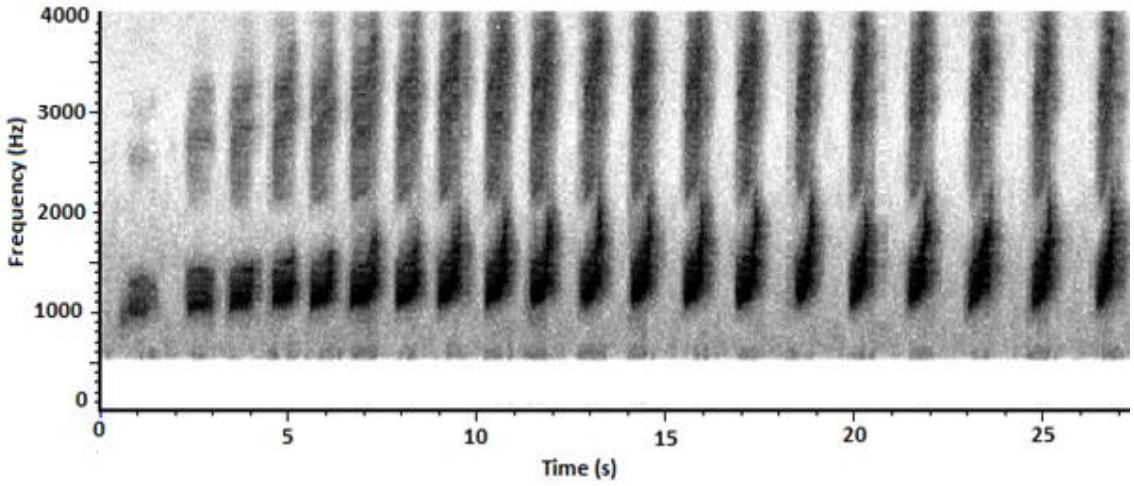
Bonnie



Punga



Flo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2000
1000
0
Frequency (Hz)
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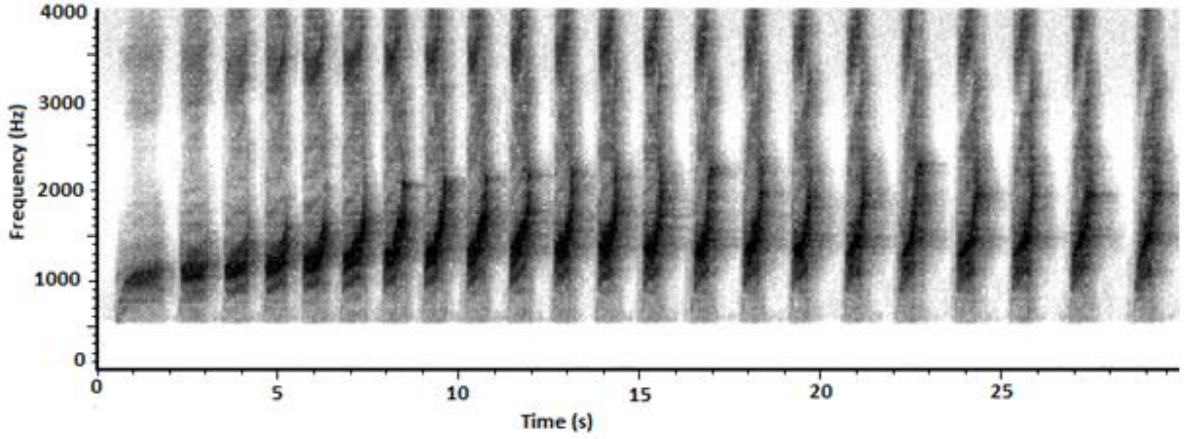
5
10
15
20
25
Time (s)

Beth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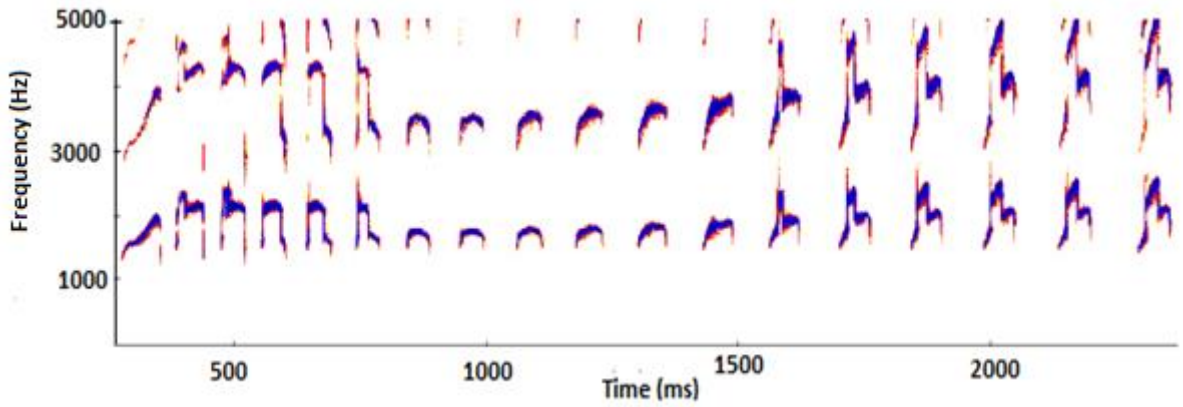
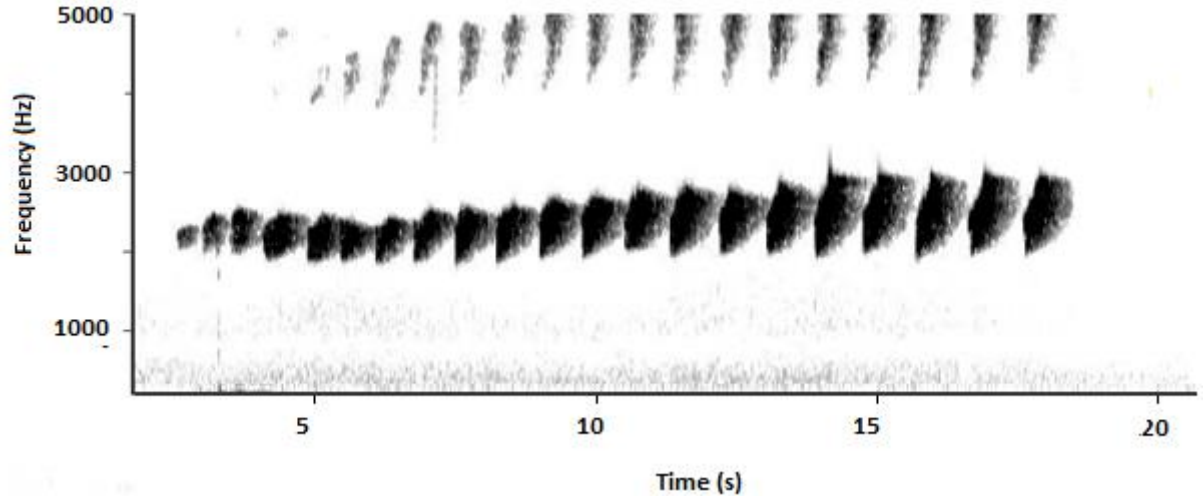
3000
2000
1000
0
Frequency (Hz)
0
5
10
15
20
25
Time (s)

B.3 Visual comparison of male *Apteryx* calls. All spectrograms have been truncated to show lower harmonics only.

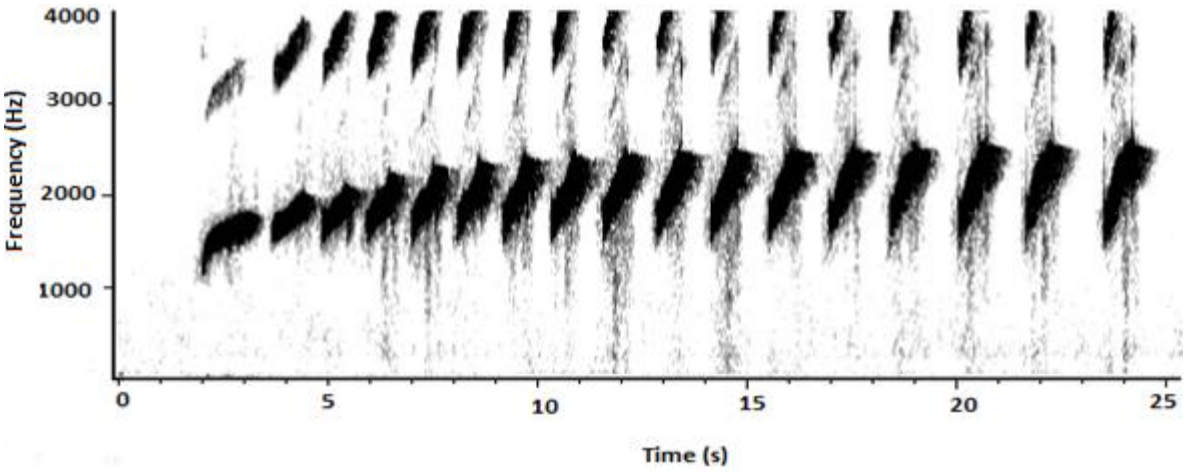
North Island Brown Kiwi: Modified from Corfield 2004 (0 - 5000Hz).



Little Spotted Kiwi: Modified from Digby 2013 (0 - 5000 Hz)

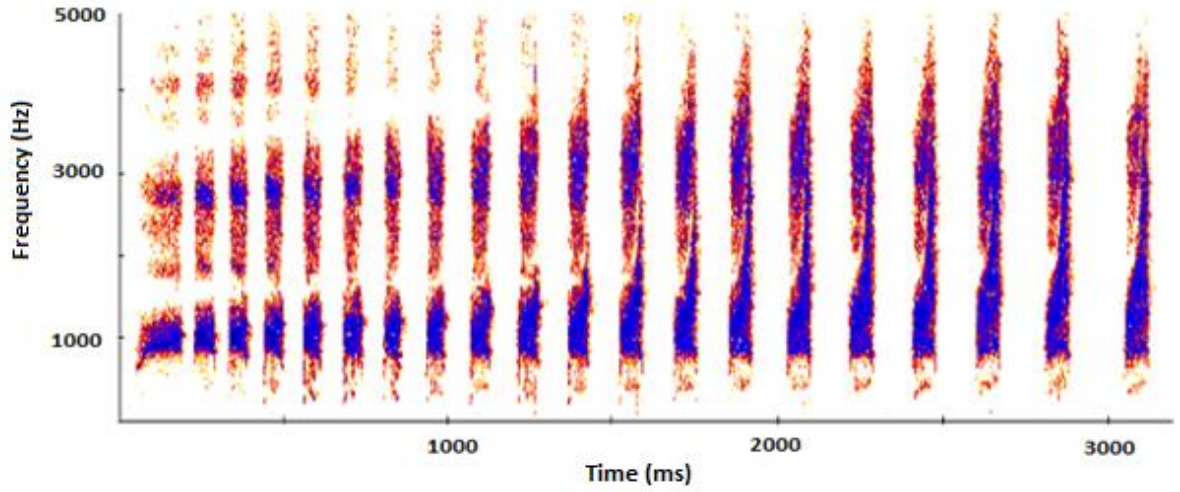


Great Spotted Kiwi (0 - 4000 Hz)

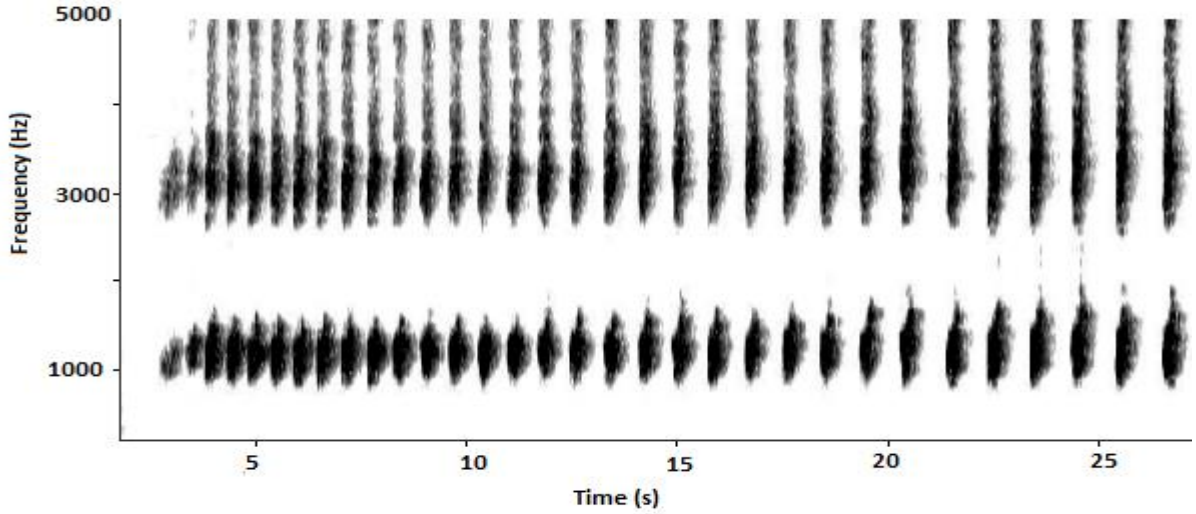


B.4 Visual comparison of female *Apteryx* calls. All spectrograms have been truncated to show lower harmonics only.

North Island Brown Kiwi: Modified from Corfield 2004 (0 - 5000Hz).



Little Spotted Kiwi: Modified from Digby 2013 (0 - 5000 Hz)



Great Spotted Kiwi (0 - 4000 Hz)