Who goes there? An analysis of North Island brown kiwi (*Apteryx mantelli*) vocal anatomy, vocalisations, and associated behaviours

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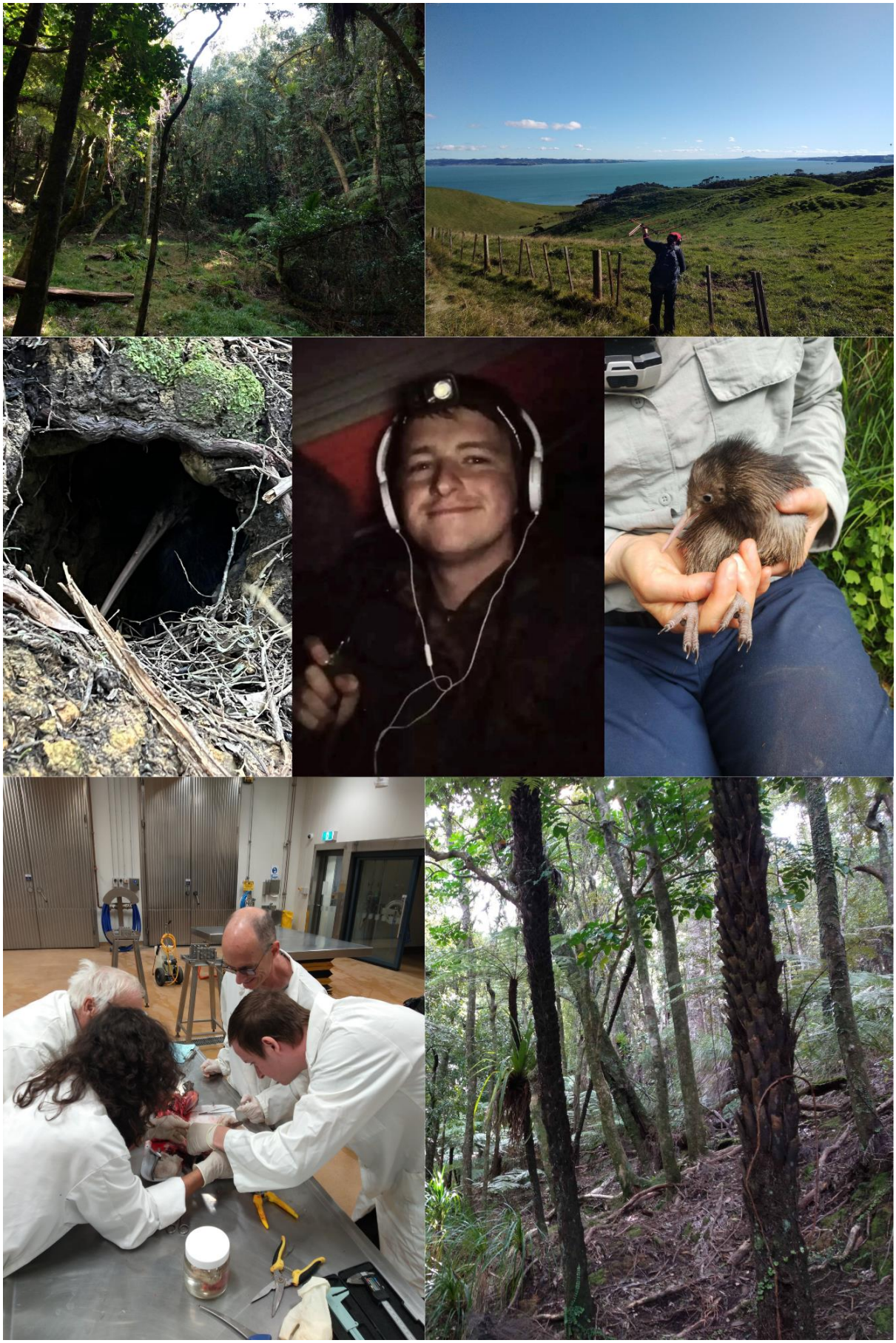

A brief overview of my masters experience

Abstract

This thesis explores individual variations in the vocal tract, vocalisations, and calling behaviour of the North Island brown kiwi (*Apteryx mantelli*). Kiwi are cryptic, nocturnal birds and are commonly monitored using acoustic methods – either manual call counts, or automated field recordings. Kiwi are loud callers with males and females producing very different calls. The number of times an individual bird calls per night varies, therefore turning call rates into estimates of population abundance is challenging and thus call counts fall short of estimating population numbers. This thesis aims to improve the knowledge we have of kiwi vocal behaviour using two approaches: (i) examining and describing for the first time the complete vocal tract of kiwi looking for differences between the sexes that could explain the different sounds they produce, and (ii) attempting to identify individuals through call variables obtained through multiple manual and automated call recordings. I also utilised calls shared between multiple recorders in an area to triangulate their location and identify a trend in call location selection. I investigated this to link calling behaviour to calling purpose, as the close proximity of kiwi nests on Ponui Island may influence calling for nest defence.

Anatomical analysis of six brown kiwi (male = 3, female = 3) revealed a considerable difference in lateral labium area between the sexes (male = 2.43 mm^2 ± 1.1, female = 1.19 mm^2 ± 0.95), though this was not statistically significant (Mann-Whitney U test: n = 6; p = 0.3827), likely influenced by a small sample size. The syrinx was of the tracheobronchial type, which was larger in females (length = 8.98mm ± 2.78; width = 9.24mm ± 0.96), than in males (length = 6.13mm ± 0.8; width = 8.51mm ± 0.47). The tongue was spoon-like with a cartilaginous tip, and the oropharyngeal cavity contained two pairs of pharyngeal folds posterior to the glottis and choana.

Call recordings, collected passively from 29 recorders near nine nests on Ponui Island and manually from six males, were analysed using k-means clustering to assess individual call distinctiveness. Results indicated that individual calls could not be reliably classified (percentage of correct identifications = 9%) using the selected call variables.

Choice of calling location was examined using a three-tiered call quality ranking system. I evaluated call quality based on the number of harmonics visible in the call recording, which correlates with distance between calling bird and the recorder. Using a negative binomial GLM I found that altitude was not a predictive factor in site selection; however, high-elevation sites functioned as good listening vantage points for the acoustic recorders, with higher ranked calls significantly correlated with increasing altitude.

These findings highlight important considerations for future research. The differences in the sound generation source between the sexes highlights a potential source of the brown kiwi's sexually dimorphic calls, however, the degree of neuromuscular control of call production must be investigated. Additionally, utilising syllable (a distinct segment of harmonics in a bird’s call) variables for individual identification is paramount as they seem to be more informative than using call (the full vocalisation) variables alone, thus potentially providing more evidence for vocal individuality in kiwi. More time is needed for both studies to provide informative results to account for limitations in sample sizes and to account for seasonal variability of kiwi calls. Addressing these challenges could improve passive acoustic monitoring techniques for kiwi and other cryptic nocturnal species.

Acknowledgements

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I would also like to thank Stuart Hunter for supplying Brown Kiwi for the anatomy study, without you, this study would have struggled to provide adequate specimens. I would like to thank David Chamberlin, and Di Archer for ensuring I survive Ponui in addition to providing lodging, amenities, and transport to and from the island. Both were incredibly important to this study and improved my time on Ponui Island substantially. I would like to thank the staff of the Histology laboratory at Massey University as without them, none of my anatomical samples would have been examinable at a sub-gross level. I would also like to thank my family, my flatmates, and Sam for tolerating my rants and supporting me throughout this degree.

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Naming Rubric for kiwi specimens:

BECG- ID code	Species	Location of source	Study type
F = Female	BK = Brown kiwi	NatP= National Park	VA= Vocal apparatus
M = Male	LSK= Kiwi pukupuku	SP = South Ponui	
	GSK = Roroa	NP = North Ponui	
	RT = Rakiura Tokoeka	R = Remutaka	
	T = Tokoeka	TP = Te Puia	
		W = Wellington	
		Z = Zoo	
		PP = Paparoa	
		I = Invercargill	

1 Introduction

This thesis was born out of an interest in helping brown kiwi (*Apteryx mantelli*) populations and other bird species for which we use bioacoustics for monitoring. Current methods for estimating population sizes could be enhanced by incorporating individual identification. Vocal individuality is known to exist in many species, and the differences are determined by the characteristics of an individual's vocal anatomy. This is the focus of my second chapter. The sounds produced can be identified by conspecifics, presumably using their distinctive frequencies, the duration (cadence) of silence and call, and other structural parameters. This is the motivation of my third chapter. In this introduction, I will briefly introduce these subjects and describe what I did in each chapter.

1.1 Vocal anatomy

A central aim of this thesis is to characterise the vocal apparatus of the brown kiwi (*Apteryx mantelli*) at both the gross morphological and microscopic (histological) levels, in order to understand its role in shaping species, and individual-specific vocal characteristics. While gross morphological examination provides information about the overall structure of the vocal tract, it is the histology of its components (including cartilages, soft tissue layers, connective elements, and glandular structures) that allows us to pinpoint the cellular and structural specialisations responsible for sound generation and modulation (e.g., Elemans et al., 2015).

Through detailed histological analyses, this study aims to reveal how tissue composition and layering, relate to the acoustics of the kiwi's calls, thereby providing a mechanistic link between the anatomy of the vocal tract and its role in producing individual vocal signatures

(Riede & Goller, 2010a). This approach allows the findings to move beyond simple description towards an understanding of the functional basis of vocal individuality, offering insights applicable across the Palaeognathae and other avian lineages.

An individual's vocal anatomy is the system of bodily components that create and contribute to the formation of vocalisations (Fitch, 2006). Fant (1960) introduced the source-filter theory of sound production, which divided the vocal anatomy into two categories, the source and the filter.

The source refers to the mechanism that generates the sound itself, which in most animal groups is the larynx (Colafrancesco & Gridi-Papp, 2016; Fitch, 2006; Frankel, 2009). This is either absent or heavily reduced in birds, which instead have a syrinx (Goller, 2022). Both source structures operate by air from the lungs flowing through the bronchi to the respective vibratory structures (vocal folds in mammals, lateral and medial labia in birds). These structures then produce various sounds that are determined by the size and tension of these tissues (Fitch, 2006). The vibrations then pass through the rest of the vocal anatomy (the filters) which include the trachea, pharyngeal, oral, and nasal cavities (Fant 1960). The sound is modified as it travels through these filters via their shape, length, and movements, ultimately producing a vocalisation modified from what the source created.

The process of sound production is therefore shaped by the unique vocal anatomy of an individual, which in turn can create unique vocalisations. Thus, it becomes important when investigating calls of an individual to understand the degree of variation possible between individuals, as that variation provides the basis for the individuality of calls.

Kiwi are known to have sexually dimorphic calls with current literature suggesting an anatomical basis to this dimorphism (Dent, 2013; Digby et al., 2013). As brown kiwi are territorial (Corfield, 2004; Digby et al., 2013), it is likely that they would signal their identity

through territory maintenance calls (Corfield, 2004; Kirschel et al., 2011), which may be influenced either by anatomical differences or call structure differences (Corfield, 2004; Dent, 2013; Digby et al., 2013).

1.2 Conservation Monitoring

Monitoring serves to provide accurate and relevant information about species that need conservation management (Jones et al., 2013). Various kinds of monitoring methods exist and are utilised to gain information about a variety of organisms through specialised tools and methods fit for purpose for the organism in question.

In this thesis I utilised monitoring methods that I classified as active or passive (Browning et al., 2017; Hallett et al., 2018; Zwerts et al., 2021). Active monitoring is when an animal is tracked and monitored by people, with or without aids such as dogs or radio telemetry. Passive monitoring typically involves the use of automated equipment such as automated recording units and camera traps, with less direct involvement from people. Active monitoring can include such methods as capture-mark-recapture, line transect sampling (Burnham et al., 1980; Navarro & Díaz-Gamboa, 2015), call surveys (Colbourne & Kleinpaste, 1984; Robertson, 2004), and visual monitoring (Bertoia et al., 2023; Cunningham & Castro, 2011; Havens & Sharp, 2015). Examples of passive monitoring include pitfall traps (Bertoia et al., 2023), tracking tunnels (Watts et al., 2011; Watts et al., 2008), trail cameras (Bertoia et al., 2023; Shiels et al., 2018), and for vocal species, automatic recording units (Pérez-Granados et al., 2018; Shonfield & Bayne, 2017).

Monitoring methods often have their positives and negatives whether it be through disturbance of the monitored species, the costs to monitor, and the accuracy of the monitoring

regiment. Despite the costs of monitoring, the benefits are substantial. Monitoring can provide conservationists with early warning if a population starts to decline, allowing time for proactive decision-making to prevent further losses (Gibbs, 2000; Gibbs et al., 1998). Monitoring also provides insights into the life history traits of the studied organism, as trends in population, habitat selection, and territoriality can all be observed through consistent monitoring (Gagnon et al., 2011; Sutherland, 2006). With accurate monitoring, effective management decisions can be made to help positively impact study species while minimizing the impacts during monitoring such as disturbance and the cost of monitoring, as poor planning often leads to poor results.

With regards to brown kiwi, there are a variety of monitoring methods employed. An example of monitoring method is call-count surveys (Colbourne & Kleinpaste, 1984), which record the number of calls heard in an area with notes on direction, distance, and sex. Capture-mark-recapture (CMR) (McCartney et al., 2006; Wilson et al., 2007), is another monitoring tool used to investigate population trends (Robertson & Westbrooke, 2005). CMR is useful for monitoring a population as it allows for radio transmitters or other identifying tags to be fitted to individuals (Wilson et al., 2007). Population can then be estimated by comparing the number of untagged individuals that are located during the recapture period (Wilson et al., 2007). The radio transmitter tags are useful tools as they allow the individual to be located using radio telemetry tracking equipment which can be carried out on foot or even in the air (Robertson & Westbrooke, 2005; Seddon & Maloney, 2004). Other examples of brown kiwi monitoring tools include the use of audio recorders (Stewart & Hasenbank, 2018), and camera traps (Fan, 2023).

Utilising information from vocalisations has become more prevalent in bioacoustic studies. Various components of vocalisations have been known to contain individually distinct vocal signatures as individuals need to communicate identity at times (Beecher, 2015; Levréro et

al., 2009). If these signatures can be identified, they can be used to monitor individuals and populations alike, providing an opportunity to improve the accuracy of call count surveys if utilised. Literature investigating vocal individuality and its detection use call variables or syllable variables, such as frequency, duration, amplitude, and timing of syllables to classify vocal signatures unique to individuals (Corfield et al., 2008; Digby et al., 2014b). Recognition of individuals by calls is important for animals as they may adjust their behaviour depending on the individual (mates or competitors). Researchers can use individual identification to help track pairs, map territories, and identify behavioural patterns that may be unique to individuals. As such, this thesis aims to identify features of brown kiwi calls that are individually distinct.

1.3 New Zealand and Brown Kiwi

Mountain ranges, numerous offshore islands, historic floodplains, shrubland, exotic and native forests all contribute to the landscape of New Zealand (Skipworth, 1974). New Zealand's variation of ecosystems provides ample opportunity for a variety of species, which has historically been dominated by birds but also includes reptiles, amphibians, and invertebrate fauna (Cooper & Millener, 1993; Fleming, 1975; Skipworth, 1974). The avifauna of New Zealand are representatives of one of the oldest avian lineages on earth, the paleognaths, which are represented by moa (*Dinornithiformes*), and kiwi (*Apteryx*) (Widrig & Field, 2022). Kiwi are culturally and biologically significant in New Zealand as they are the national bird (Dunleavy, 2014), with Robertson et al. (2017) suggesting they should be an indicator of ecosystem health. Of the five species of kiwi described currently, two are declining, two are improving, and one is stable, with North Island brown kiwi listed as stable (IUCN, 2017).

On Ponui Island a considerable population of North Island brown kiwi is present. Ponui Island is comprised of a variety of habitat types with swamps, kauri forests, scrub, and large swathes of plains for farmland present (Cameron & de Lange, 2005; Dixon, 2015).The geography of Ponui Island has a series of gullies all concentrated along the same ridgeline that provide water for a large portion of southern Ponui, important for the flora and fauna of the forest, in addition to the livestock and human inhabitants. These gullies also contain multiple kiwi nests within relative proximity to each other. Kiwi use burrows, logs, native grasses, and swamp as day shelters, and at night forage across the whole island (Dixon, 2015). Accessibility, the relatively compact site size, and the high population density of brown kiwi all contribute to making South Ponui Island an ideal research site.

Kiwi are primarily insectivores, probing soil and leaf litter with a unique bill-tip organ (Buller & Keulemans, 1873; Cunningham et al., 2013) to find ground-based invertebrates such as worms and beetle larvae (Buller & Keulemans, 1873). Brown kiwi are sexually dimorphic, with females being larger than males on average (Buller & Keulemans, 1873) and drastically different in the sound of their calls (Corfield, 2004). Brown kiwi are variable in their breeding systems, as characteristics and life history traits for monogamy and polygamy are present (Potter, 1989; Taborsky & Taborsky, 1999; Undin & Castro, 2022; Undin et al., 2021), with females laying the eggs, and males as the primary incubators (Potter, 1989; Taborsky & Taborsky, 1999).

1.4 Benefits to conservation

Fant's (1960) classic work on the acoustic theory of speech laid the foundation for understanding how a vocal tract's filter characteristics shape sound, providing a framework for why individual animals (and humans) have uniquely identifiable vocal signatures. In this context, formants — the resonant frequencies shaped by the vocal tract — serve as critical acoustic markers that encode individual identity within vocalisations (Suthers, 1994), while body size influences the overall frequency of sounds an animal produces (Bertelli & Tubaro, 2002; Fitch, 1999). As a result, the structural characteristics of vocalisations can be used to identify individuals (Corfield, 2004; Dent, 2013; Digby et al., 2013), to estimate their body size (Bertelli & Tubaro, 2002; Fitch, 1999; Hall et al., 2013), and potentially even to assess their age (Fontana et al., 2016).Utilising individual identification will improve call surveys by increasing the accuracy of the population estimates by reducing repeated counts of individuals, helping to highlight the true size of populations. Employing ARUs combined with the identification of individuals through calls will allow for long term population monitoring with the ability to track individuals without the need for tracking tags or other invasive measures. Vocal individuality may also be used when individuals are low in number and difficult to locate, or in periods when they are sensitive to disturbance such as incubation (Terry et al., 2005).

1.5 Objectives

This thesis will highlight the mechanisms of vocal control and investigate to which degree this control results in the sexual dimorphism of brown kiwi calls. The mechanisms of vocal control and variability of the vocal anatomy will then be used to extrapolate differences in vocal anatomy, to differences in vocalisations, thus providing a form to function link. In addition, this thesis aims to investigate whether common structural characteristics of calls can be used to identify individual vocalisations which later could be used in the monitoring of brown kiwi to improve current monitoring techniques to produce more accurate estimates of population abundance.

This thesis has two objectives:

- **Objective 1**: Investigate and describe brown kiwi vocal anatomy, to illustrate variability between individuals, males, and females, highlighting form-to-function links (Chapter 2).

- **Objective 2**: Investigate the vocalisations and associated behaviours of brown kiwi for evidence of vocal individuality using call and location data of known and unknown individuals within a high-density population (Chapter 3).

1.6 Thesis outline

There are four chapters to this thesis. Chapter one provides a general background to the thesis, aims and objectives. Chapter Two presents a study of the brown kiwi's vocal anatomy. It consists of a combined introduction and literature review that provides an overview of vocal communication, a general description of avian vocal anatomy and its function, and a taxonomic review of the Palaeognathae with a focus on the current literature describing vocal

anatomy within this group. The results section describes the morphology of the vocal tract in both male and female kiwi and includes corresponding histological analyses of its various components. The discussion then places these findings in the context of other paleognathous birds and a wider range of avian species, including a comparative examination of sex-based differences in brown kiwi vocal anatomy. Chapter three presents a study on the vocal behaviours of brown kiwi. It consists of a combined introduction and literature review that provides an overview of kiwi conservation and monitoring methods, issues with these methods, vocal individuality and how it may contribute to kiwi monitoring, and calling location selection. The results section includes an analysis of call spectral variables used to identify individuals, and call data combined with geographic data to analyse calling behaviours. The discussion then compares the outcomes of this study in context with other vocal behaviour and individuality studies, highlighting the differences in methods and outcomes while considering the factors which may have contributed to the results. Chapter four presents a reflection of the thesis, discussing the strengths and weaknesses, what could be done differently in future, and suggestions for future work.

2 The anatomy of the brown kiwi (*Apteryx mantelli*) vocal tract

2.1 Abstract

The North Island brown kiwi (*Apteryx mantelli*) is a small flightless bird belonging to the infraclass Palaeognathae. Paleognathous birds except for kiwi and tinamous were once thought to be a silent group (Pérez-Granados & Schuchmann, 2021), but it was later found that all extant species in the group produce sounds, with kiwi being particularly vocal. There is sparse knowledge of the vocal tract anatomy of the paleognathous birds and even less for the genus *Apteryx*.

This study investigated the entire vocal tract anatomy of the North Island brown kiwi. The vocal tract of the brown kiwi exhibited differences from other paleognaths, such as a spoon-like tongue with a cartilaginous tip, and two sets of pharyngeal folds. We found that brown kiwi lack the intrabronchial ligament, extrinsic syringeal muscles, and a cartilaginous pessulus present in other paleognaths. Additionally, the trachea had interlocking cartilaginous rings lined with circular, longitudinal striated, muscle to support movement in the trachea.

Various features of the brown kiwi vocal tract may account for the differences in their dimorphic vocalisations. The syrinx of the brown kiwi was of the tracheobronchial type with large lateral labia in males (2.43 mm^2 ± 1.1), and smaller in females (1.19 mm^2 ± 0.95). The female syrinx was larger (length 8.98 mm ± 2.78; width 9.24 mm ± 0.96) than the male syrinx (length 6.13 mm ± 0.8; width 8.51 mm ± 0.47). The average lateral labium area (mm^2) was larger in males than females, but not to a significant degree (Mann-Whitney U test: n = 6; p value = 0.3827, Table 5). Overall, the sexual dimorphisms of brown kiwi vocalisations

were consistent with the morphology differences between males and females, forming a connection between the functional morphology and the resulting calls.

2.2 Introduction & Literature review

Communication, whether by chemical, visual, or auditory signals is an important aspect of animal behaviour (Fögen, 2014; Marler, 1957; Rendall et al., 2009; Winkler, 2001). It is ubiquitous throughout the animal kingdom and is frequently used to convey a plethora of information to conspecifics and members of other species alike (Rowe & Skelhorn, 2004; Wilson, 1972). Territorial displays, mating rituals, and alarm calls are all examples of communication and are the framework of many species' existences (Nemeth et al., 2013; Rendall et al., 2009; Seyfarth & Cheney, 2003). An understanding of the signals will help us know what is communicated and why (Cullen, 1972; Rowe & Skelhorn, 2004; Seyfarth & Cheney, 2003; Wilson, 1972). Investigating communication helps further various fields of study through questions about the function, mechanisms, and how they evolved (McGregor, 2005; Winkler, 2001). To understand the function, mechanisms, and evolution of communication we need to make the connection between the anatomical features of the organs involved and their function.

Vocalisations are a major medium of communication, being one of the most widespread. They convey information at long distances, in environments where other communication methods such as visual or chemical signals, are not viable. Amongst animals, birds' vocalisations stand out as a method of communication, because the sounds display a wide range of variability and complexity (Marler, 1957; Rowe & Skelhorn, 2004). In some species bird calls are innate (Marler, 2004; Searcy & Marler, 1987), in others partially learned (some species are age-limited learners), and in others, calls are learned during one or more distinct periods or continuously over their lifespan (open-ended learners; (Leonardo & Konishi,

1999)). Regardless of the type of learner a bird is, they can control aspects of their call through modulation of the sounds (Beckers et al., 2003; Stein, 1968).

Amplitude, or the volume of a call, is one sound characteristic the bird can control; volume alters how far a call travels, or if a call is even heard (Brumm, 2004; Brumm & Todt, 2002; Zollinger et al., 2012). Likewise, birds can change the sounds' frequency, or pitch, also changing how far a call travels. For example, a bird can mitigate the sound's degradation by lowering its pitch (Mack & Jones, 2003) or increasing a sound's pitch allowing the broadcast of a louder call (Nemeth et al., 2013). Vocalisation in birds is achieved via the vocal tract, which consists of the bill, tongue, trachea, syrinx (Laiolo & Rolando, 2003), oropharynx, pessulus, and air sacs (Figure 2-1; (Mack & Jones, 2003; Riede et al., 2016)). Differences in the anatomical features of the vocal tract between species, and between individuals of the same species account for variations in their sounds (Fant, 1960).

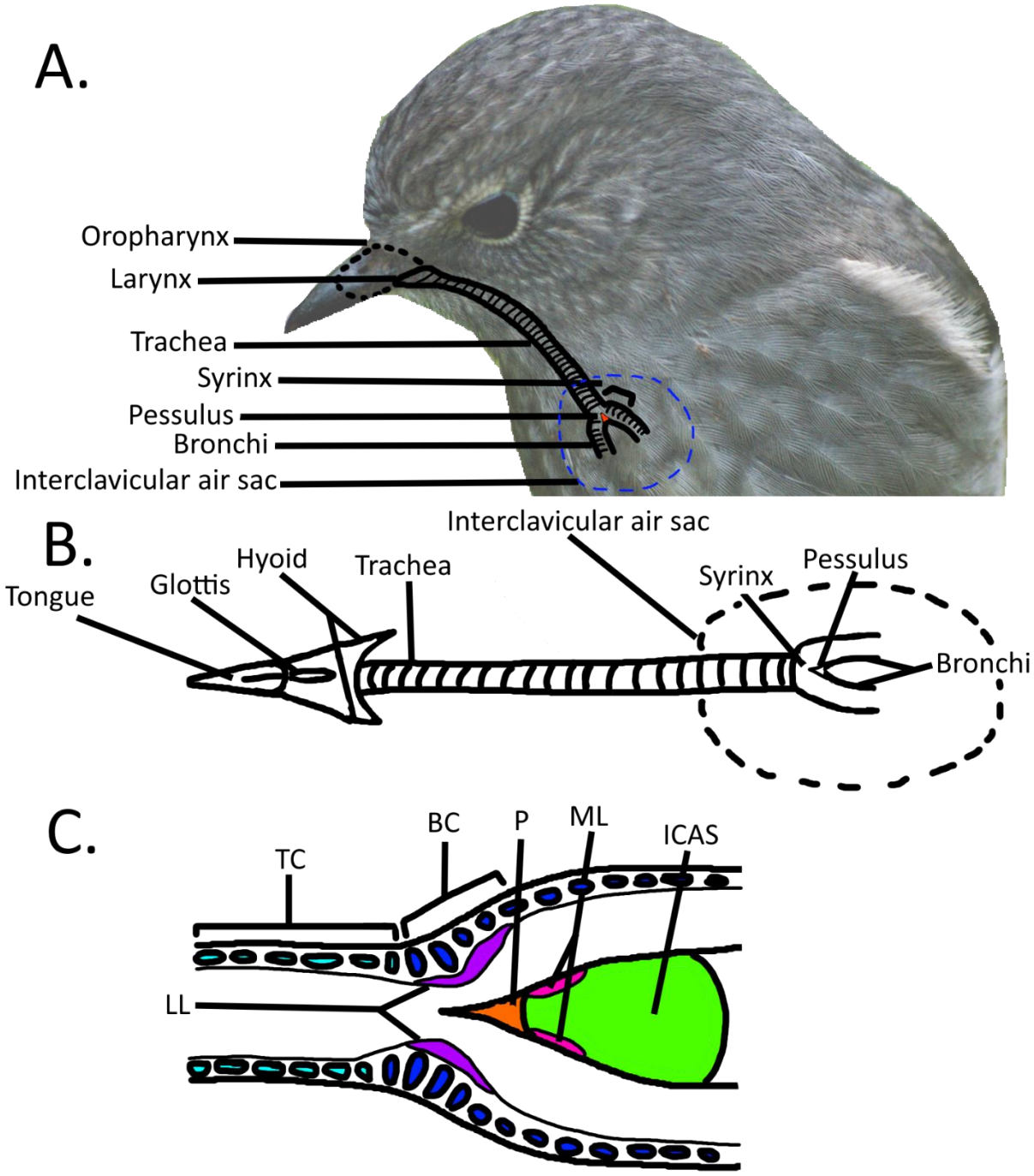

Figure 2-1) (A) Shows a generalised avian vocal anatomy in situ. **(B)** Shows a dorsal view of an extracted generalised avian vocal tract. **(C)** shows a transverse section of a generalised tracheobronchial syrinx. **LL** refers to the lateral labia and **ML** refers to the medial labia. **ICAS** refers to the interclavicular air sac and **P** refers to the pessulus. **BC** refers to the bronchial cartilage and **TC** refers to the tracheal cartilage.

In the next sections, I will describe the anatomical features of the different components of the vocal tract in birds and our current knowledge of how they relate to sound production.

2.2.1 Syrinx

The syrinx is a unique feature of the avian vocal tract. It is considered analogous to the human larynx (Riede & Goller, 2010b), but has one major morphological difference: it bifurcates into two bronchi, one per lung, potentially allowing the production of two different sounds simultaneously. While the syrinx is just one part of the vocal tract, various sources agree that it is one of the most important features in sound production in birds and is also important for taxonomic purposes (Casteleyn et al., 2018; Hérissant, 1753; Warner, 1972).

Syrinx morphology varies with differences in cartilage arrangement, presence of ossification, presence of a pessulus, musculature, and presence and shape of internal and external membranes (Chiappone et al., 2024; Forbes, 1881; Garitano-Zavala, 2009; Picasso & Carril, 2013).

The syrinx can be divided into three types depending on its anatomical position. Tracheal syringes result from modification of the lower end of the trachea, bronchial syringes form from modification of the bronchi, and tracheobronchial syringes form at the junction of the trachea and bronchi (Warner, 1972). The syrinx typically contains a pessulus, a structure located at the bifurcation where the trachea splits into the bronchi, two lateral labia lining the syringeal cartilage, a pair of medial labia on either side of the pessulus, and tympaniform membranes (ÇEvik-Demirkan et al., 2007). Sound is produced through the syrinx utilising the labia with variations in size and tension of the labia being attributed as the cause of variations in the resulting sound (Casteleyn et al., 2018; Riede & Goller, 2010b). Labial tension interacts with sound production by increasing the velocity of the syringeal membrane,

producing increasingly quicker oscillations resulting in higher fundamental frequencies and greater amplitudes (Elemans et al., 2009).

The labia of the syrinx are controlled by muscles such as the ventral and dorsal syringeal muscles (Goller & Riede, 2013; Nojiri et al., 2025), and act to change the internal shape of the syrinx. Changes in the internal shape of the syrinx cause shifts in internal pressure, which in turn causes the airflow rate to change (Goller & Riede, 2013). In addition to the muscles of the syrinx, pressure from the surrounding air sacs such as the interclavicular air sac, impacts the internal cavity of the syrinx as the second component of the resulting vocalisation (Alonso et al., 2014). The interclavicular air sac supports birds' high metabolic lifestyle as well as the respiratory behaviours that aid in vocal production (Goller, 2022).

Studies of sound production have focussed on neognathous birds, and there is a wealth of studies of the song of many species of Passerines, a group that displays a wide variety of vocalisations. The studies of neognathous birds all agree that the syrinx is the most important feature of avian vocal anatomy, but its structure is also incredibly varied throughout the group (Casteleyn et al., 2018; Goller, 2022; Warner, 1972). Variability of the syrinx resulted in many studies on neognath's vocal anatomy with the discovery of features like the mallard (*Anas platyrhynchos*) syringeal bulla (Yilmaz et al., 2012) and the presence of ossification within the syringeal cartilage in domestic chicken (*Gallus gallus domesticus*) (Hogg, 1982; Piperno & Peirone, 1975).

The syrinx has historically been important for taxonomic purposes in neognaths' clades. For example, the morphological characteristics of the syrinx helped determine the position of the family Rhinocryptidae within a neognaths' phylogeny (Maurício et al., 2012). The morphology of the syrinx combined with molecular data helped clarify the position of Rhinocryptidae on a phylogenetic tree when conflicting osteological characteristics confused

taxonomy. Another example of the syrinx's importance to phylogenetic classification was presented in McInerney et al. (2019). Morphological data of the syrinx, hyoid, and larynx, of the southern cassowary *(Casuarius casuarius*) were compared to phylogenetic trees made using molecular data. Within Palaeognathae, the morphological traits of the vocal tract were a more reliable method of classification than using other post-cranial characters and ultimately closer to the conclusions reached with molecular data (McInerney et al., 2019). Other features of the vocal tract, such as the trachea and tongue, may play a role in vocal modulation rather than production (Suthers, 1994).

Descriptions of the paleognathous vocal anatomy range from descriptions of the skeletal elements (Forbes, 1881; McInerney et al., 2019), to more recent investigations into the tissues of the vocal tract (Chiappone et al., 2024; Picasso & Carril, 2013; Yildiz et al., 2003). While these studies focus on muscular or skeletal components, there is a lack of studies on the other parts of the vocal anatomy, resulting in a fragmented image of paleognaths' vocal anatomy (Table 2-1). These gaps create a lack of comparability between paleognaths, making comparisons of morphological features for taxonomy difficult. As a result, the best feature available for comparison is the cartilage of the syrinx, which was described by Forbes (1881), then extended in modern literature (Garitano-Zavala, 2009; Picasso & Carril, 2013). The lack of knowledge of many features of the vocal tract of paleognaths makes it impossible to understand how basal birds have developed and utilised a vocal tract that is fit for a variety of vocalisations ranging from booming to trills (Chiappone et al., 2024; Digby, Bell, et al., 2014a).

Filling this gap would lead to a better understanding of how early birds produce sounds. It would allow us to compare the vocal mechanisms and vocalisations of some of the earliest known living birds with those of extinct and extant species. This could potentially help us advance our understanding of how vocal mechanisms and vocalisations have evolved.

2.2.2 Trachea

The trachea is a narrow cartilage-ringed tube that typically extends from the larynx to the syrinx and is a core component of the avian respiratory system. The role of the trachea is to transport inhaled and exhaled air. The trachea is composed of rings of cartilage that in some species overlap with each other (Atalgin et al., 2021; Kabak et al., 2007; McLelland, 1965), separated by connective tissue, elastic fibres (Duncker, 1974), and thin muscle layers (McLelland, 1965) that all allow for the extension and collapse of the trachea.

The trachea commonly acts as a resonant tube in which formants are thought to arise, and in some species, formants act as a vocal signature of an individual (Fitch, 1999; Gaunt et al., 1987; Suthers, 1994). Formants are sounds that arise from vocal tract resonances identified by peaks of amplitude centred around certain frequencies (Aalto et al., 2018; Briefer, 2012). The frequencies are thought to arise from the filtering of sound as it travels through the vocal tract to form specific sounds like consonants and vowels in human speech and in animals, they convey individual-specific information (Aalto et al., 2018; Briefer, 2012).

Extension of the trachea has been noted to modify the resulting sound (Daley & Goller, 2004). Some birds have the trachea coiled, with coils present within the thorax to exaggerate the size of the bird, which is communicated via vocalisations (Fitch, 1999). The coils allowed for a longer total length of the trachea and resulted in a vocalisation of lower frequency, thus falsely advertising as a bird of larger body size (Fitch, 1999). Other species have been noted to extend the length of the trachea using pressure from the interclavicular air sac, with high-frequency calls being produced as the trachea was extended (Daley & Goller, 2004).

Studies of the trachea have focussed on neognathous species, with studies on paleognathous birds being limited and often brief in their description. Nevertheless, these few studies have shown that overlapping cartilage of trachea are found in rhea (*Rhea americana*) and Darwin's

nothura (*Nothura darwinii*) (Crole & Soley, 2012b; Garitano-Zavala, 2009; Jayachitra & Balasundaram, 2015; Kummrow, 2014; Sousa et al., 2018). One unique feature of the trachea in paleognaths was found in the emu; they possess a tracheal pouch, where incomplete cartilage rings form a brief cavity in the otherwise continuous cartilage (Jayachitra & Balasundaram, 2015). There was a lack of consensus regarding ostrich trachea changing in width caudally as conflicting results were found between studies (Chiappone et al., 2024; Jayachitra, 2007). There is little information available in kiwi and cassowary species (Table 2-1).

2.2.3 Oropharyngeal cavity, Tongue, and Bill gape

The oropharynx comprises the middle part of the throat, behind the mouth. The oropharynx includes the soft palate (the back muscular part of the roof of the mouth), the side and back walls of the throat, the tonsils, and the back one-third of the tongue. The oropharynx combines the oral and pharyngeal cavities into one cavity with it being an essential part of respiration and food intake (Abumandour & El-Bakary, 2017; El-Mansi et al., 2020; Gupta et al., 2015; Igwebuike & Eze, 2010). Its role in sound production is passive, limited to changes in shape caused by manipulations by either the tongue (lingual articulation (Beckers et al., 2004; Riede et al., 2016; Suthers et al., 2016) or through shifting of oral bones (Homberger, 1999). The beak or bill of birds has been identified as a source of vocal modulation as beak movements and gape width were correlated with shifts in vocalisations' frequency patterns (Goller et al., 2004; Hoese et al., 2000; Ohms et al., 2010; Westneat et al., 1993). The vocal modulation caused by movements in the beak is similar to the changes caused by lingual (tongue) articulation by changing the available space of the oropharyngeal cavity (Ohms et al., 2010).

The tongue consists of various elements, with the hyoid bone supporting the tongue, cartilaginous components, and dense musculature all contributing to tongue structure and function (Erdoğan & Iwasaki, 2014). Functions of the tongue include food manipulation, capturing, filtering of food (Erdoğan & Iwasaki, 2014), and vocal filtering (Beckers et al., 2004).

Lingual filtering has been highlighted as potentially one of the reasons parrots and songbirds can produce complex vocalisations by changing the shape of resonance chambers. Other literature suggests that complex vocalisations, while influenced by lingual filtering, are also impacted by the mechanism by which the laryngeal mound is raised (Homberger, 1999). Skeletal elements of the larynx changing the configuration of the laryngeal chamber create differences in the resulting vocalisations potentially allowing for complex vocalisations (Homberger, 1999).

The study of paleognathous oral morphology tends to be focused on feeding mechanisms (Crole & Soley, 2009, 2012b; Jackowiak & Ludwig, 2008; Johnston, 2014; McInerney et al., 2019) as the tongues of ratites have often been designated as rudimentary, lacking the features to enable vocal modulation (Erdoğan & Iwasaki, 2014; Johnston, 2014).

2.2.4 Study Species and study aims

This study focuses on a bird of the infraclass Palaeognathae, the North Island brown kiwi (*Apteryx mantelli*) here referred to as brown kiwi. Paleognathous birds are a largely flightless group of birds that include the following extant species: rheas (Rheidae), kiwi (Apterygidae), ostrich (Struthionidae), cassowaries, emu (Casuariidae), the flight-capable tinamous (Tinamidae), and the following extinct species: moa (Dinornithiformes), elephant birds (Aepyornithiformes), and the false tinamous (Lithornidae).

Birds of the group infraclass Paleognathae have been studied since the 19th century, with the gross anatomical features of many paleognaths described by Owen (1879) and Forbes (1881). These references provided only partial descriptions of the vocal tract of kiwi (*Apteryx*), as few specimens were available for analysis, and the equipment and methods required for thorough sub-gross analysis were not yet developed (Crole & Soley, 2009, 2012a, 2012b; Forbes, 1881; Owen, 1879; Pérez-Granados & Schuchmann, 2021). The vocal tract of paleognaths has been historically under-studied when it comes to vocalisations as this group was regarded as lacking vocalisations except in the case of tinamous and kiwi (Table 2-1). Vocal anatomy descriptions have been updated in some paleognaths (Chiappone et al., 2024; Jayachitra, 2007; Jayachitra & Balasundaram, 2015; Longtine et al., 2024; McInerney et al., 2019; Pérez-Granados & Schuchmann, 2021; Picasso & Carril, 2013; Yildiz et al., 2003). Regardless of the lack of historical studies on paleognathous birds, recent studies have acknowledged the value of studying their vocalisations and their sound production mechanisms (Benedict & Krakauer, 2013). This comes as attention turns to birds outside of the order Passeriformes, with a wide array of complexity in calls and structures being uncovered, prompting further investigation (Crole & Soley, 2012b; Krakauer et al., 2009; Livezey, 1986).

Table 2-1: Key literature of Palaeognathae vocal anatomy

	Tongue	**Oropharynx**	**Trachea**	**Syrinx**	**Characteristics**
Tinamous (*Nothura darwinnii, Rhynchotus rufescens*)	(Tomlinson, 2000)	No literature	No literature	(Garitano-Zavala, 2009; Oliveira et al., 2023)	Tracheobronchial syrinx type. Syrinx lacked sternotracheal muscle but had an interbronchial ligament. Syrinx contained a pessulus. Large lateral tympaniform membrane compared to cartilage of syrinx. The cartilage of the trachea overlapped and was covered by a thin epithelial layer.
Emu (*Dromaius novaehollandiae*)	(Crole & Soley, 2009, 2011; Jayachitra et al., 2015; Smith, 2018; Tomlinson, 2000)	(Crole & Soley, 2011, 2012a)	(Cho et al., 1984; Fowler, 1991; Jayachitra & Balasundaram, 2015; Smith, 2018)	No literature	Tracheobronchial syrinx type. The tongue was triangular with a blunt pointed end. Trachea was similar to ostrich but featured a tracheal pouch that led to an air sac. Tonsils present on the dorsal surface of the pharyngeal folds with lymphoid tissue but lacked crypts.
Ostrich (*Struthio camelus*)	(Jackowiak & Ludwig, 2008; Johnston, 2014; Smith, 2018; Tivane et al., 2011; Tomlinson, 2000)	(Crole & Soley, 2012a; Tivane et al., 2011)	(Cho et al., 1984; Forbes, 1881; Fowler, 1991; Jayachitra, 2007)	(Chiappone et al., 2024; Forbes, 1881; Yildiz et al., 2003)	Tracheobronchial syrinx type. The syrinx had no extrinsic muscle and no well-developed pessulus. The tongue was short, broad, with a rounded tip. Trachea was long and flexible with no unusual features present. Tonsils present on the dorsal surface of the pharyngeal folds with lymphoid tissue but lacked crypts. The oropharyngeal cavity was bell shaped and dorso-ventrally flattened.

Kiwi (*Apteryx mantelli, A. australis, A. haastii, A. owenii*)	(Mccann, 1973)	No literature	(Owen, 1879)	(Forbes, 1881)	Syrinx lacked extrinsic muscle and had no well-developed pessulus. The tongue included a large laryngeal pad posterior to the glottis. Three quarters of the tongue was cartilaginous with a depression running posteriorly until reaching the fleshy portion of the tongue. Overlapping cartilage rings were present in the trachea. The trachea gradually narrows distally.
Rhea (*Rhea americana*)	(Crole & Soley, 2012b; Rodrigues et al., 2012; Santos et al., 2011; Smith, 2018; Tomlinson, 2000)	(Crole & Soley, 2012b; Fowler, 1991; Rodrigues et al., 2012)	(Picasso & Carril, 2013; Sousa et al., 2018)	(Forbes, 1881; Picasso & Carril, 2013; Sousa et al., 2018)	Tracheobronchial syrinx type. Bell shaped oropharyngeal cavity; tongue filled with salivary glands and hyaline cartilage found internally. The trachea was formed into a slightly flattened oval shape. The cartilage of the tracheal rings overlapped and was covered by a thin epithelial layer.
Cassowary (*Casuarius casuarius*)	No literature	(McInerney et al., 2019)	(Forbes, 1881)	(Forbes, 1881; McInerney et al., 2019)	Ossification of the last tracheal and first bronchial cartilage found in the syrinx. The end of the trachea developed into an expanded tympanum. There was no pessulus in the syrinx. The tracheal rings were dilated compared to other palaeognathous birds.

In particular, there are no studies on vocal modulation of paleognath calls via the tongue. This has resulted in sparse literature surrounding kiwi oral anatomy for the tongue, bill, and oropharynx with exceptions including a description of the bill tip organ found in brown kiwi used in feeding (Cunningham et al., 2013).

2.2.5 Kiwi vocalisations and vocal tract anatomy

Brown kiwi are strongly sexually dimorphic in both physical features and behaviour, with differences in vocalisations, weight, and bill length between the sexes being well-known (Fraser & Robertson, 2009).

Vocal analysis of three species of kiwi, brown kiwi, little spotted kiwi (*Apteryx owenii*), and great spotted kiwi (*Apteryx maxima*) have been conducted to date. Of these analyses, all show that there are sexually dimorphic calls between the males and females of their respective species (Corfield, 2004; Dent & Molles, 2015; Digby et al., 2013). Qualitative descriptions of the calls of brown kiwi agree that males produced a "shrill whistle call" with frequency range of ~1.5 kHz to ~13 kHz and females produced a "hoarse series of croaks" with frequency range of ~0.1 kHz to ≤7.0 kHz (Figure 2-2; Colbourne & Kleinpaste, 1984; Corfield, 2004; Corfield et al., 2008; Taborsky & Taborsky, 1992). While variation in calls between species has not been studied, in a Northland population male brown kiwi calls contained an average of 24 syllables, while female calls contained an average of 22 syllables (Corfield, 2004). In the same study, male and female calls also vary in fundamental frequency with male calls ranging from 398-2911 Hz whereas female calls ranged from 90-4150 Hz (Corfield, 2004).

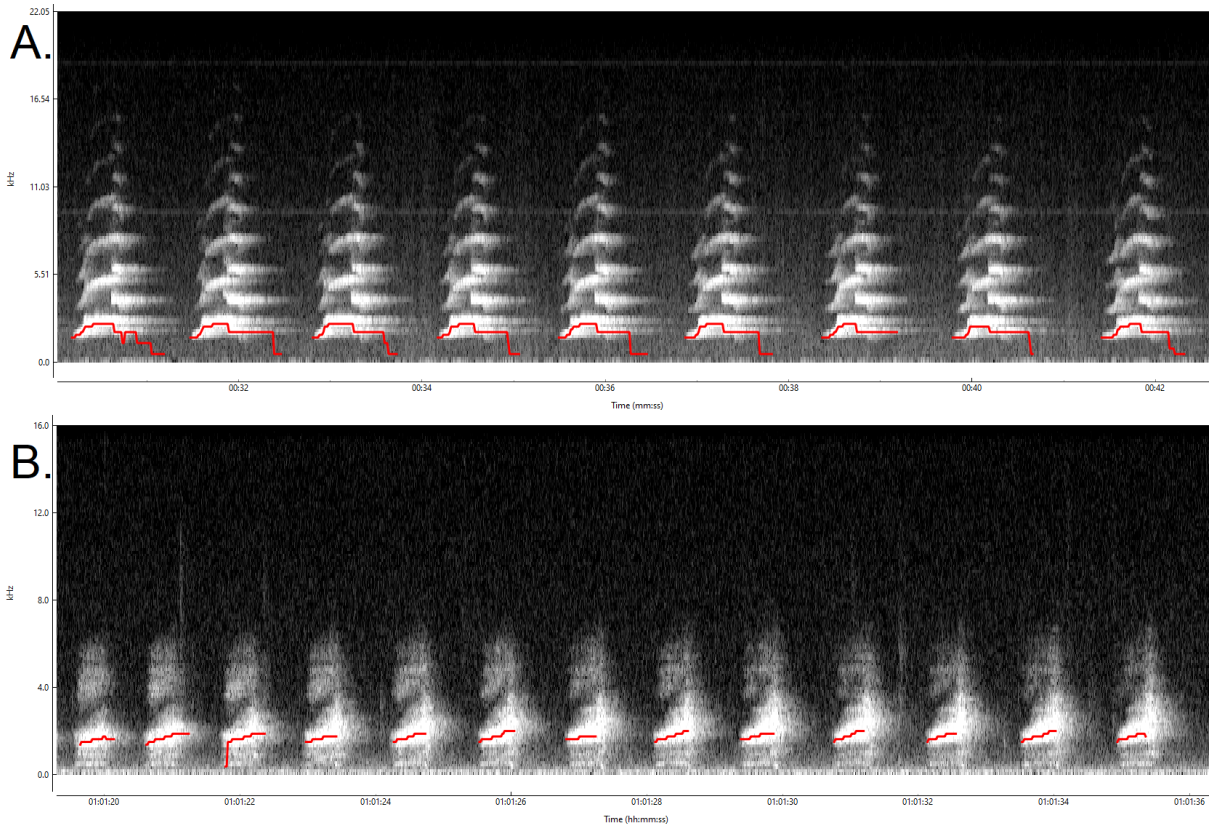

Figure 2-2) Spectrograms of kiwi calls. **(A)** Shows a segment of a male brown kiwi call with the red line showing the fundamental frequency of the call. **(B)** Shows a segment of a female brown kiwi call with the red line showing the fundamental frequency.

The current knowledge of kiwi vocal anatomy consists of a description of the syrinx cartilage with comparisons made to other paleognaths such as the cassowary and ostrich (Forbes, 1881). Tissues of the syrinx were noted but were limited to fundamental descriptions discussing presence and absences of sections of the tract and showing the locations of the components of the vocal tracts of different species (Forbes, 1881). The main gaps in the study of vocal tract anatomy in brown kiwi include information about the kiwi trachea and its associated tissues, information about the tissues and membranes of the syrinx, and information about the general morphology of the oropharyngeal cavity.

In this study, we describe the vocal tract of the brown kiwi and discern differences between male and female specimens, as well as highlight differences from other members of the

Palaeognathae group and birds more generally. Detailed morphological and histological analyses of the vocal tract are critical for understanding how its structure shapes sound production, as variations in its anatomy and tissue composition directly affect vocal characteristics (Fant 1960). Moreover, morphological variation in the vocal tract (including differences in tube lengths and cross-sectional areas) directly shapes acoustic resonances such as formants, enabling the production of distinct vocal signatures that allow individual recognition across animal species (Garcia and Favaro, 2017).

An updated description of the vocal anatomy could identify common or novel vocal characteristics across all *Apteryx* species. This would allow for use in taxonomy as morphological characteristics can be used alongside genetic data (Padial et al., 2010) to better inform the relationships of *Apteryx* to other paleognathous birds and potentially beyond. Morphological investigations may also uncover the mechanisms present that contribute to the sexually dimorphic kiwi vocal production (Corfield et al., 2008; Dent & Molles, 2015; Digby et al., 2013; Digby, Bell, et al., 2014a).

2.2.6 Research aims

As a result of the gaps elucidated in the literature review, this study proposes to investigate the brown kiwi vocal anatomy to provide a basis for future taxonomic, anatomical, and behavioural research. I seek to do this by describing the brown kiwi vocal tract to highlight any differences between the male and female vocal anatomy. To answer the questions:

1. Could the source of brown kiwi's sexually dimorphic calls result from anatomical differences?
2. Does the brown kiwi vocal anatomy differ from that of other Paleognaths?

2.3 Materials and Methods

2.3.1 Specimen sourcing

Studies of kiwi face various limitations with the primary ones being the scarcity of specimens and the condition of specimens. Kiwi are often victims of predation and thus specimens available are decayed or eaten partially. Specimens are most often available frozen, and therefore likely to have damaged mucous membranes limiting the ability to describe tissues within the vocal tract accurately and thoroughly. Nevertheless, seven brown kiwi (4 female, 3 male; Table 2-3 & 2-4) from various North Island sources (Ponui Island, Tongariro National Park; Table 2-2) submitted to Wildbase Pathology, Massey University, for postmortem examination, were used as the study material for this research. The anatomical data was collected from January 2022 to June 2023 from various male and female specimens.

Table 2-2: Specimen ID with source location.

Bird ID:	Sex:	Source:	Extra notes:
F-BK-SP-VA-1	Female	South Ponui	Missing syrinx
F-BK-NP-VAG-2	Female	North Ponui	
F-BK-NatP-VAG-4	Female	National Park	
F-BK-SP-VAG-7	Female	South Ponui	
M-BK-SP-VAG-1	Male	South Ponui	Broken bill
M-BK-SP-VA-4	Male	South Ponui	
M-BK-SP-VAG-5	Male	South Ponui	

2.3.2 Bird and vocal tract morphometrics

Prior to dissection, the body weight, the length and width of the head, length of the bill, width at the widest point of the bill. Tarsus length was measured from the base of the foot to the joint of the tarsometatarsus and tibiometatarsus. Tarsus width was measured from the lateral sides of the tarsus. Tarsus depth was measured from the cranial to caudal face of the tarsus. All measurements were taken by the same operator using callipers and repeated three times,

to compare specimens and assign sex. Sex was assigned by bill length and by visual confirmation of gonads during dissection. Male birds had bills between 85 mm and 116 mm and females had bills longer than 117 mm (Colbourne & Kleinpaste, 1983; Reid & Williams, 1975).

2.3.3 Dissection process

The thorax was opened on the ventral surface shallow enough to cut only the skin. The cut was extended from the cloaca to the bill and the vocal tract was removed intact. The extracted tract included the tongue and lower palate, the trachea, and the syrinx with 10mm of bronchi attached.

Once dissected, the removed vocal tract was arranged on a flat surface and aligned to be parallel to the ruler used for scale in images. Photographs of the dissections were taken using a camera (Oppo AX5, Canon EOS 1100D, Figure 2-3A, B & C), with each view having a 30cm ruler or 20cm set of callipers to provide scale. ImageJ (Schneider et al., 2012) was used to gather measurements after the dissections if some were missed. Measurements of the histological analysis and adjustments of the scale bar were also made using ImageJ by measuring the original scale bar produced by CellSens standard (Olympus, 2024), cropping the image, and creating a more visible scale bar using the original scale bar for size reference. The resulting measurements were collated into Microsoft Excel (Microsoft Corporation, 2023), where the data were averaged across the three measurements, and the standard error was then calculated for each sex group.

Trachea start width was measured where the trachea meets the glottal opening on the ventral surface (Figure 2-3A). Trachea end width was measured where the trachea begins to bifurcate into the bronchi. The trachea length was measured from where the trachea meets the glottal opening, caudomedially until the start of the bifurcation was met. Tongue length was

measured in two ways (Figure 2-3B): (i) from the cartilaginous tip of the tongue to the cranial-most point of the glottal opening, (ii) starting from the same point and then measuring to the caudal-most point of the pharyngeal fold (typically caudally along the midline). The syrinx length and width were measured as shown in Figure 2-3C. The length was chosen by using the change in cartilage shape and then measured caudomedially till the pessuliform process was reached. The width was chosen by taking the bulge produced by the largest syringeal cartilage and measuring transversely across the syrinx.

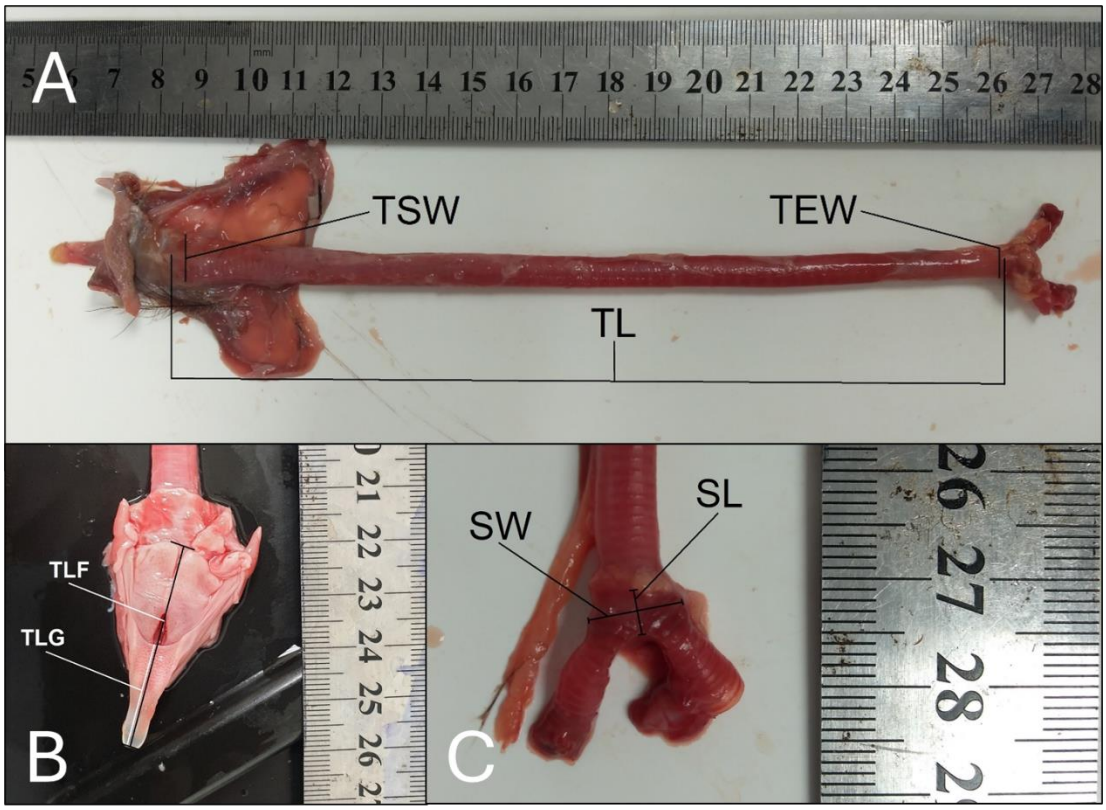

Figure 2-3) (A) The dissected vocal tract of a brown kiwi ventral view. **TSW**: width at the start of the trachea. **TEW**: width at the end of the trachea. **TL**: trachea length. **(B)** Dissected tongue and trachea of a brown kiwi dorsal view. **TLF**: tongue length from pharyngeal folds to tongue tip. **TLG**: tongue length from the opening of the glottis. **(C)** Dissected syrinx and trachea of a brown kiwi dorsal view. **SW**: syrinx width. **SL:** syrinx length.

2.3.4 Sectioning for histology

After measuring and photographing, the vocal tract was excised and fixed in a 10% neutral buffered formalin solution for a minimum of three days before sectioning. Transverse and longitudinal sections of the trachea were taken recording the dorsal and ventral surfaces and approximate distance from the pharyngeal junction. The sections taken from the trachea were approximately 3.75mm long to fit the cassette with room to fit multiple sections per cassette to better utilise space. The syrinx was sectioned by cutting 1.5cm anterior to the bifurcation, including a small piece of trachea to highlight the differences in cartilage between syrinx and trachea.

Once detached from the trachea, the syrinx was cut laterally with care taken not to tear the tissue wall in the pessulus region as this was notably fragile. The hyoid bone was removed from the tongue and some blocks were decalcified if necessary to prevent tearing of ossified cartilage. All tissues were processed routinely into paraffin and 4µm sections were cut and stained with H & E as well as Masson's trichrome to identify collagen (Culling et al., 2014).

2.3.5 Statistics

The data was analysed using R Studio (R Core Team, 2022) using a Mann-Whitney U test to test for differences between the sexes, with the independent variable being sex, and the dependent variables being anatomy features such as bill, tarsus, and syrinx measurements (width, length, and occasionally depth). The Mann-Whitney U test was chosen as it works for two independent samples that do not follow a normal distribution. For a test of normality, the Shapiro-Wilk test was used as it is suitable for small sample sizes.

2.4 Results

2.4.1 General morphology

The morphometrics of the birds sampled did not differ greatly from the general morphology of the brown kiwi (Tables 2-3 & 2-4). The trend for the results shows a pattern of male and female morphometrics being proportionate to each other except in the cases of bill length, and the area of the lateral labia (Fig. 2-4). Testing the dataset of all morphometrics showed that all but tongue length to tip were normally distributed (Table 2-5). The females were larger in general, with disproportionately large bill length, but not to a statistically significant degree probably due to the small sample size and the possible inclusion of juvenile animals in the sample (Fig. 2-4, Table 2-6).

Table 2-3: Measurements of female body and vocal tract characteristics.

Bird ID:	F-BK-SP-VA-1	F-BK-NP-VAG-2	F-BK-NatP-VAG-4	F-BK-SP-VAG-7	Mean of female specimens with standard deviation
Weight (Kg)	2.59	2.85	1.88*	2.58	2.47 ± 0.42
Bill length (mm)	129	119.27	130.40	121.78	125.11 ± 5.42
Bill depth (mm)	NC	15.11	14.70	13.47	14.43 ± 0.86
Bill width (mm)	NC	30.48	29.02	28.15	29.22 ± 1.18
Head length (mm)	NC	68.94	65.60	68.98	67.84 ± 1.94
Head width (mm)	NC	35.41	34.73	35.47	35.20 ± 0.41
Tarsus depth (mm)	21	18.86	14.9	18.2	18.24 ± 2.53
Tarsus width (mm)	16	14.67	11.80	15.43	14.48 ± 1.87
Tarsus length (mm)	90	96.45	95.55	95.57	94.39 ± 2.96
Trachea start width (mm)	9.61	11.24	11.93	10.30	10.77 ± 1.02
Trachea end width (mm)	5.19	5.48	6.2	6.9	5.94 ± 0.77
Trachea length (mm)	153.95	178	182.10	150.26	166.08 ± 16.85
Tongue length tip to fold (mm)	50.16	42.2	42.56	39.21	43.53 ± 1.4.67
Tongue length glottis to tip (mm)	30.80	20.73	21.70	22.81	24.01 ± 4.6
Syrinx length (mm)	NC	6.59	8.32	6.39	7.10 ± 1.06
Syrinx width (mm)	NC	8.15	9.97	9.59	9.24 ± 0.96
Average area of lateral labia (mm^2)	NC	0.936	2.242	0.39	1.19 ± 0.95

*This specimen was underweight, which probably affected the tarsus depth and width measurements. NC = not collected, refers to parts of the anatomy that could not be measured due to damage/injury, or if the feature was missing.

Table 2-4: Measurements of male body and vocal tract characteristics.

Bird ID:	M-BK-SP-VAG-1	M-BK-SP-VA-4	M-BK-SP-VAG-5	Mean of male specimens with standard deviation
Weight (Kg)	1.80	1.65	1.54	1.66 ± 0.13
Bill length (mm)	NC	87.3	92.83	90.07 ± 3.91
Bill depth (mm)	13.95	12.58	13.97	13.5 ± 0.79
Bill width (mm)	29	28.37	23.4	26.92 ± 0.45
Head length (mm)	63.2	64.57	65.03	64.27 ± 0.95
Head width (mm)	31.5	33.43	32.67	32.53 ± 0.97
Tarsus depth (mm)	15.2	15.2	13.3	15.79 ± 1.1
Tarsus width (mm)	12.2	12.64	10.17	11.67 ± 1.32
Tarsus length (mm)	88.55	93.20	83.17	90.94 ± 5.02
Trachea start width (mm)	11.53	10.34	9.71	10.53 ± 0.92
Trachea end width (mm)	6.57	5.90	6.38	6.28 ± 0.34
Trachea length (mm)	155	176.81	148.27	160.03 ± 14.92
Tongue length tip to fold (mm)	42.17	39.56	35.97	39.23 ± 3.11
Tongue length glottis to tip (mm)	19.85	21.07	21.72	20.88 ± 0.95
Syrinx length (mm)	6.84	6.29	5.26	6.13 ± 0.8
Syrinx width (mm)	8.62	8.91	8	8.51 ± 0.47
Average area of lateral labia (mm^2)	1.70	1.896	3.689	2.428 ± 1.1

Table 2-5: Results of the Shapiro-Wilks normality test.

MORPHOMETRIC	W STATISTIC	P VALUE	NORMALITY
WT	0.872	0.193	Normal
BL	0.833	0.114	Normal
BD	0.970	0.895	Normal
BW	0.799	0.057	Normal
HL	0.875	0.247	Normal
HW	0.914	0.463	Normal
TD	0.922	0.489	Normal
TW	0.943	0.662	Normal
TL	0.893	0.290	Normal
TCSW	0.918	0.451	Normal
TCEW	0.973	0.921	Normal
TCL	0.821	0.065	Normal
TLTP	0.899	0.325	Normal
TLTG	0.692	0.003	Not Normal
SL	0.925	0.540	Normal
SW	0.938	0.644	Normal
SA	0.951	0.735	Normal

Table 2-6: Mann-Whitney U test for significant differences in vocal tract component size.

Morphometrics	Males	Females	M (n)	F (n)	U	P value
Weight (Kg)	1.66 ± 0.13	2.47 ± 0.42	3	4	12	0.05714
Bill length (mm)	90.07 ± 3.91	125.11 ± 5.42	2	4	8	0.1333
Bill width (mm)	13.5 ± 0.79	14.43 ± 0.86	3	3	7	0.4
Bill depth (mm)	26.92 ± 0.45	29.22 ± 1.18	3	3	7	0.4
Head width (mm)	64.27 ± 0.95	67.84 ± 1.94	3	3	9	0.1
Head length (mm)	32.53 ± 0.97	35.20 ± 0.41	3	3	9	0.1
Tarsus length (mm)	90.94 ± 5.02	94.39 ± 2.96	3	4	10	0.2218
Tarsus width (mm)	11.67 ± 1.32	14.48 ± 1.87	3	4	10	0.2286
Tarsus depth (mm)	15.79 ± 1.1	18.24 ± 2.53	3	4	11	0.1143
Trachea start width (mm)	10.53 ± 0.92	10.77 ± 1.02	3	4	6	1
Trachea end width (mm)	6.28 ± 0.34	5.94 ± 0.77	3	4	4	0.6286
Trachea length (mm)	160.03 ± 14.92	166.08 ± 16.85	3	4	8	0.6286
Tongue length tip to fold (mm)	39.23 ± 3.11	43.53 ± 1.4.67	3	4	10	0.2286
Tongue length tip to glottis (mm)	20.88 ± 0.95	24.01 ± 4.6	3	4	9	0.4
Syrinx length (mm)	6.13 ± 0.8	7.10 ± 1.06	3	3	7	0.4
Syrinx width (mm)	8.51 ± 0.47	9.24 ± 0.96	3	3	7	0.4
Lateral Labia area (mm^2)	2.428 ± 1.1	1.19 ± 0.95	3	3	2	0.3827

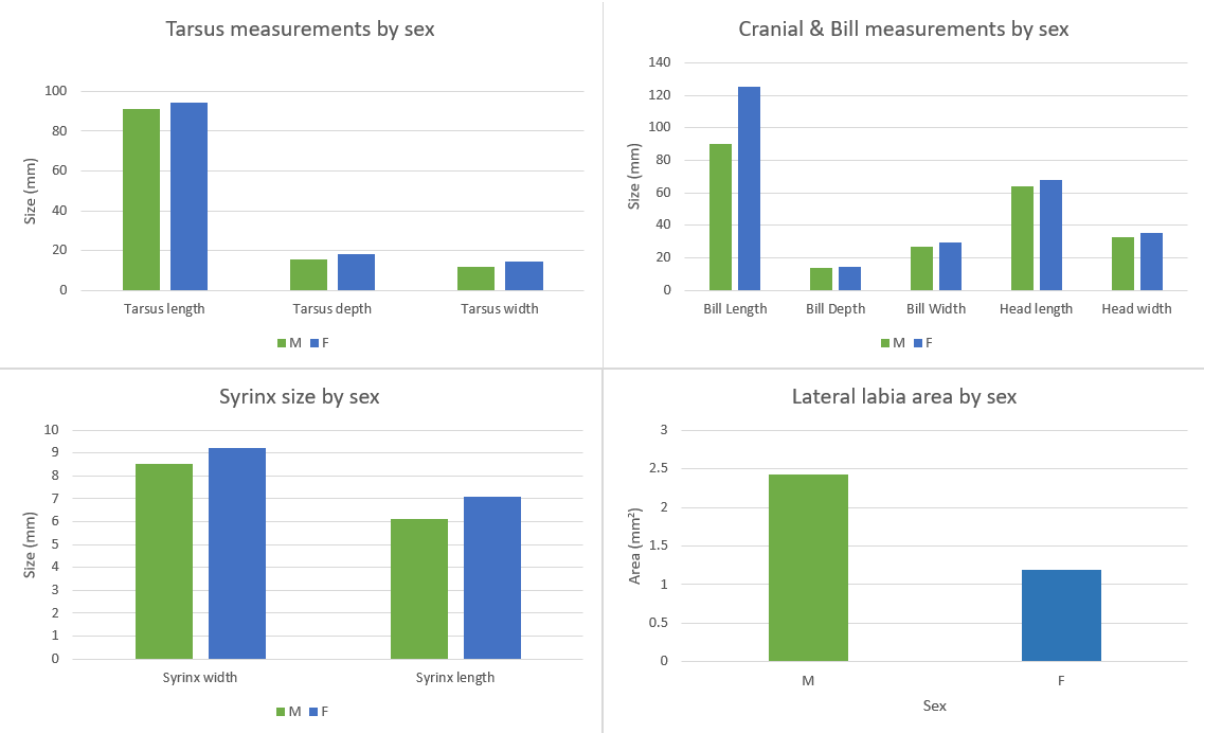

Figure 2-4) Graphs showing sample measurements of brown kiwi morphological characters with standard errors. Graphs are grouped by tarsus measurements, cranial & bill measurements, syringeal measurements, and lateral labia area.

2.4.2 Syrinx

The syrinx mucosal surface was lined by ciliated pseudostratified columnar epithelium, which differentiated to stratified squamous epithelium along the lateral labium and then returned to pseudostratified columnar epithelium once reaching the bronchi (Fig. 2-5A). The lateral labium comprised areas with different types of collagen fibres (Fig. 2-5B). Fibres towards the lumen of the syrinx were less densely packed and were loose elastic and collagen fibres that form the lamina propria. Further from the lumen of the syrinx were multiple irregular tight bundles of collagen forming a layer of greater density than that of the lamina propria. The size and extent of the layers of differing densities varied between individual specimens with the separation being more noticeable in male specimens.

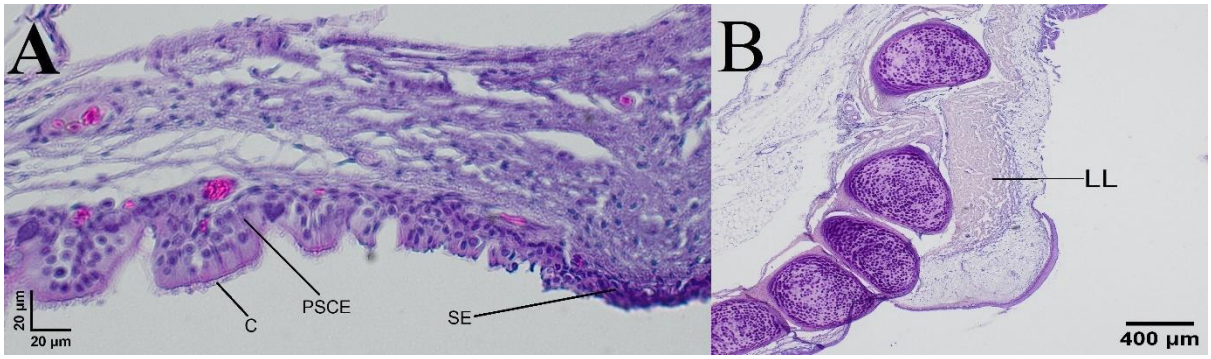

Figure 2-5) (A) The dorsal view of the epithelial lining of a female brown kiwi (F-BK-SP-VAG-7) syrinx, stained with H&E. **C**: cilia of the ciliated pseudostratified columnar epithelium. **PSCE**: ciliated pseudostratified columnar epithelium of the respiratory tract changing into the **SE**: squamous epithelium of the medial labia. **(B)** Ventral view of a male brown kiwi (M-BK-SP-VA-4) syrinx, stained with H&E cut on the frontal plane. **LL**: Lateral labium, the epithelial layer is damaged, but the size of the labium is comparable to the cartilage.

The cartilaginous pessulus in brown kiwi was absent. In its place there was a pessuliform process (following the terminology of Forbes (1881)). The pessuliform process was a projection of submucosal connective tissue covered by a thickened and folded, respiratory epithelium (Fig. 2-6A). It had a core of 2 to 10 tight bundles of collagen resembling a tendon joining similar bundles running down the medial bronchial submucosa. In one specimen there was a small cartilaginous remnant at the base of the membrane (Fig. 2-6B) where the pessulus normally meets the interclavicular air sac in other species.

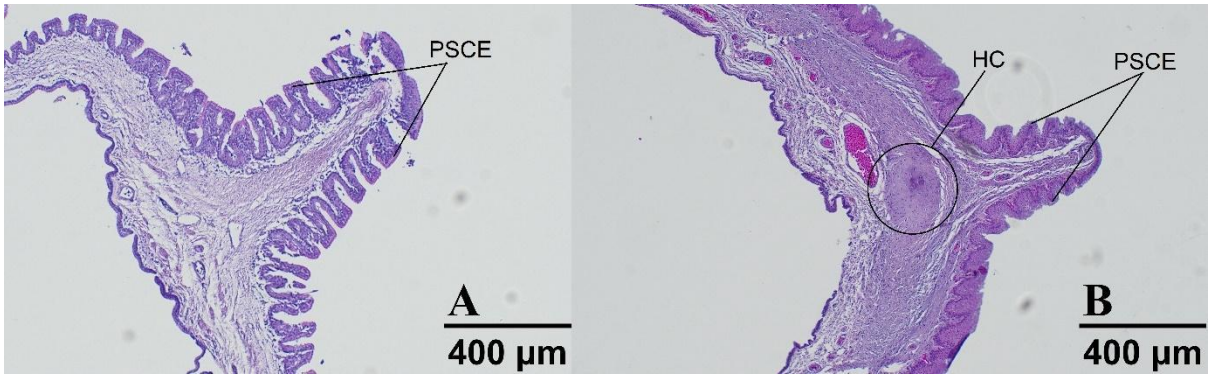

Figure 2-6) (A) Dorsal view of a male brown kiwi (M-BK-SP-VA-4) pessulus region, cut on the frontal plane, and stained with H&E. **PSCE**: Pseudostratified columnar epithelium. **(B)** Dorsal view of a female brown kiwi (F-BK-SP-VAG-7) pessulus region, cut on the frontal plane, and stained with H&E. **PSCE**: Pseudostratified columnar epithelium. **HC**: Hyaline cartilage.

The hyaline cartilaginous rings of the syrinx could be differentiated from those elsewhere by shape, forming wedge-shaped cross sections as opposed to more oblong shapes found in the bronchi and trachea. In addition to the lateral and medial labia, there were the *membrana tympaniformis lateralis* and *membrana tympaniformis medialis*. The lateral tympaniform membrane was found in the gaps between the cartilage of the syrinx, from the medial labia. The *membrana tympaniformis medialis* was situated caudally to the medial labium (Fig. 2-7).

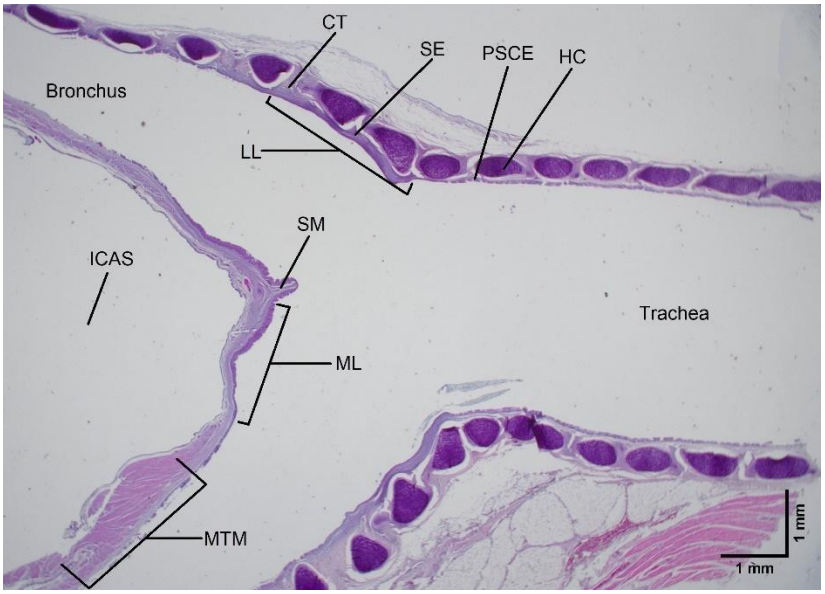

Figure 2-7) Dorsal view of the syrinx of a female brown kiwi (F-BK-SP-VAG-7) stained with H&E. **HC**: Hyaline cartilaginous rings supported the vocal tract from trachea to the bronchi. **CT**: Loose connective tissue filled the gaps between the hyaline cartilage. **SM**: Pessuliform process. **ML**: Medial labium. **LL**: Lateral labium. **ICAS**: Interclavicular air sac. **PSCE**: Ciliated pseudostratified columnar epithelium. **SE**: Squamous epithelium. **MTM**: *Membrana tympaniformis medialis*.

The lateral labia of the syrinx differed in total area between males and females (Fig. 2-8A & B, Table 5). The area of the lateral labia for males on average was larger than the females (Male = 2.428 mm^2 ± 1.1, Female = 1.19 ± 0.95 mm^2). This size difference was not significant possibly due the small sample size and the possible inclusion of juvenile animals in the sample (Mann-Whitney U test; U = 2; n = 6; p-value = 0.3827).

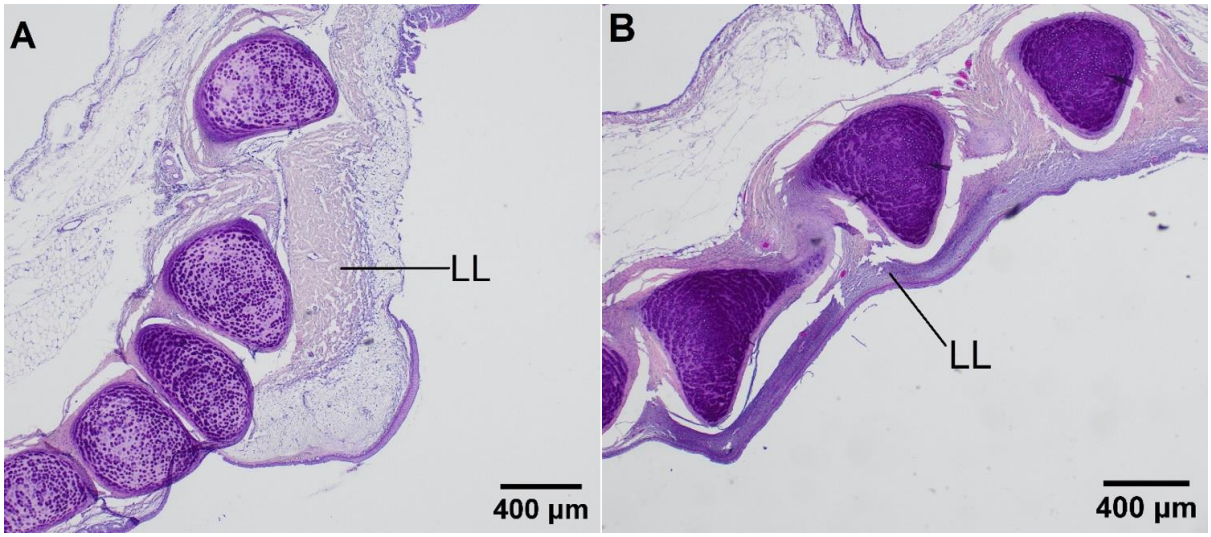

Figure 2-8) (A) Ventral longitudinal section of a male brown kiwi (M-BK-SP-VA-4) syrinx stained with H&E cut in the frontal plane. **LL**: Lateral labium, the epithelial layer was damaged, but the size of the labium was comparable to the cartilage. **(B)** Ventral view of a female brown kiwi (F-BK-SP-VAG-7) syrinx stained with H&E cut on the frontal plane. **LL**: Lateral labium was much thinner than that of the males.

2.4.3 Trachea

The trachea of the brown kiwi was lined with pseudostratified ciliated columnar epithelium that folded into crypts and peaks when collapsed (Fig. 2-9B). This epithelial layer lined the trachea and the bronchi, and therefore will be called respiratory epithelium. The cartilage of the tracheal rings overlapped when the trachea was folded and interlocked with the adjacent cartilage. The rings were triangular in a transverse section with the longest flat side alternating in position likely to allow for collapse and extension of the trachea. This was likely to be activated by the longitudinal striated muscle layer that lay adjacent to the cartilage. Circular striated muscle was also present in small clumps peripherally to the longitudinal muscle layer (Fig. 2-9A & Fig. 2-9C). At the base of the trachea, where it connected into the oral cavity via the larynx, there was a small, serrated ridge composed of an unknown solid material that ran medially down a small section of the larynx before it transitioned to the trachea. This ridge partially divided the laryngeal chamber as the ridge did not reach the dorsal surface of the larynx.

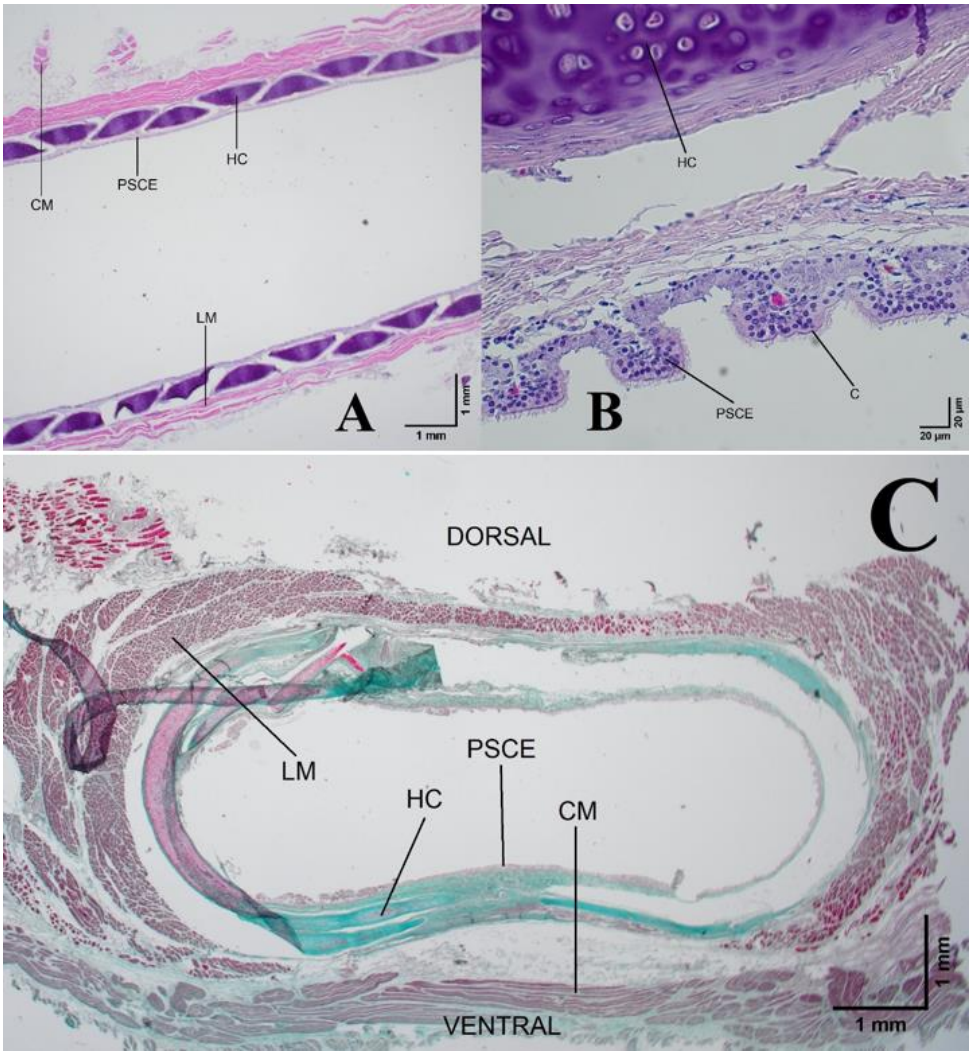

Figure 2-9) (A) Female brown kiwi (F-BK-SP-VAG-7) trachea cut on the frontal plane, stained with H&E. **HC**: Hyaline cartilage. **PSCE**: Ciliated pseudostratified columnar epithelium. **LM**: Longitudinal striated muscle. **CM**: Circular striated muscle. **(B)** Dorsal view of the syrinx of a female brown kiwi (F-BK-SP-VAG-7) stained with H&E. **HC**: Hyaline cartilage. **PSCE**: Ciliated pseudostratified columnar epithelium. **C**: Cilia. **(C)** Transverse view of the trachea of a male brown kiwi (M-BK-SP-VAG-5) stained with Masson's trichrome. **LM**: Longitudinal striated muscle. **CM**: Circular striated muscle. **HC**: Hyaline cartilage. **PSCE**: Ciliated pseudostratified columnar epithelium.

2.4.4 Bronchi

The bronchi were supported by C-shaped cartilage and lined with a pseudostratified columnar epithelium similar to the tracheal epithelium. The only part of the bronchi that lacked cartilage was the cranial medial section where the *membrana tympaniformis lateralis* was located (Fig. 2-10).

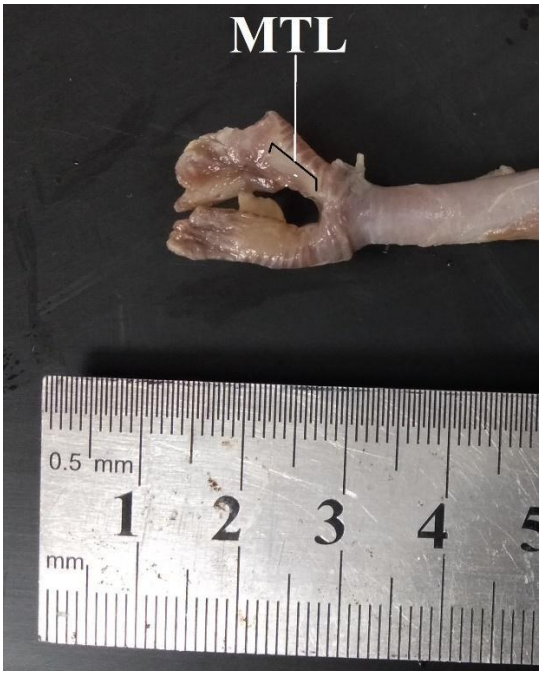

Figure 2-10) Ventral view of a male brown kiwi (M-BK-SP-VAG-1) syrinx with the medial tympaniform membrane shown as **MTL**.

2.4.5 Tongue & Palate

The oral cavity could be divided into easily recognisable sections; the tongue tip, the muscular section of the tongue, and the two pairs of pharyngeal folds that were found with one pair caudal to the choana on the upper palate and one pair caudal to the glottis on the lower palate. The entire tongue and the four pharyngeal folds were lined with keratinised stratified squamous epithelium.

The tip of the tongue had a thin layer of secretory cells forming glandular acini beneath the dorsal layer of epithelium (Fig. 2-11A). The epithelium dorsal to the cartilaginous tip was thickened and showed evidence of dense keratinisation (Fig. 2-11C). The remainder of the tongue tip was dominated by a large cartilaginous plate that formed a spade-like shape when viewed dorsally (HC in Fig. 2-11B, although note that only half of the spade is visible).

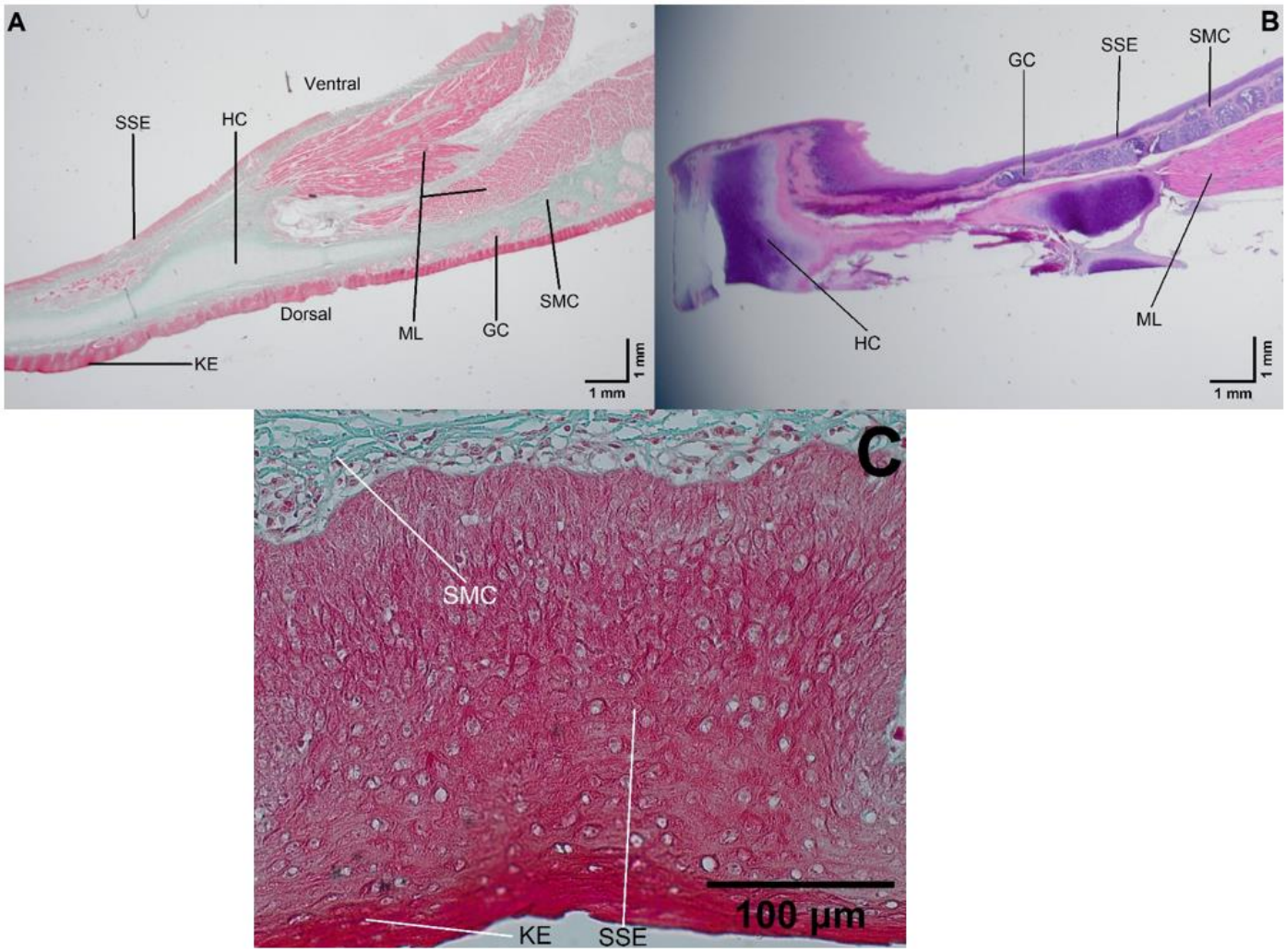

Figure 2-11) (A) Section of male brown kiwi (M-BK-SP-VA-4) tongue cut on the sagittal plane, stained with Masson's trichrome. **(B)** Half a section of female brown kiwi (F-BK-SP-VAG-7) tongue cut on transversely, stained with H&E. **SSE**: Stratified squamous epithelium. **HC**: Hyaline cartilage. **KE**: Keratinised epithelium (staining as densely eosinophilic tissue). **GC**: Secretory glands. **ML**: Longitudinal striated layer. **SMC**: *Lamina propria*. **(C)** Section of male brown kiwi (M-BK-SP-VA-4) tongue cut on the sagittal plane, stained with Masson's trichrome. **SMC**: Submucosal collagen layer (*Lamina propria*). **SSE**: Submucosal squamous epithelium layer. **KE**: Keratinised epithelium.

The muscular section of the tongue had three layers. The first was the oral epithelial layer which consisted of stratified squamous epithelium. Beneath this were glands of salivary secretory cells that lay superficially with ducts opening to the non-cartilaginous part of the tongue. Glands of secretory cells were also embedded in the second layer, which was the

submucosal connective tissue layer. Lastly, ventral to the submucosal layer was the muscular layer of the tongue, which consisted of longitudinal striated muscle that connected the cartilage at the tongue tip to cartilage present distal to the glottis. The longitudinal striated muscle contained groups of multidirectional fibres. The tip of the tongue was broad and spoon shaped, with a rigid cartilaginous tip. The tongue was relatively smooth aside from various small indentations found along the dorsal surface from the glottis to the beginning of the cartilaginous tip. Immediately caudal to the glottis on the lower and upper palate were four distinct, slightly raised folds. The folds were not symmetrical, and the line that divided the two adjacent folds was incomplete and became indistinct rostrally (Fig. 2-12A). The folds, like the muscular section of the tongue, were lined by stratified squamous epithelium that was folded caudally (pharyngeal folds) beneath which were large acini of secretory glands surrounding ducts with cilia in places located within a collagenous submucosal layer (Fig. 2-12D). The striated muscular layer (Fig. 2-12B) differed from that of the tongue in that it contained many secretory cells over a smaller area (Fig. 2-12C).

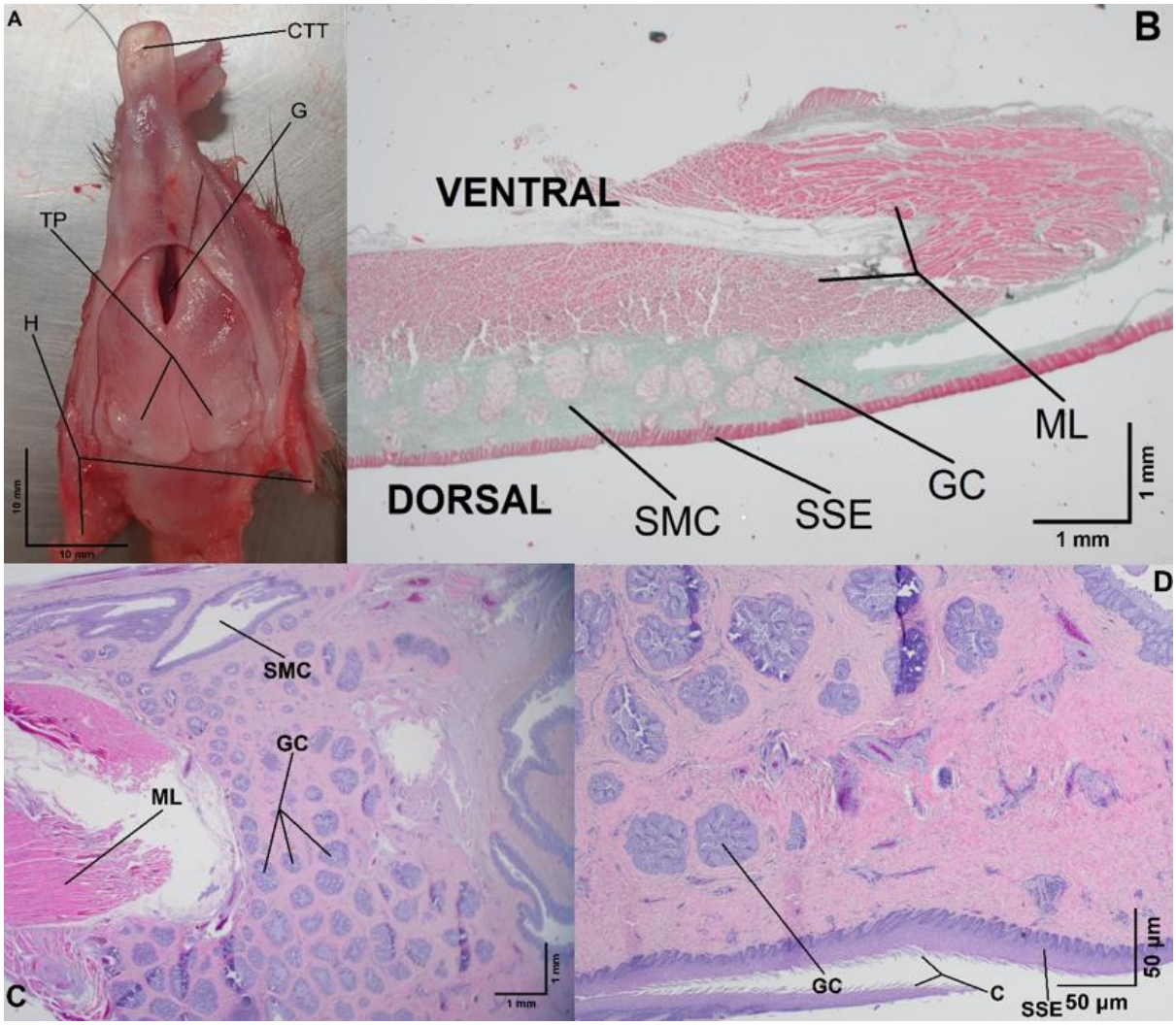

Figure 2-12) (A) Dorsal view of a female brown kiwi (F-BK-SP-VAG-7) tongue. **CTT**: Cartilaginous tongue tip. **G**: Glottis. **TP**: Pharyngeal folds **H**: Hyoid bone tips. **(B)** Section of the male brown kiwi (M-BK-SP-VA-4) pharyngeal fold cut along the sagittal plane stained with Mason's Trichrome. **SMC**: Submucosal collagen. **SSE**: Stratified squamous epithelium. **GC:** Secretory glands. **ML**: Circular striated muscle. **(C)** Section of the female brown kiwi (F-BK-SP-VAG-7) pharyngeal fold cut frontally, stained with H&E. **SMC**: Submucosal collagen. **GC**: Secretory glands. **ML**: Longitudinal striated muscle. **(D)** Section of the female brown kiwi (F-BK-SP-VAG-7) pharyngeal fold cut frontally, stained with H&E. **GC**: Secretory glands. **C**: Cilia. **SSE**: Stratified squamous epithelium.

The upper palate of the brown kiwi's mouth consisted of the medial nasal ridge that extended from the tip of the bill to the opening of the choana. The kiwi had two choanal slits like those found in ostrich, rhea, and emu (Crole & Soley, 2011, 2012a, 2012b). Past the choana were two pharyngeal folds that were separated by the infundibular cleft (Fig. 2-13).

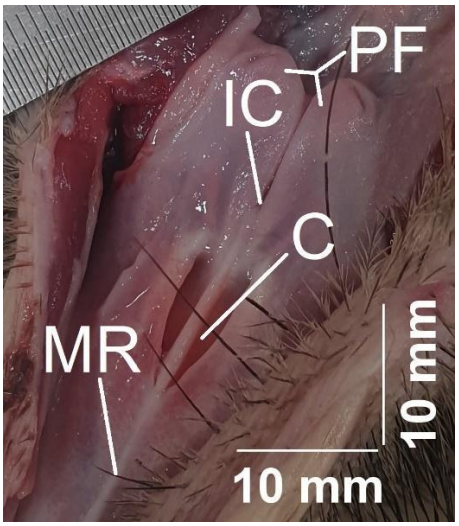

Figure 2-13) Upper palate of a female brown kiwi (F-BK-SP-VAG-7). **MR**: Medial nasal ridge. **C**: Choana. **IC**: Infundibular cleft. **PF**: Pharyngeal folds.

2.5 Discussion

The main findings of this anatomical study were the structure of the kiwi tongue, the structural differences between kiwi and other paleognaths studied, and the differences between the two sexes. In the next sections, I will focus on the findings of this study concerning our current knowledge of bird vocal anatomy, and paleognathous birds' vocal anatomy in particular.

2.5.1 Syrinx

In brown kiwi, the females seem to have a slightly larger syrinx, although this needs to be confirmed with a larger sample size. The difference in syrinx size may contribute to the production of sexually dimorphic calls. Mallard ducks (*Anas platyrhynchos;* Mohamed, 2017) present similar size dimorphism as well as dimorphic calls. There was also sexual dimorphism in lateral labia size, with males having larger labia than females, a feature that is not exhibited by the southern cassowary (previously known as *Casuarius galeatus*, now as *Casuarius casuarius*) the only other paleognath studied thus far (McInerney et al., 2019). Beani et al. (1995) reported that the increased levels of testosterone in male grey partridges (*Perdix perdix*) modified acoustic anatomical structures, with the lateral labia thickening resulting from additional testosterone. This suggests that differences in testosterone concentration in males may cause the variation in lateral labia size we noted between the sexes and possibly between individual males as well. Contrary to this finding, Dos Santos et al. (2023) found that testosterone only altered syrinx mass and the diameter of associated muscles in males, suggesting that testosterone may not account for the difference observed between male and female brown kiwi syrinx morphometrics. In addition, C. McLeod (pers. comm.) found that male and female kiwi testosterone levels are similar, also suggesting that other factors may be involved in the differences between the sexes.

Forbes (1881) highlighted differences in the cartilage between various ratite syringes (*Struthio camelus, Apteryx mantelli, Casuarius galeatus, Rhea americana*), with the ostrich's syrinx having comparatively thinner bronchial cartilage and greater spacing between rings. Brown kiwi also differs from cassowary, which has the last eleven visible tracheal cartilage rings being widely spaced and incomplete compared to the tightly packed, complete rings of brown kiwi. The cartilaginous rings of the brown kiwi syrinx are tightly packed at the tracheal end of the syrinx, but become less densely packed at the joining of the bifurcation, which continues until the semi-rings of cartilage become full rings again, past the medial tympanic membrane and into the bronchi.

The brown kiwi syrinx lacks a cartilaginous pessulus, also found lacking in tinamous, emu, and cassowary (Forbes, 1881; Garitano-Zavala, 2009; McInerney et al., 2019). Instead, a smaller mucosal projection was present where the pessulus is usually positioned and this could be termed a pessuliform process. A similar small cartilaginous process is also found in ostriches (Yildiz et al., 2003). Longtine et al. (2024) have recently described this in detail and suggested it may be vestigial and a cartilaginous pessulus may be ancestral to Aves. Of interest in our study, was the finding that one female brown kiwi specimen was observed to have a cartilage formation at the base of where the pessulus cartilage is normally positioned. The lack of a full pessulus may suggest that its role, which is to provide support for the medial tympaniform membranes (McInerney et al., 2019), is not needed in kiwi. Another feature that is absent in brown kiwi is the tympanum. This contrasts with the sparrowhawk (*Accipiter nisus*), which has very clear tympanic cartilage and a visibly elastic tympanic membrane (Ozudogru et al., 2015).

The medial labia, however, shares the same feature as the sparrowhawk, as both species medial labia have the side facing into the syrinx lined with epithelium, and the side facing the interclavicular air sac lacking epithelium (Ozudogru et al., 2015). The medial tympanic

membrane follows suit, and both membranes are lined with epithelium on both sides (Ozudogru et al., 2015). Brown kiwi also have a pessuliform process with a core of connective tissue instead of cartilage. The runs from the ventral surface of the syrinx to the dorsal surface of the syrinx acting as a connective tissue divider for the bronchi.

2.5.2 Oropharynx

The pharyngeal folds were found in two pairs, one pair on the dorsal surface, caudal to the choana, and one pair on the ventral surface, caudal to the glottis. This is different to all other paleognaths, as emu (*Dromaius*), ostrich (*Struthio*), and rhea (*Rhea*) have one pair of pharyngeal folds which in these groups, contain true pharyngeal tonsils (Crole & Soley, 2012a; Rodrigues et al., 2012). If the pharyngeal folds of kiwi also contained lymphoid tissue and mucus-secreting glands, they too could be considered true pharyngeal tonsils (Crole & Soley, 2012a; Rodrigues et al., 2012). Tonsils would likely not play a role in vocalisations for kiwi but instead function as a core component of the kiwi immune system as they are positioned at the opening of the choana and oesophagus, where they would have a role in identifying antigens that are potential threats to kiwi health (Scadding, 1990).

2.5.3 Trachea

Much like the trachea of the ostrich, the brown kiwi's trachea was also a long flexible, cylindrical cartilaginous tube (Jayachitra, 2007) that extends from the glottis caudally to the syrinx. The brown kiwi's trachea was composed of many complete cartilaginous rings that gradually decrease in diameter as they get closer to the syrinx, like the emu's trachea (Jayachitra & Balasundaram, 2015). Unlike the emu, however, the brown kiwi trachea did not feature a tracheal pouch, characterised by incomplete cartilaginous rings found along the trachea (Jayachitra & Balasundaram, 2015). We found that the trachea, at a sub-gross level was composed of many overlapping cartilaginous rings, possibly allowing for extension of

the trachea. This is supported by the presence of longitudinal and circular striated muscle in the trachea and a markedly folded tracheal epithelium when at rest and these features would potentially allow for its expansion and contraction during vocalisation. The result of the muscular control of the trachea would be elongation during calls, which would increase tracheal length in turn causing a lower frequency of calls to be produced in addition to an increase of amplitude during vocalisations (Fitch, 1999; Gaunt et al., 1987). Behavioural observations of kiwi calling support this as they show that kiwi raise their head, extending their neck (Cunningham & Castro, 2011), resulting in trachea extension or expansion.

The overlapping cartilage of the trachea is unlike that of both ostrich and emu (Jayachitra, 2007; Jayachitra & Balasundaram, 2015) but was similar to the overlapping tracheal cartilage found in the gray heron (*Ardea cinerea*). However, the heron's cartilage also features tracheal notches (Atalgin et al., 2021) that serve an unknown function.

Unique to the kiwi was the finding that the laryngeal cavity possesses cartilage, which was partially ossified, forming a toothy ridge (McInerney et al., 2019). The function of this toothy ridge is currently unknown.

2.5.4 Tongue

The tongue of the brown kiwi presented a broad spoon-shaped cartilaginous tip, a structure that is likely to aid in drinking or food manipulation but could also be used to modulate sounds during calling. The tongue could be moved by manipulations of the hyoid bones, either in isolation, or in conjunction with the muscles of the tongue. This would result in changes in the available area within the oropharyngeal cavity and thus modulate the resulting vocalisation (Beckers et al., 2004; Suthers et al., 2016).

The tongue of the brown kiwi lacked the spiked papillae, or any hair-like projections found in some other species of birds like American kestrels (*Falco sparverius*) or barn owls (*Tyto*

alba) (Johnston, 2014). Instead, the kiwi tongue was relatively smooth aside from various small indentations found along the dorsal surface from the glottis to the beginning of the cartilaginous tip. Johnston (2014) described ratite tongues as rudimentary given their short length relative to the bill length and suggested that the tongue played a minimal role in feeding (Johnston, 2014). If this were the case the kiwi tongue would be relatively unremarkable or somewhat featureless like the tongue of an ostrich which externally looks very plain, lacking spiked papillae, and in general being short and stumpy (Tivane et al., 2011). However, while kiwi tongues are similar in length to other paleognaths (Crole & Soley, 2009; Jayachitra et al., 2015; Rodrigues et al., 2012), relative to bill length they are proportionally much smaller. Further, while ostrich (*Struthio*) and rhea (*Rhea*) tongues may be rudimentary, kiwi tongues are specialised in shape. This may suggest functional use in vocalisations and food manipulation suggesting that ratite tongues are used for more functions than in catch-and-throw feeding. This is supported by the finding that the tongue is comprised of dense striated muscle, allowing for independent articulation of the tongue indicating possible use in both food manipulation and vocalisations.

While the kiwi tongue was relatively short compared to its bill length, it had the odd feature of a spoon-like cartilaginous tip which was supported by a bed of muscles caudally, providing a solid tip that could aid in prey manipulation or vocal modulation (McInerney et al., 2019). This exposed cartilage tip seems to be a feature unique to the kiwi within the birds of the ratite group.

Beckers et al. (2004), by replacing the syrinx with a speaker in dead parrots to precisely control the passage of sound through the vocal tract, found that the positioning of the tongue during calling had impacts on the frequency and amplitude of formants produced. This method could be used to help investigate the role of the kiwi's tongue. Video recordings of

vocalising kiwi also suggest that the tongue is used in modulation, as it moves during the call production (I. Castro, pers. comm.).

Another point of interest was the relative thinness of the lingual epithelium when compared to species like the domestic goose, which has a thick dorsal epithelium layer that is used in food manipulation (Jackowiak et al., 2011). The thickened epithelial layer of the tongue is not strictly limited to those birds with a herbivorous diet, as this feature is also found in the white-tailed eagle (*Haliaeetus albicilla*; Jackowiak & Godynicki,(2005).

The kiwi tongue epithelium differs from that of ostrich and emu (Crole & Soley, 2009; Jackowiak & Ludwig, 2008). These authors found that the dorsal epithelium of ostrich and emu species, respectively, was thicker than that of the ventral surface, which does not appear to be the case in kiwi. The dorsal epithelium on the kiwi tongue showed keratinisation dorsal to the cartilage of the tongue, potentially suggesting rigidity on the dorsal surface but not on the ventral. The thin epithelium and lack of keratinisation would make the tongue of kiwi flexible and thus more capable of movement for prey handling. In addition, it may allow the tongue to vibrate as air passes through the vocal cavity affecting the sounds produced.

Lastly, another feature of the kiwi tongue that seemingly has no equivalent in the ratite group was the band of connective tissue that runs to the ventro-caudal end of the oral cavity, seemingly tracing the position of the hyoid bone that lies beneath the tongue. This tissue was the only one of its kind that did not show an obvious caudal root like that of the emu, instead lying above the tissue surrounding the glottis opening and then becoming level with the glottis. This tissue was likely one of the connection points of the hyoid bone to the tongue and could act to alter the position of the tongue within the oropharynx.

2.5.5 Species and sexual differences

Brown kiwi vocal anatomy closely matched that of other paleognaths, although there were some notable differences. The differences in the brown kiwi vocal tract were the bill length, the two pairs of pharyngeal folds on the upper and lower palate, the sexually dimorphic lateral labia of the syrinx, and the tongue length. The bill length was disproportionately larger in females, but males have larger lateral labia of the syrinx. The anatomical differences found in brown kiwi, when contrasted with other paleognaths, reflect their unique behavioural and ecological circumstances. Dense forest habitats, being nocturnal, and vocal activity associated with territoriality and long-distance communication have likely imposed selection pressures that have shaped and altered their vocal tract. Long tracheas for lower frequency calls, syringes with large vibratory structures, and a unique tongue shape all contribute to the overall picture painted by the brown kiwi's unique vocal tract. As such, they provide a striking example of how ecological and behavioural differences can drive anatomical specialisation within a basal avian clade.

Overall, the findings of this study further taxonomic descriptions of paleognathous birds by providing additional morphological characters to compare against other specimens, filling a major gap in knowledge (McInerney et al., 2019).

We found three main differences in the anatomy of the vocal apparatus of male and female brown kiwi. Two of these were already known, bill length and body weight being larger in females. In addition, we found that males had larger syringeal lateral labia than females, although this difference was not significant with our sample size. Together, these differences suggest that the dimorphic vocalisations of brown kiwi could arise from the differences in vocal anatomy, as thickening of the lateral labia is known to cause intersexual variation in calls (Beani et al., 1995; Nojiri et al., 2025).

The muscular control of the trachea is likely to be a major source of vocalisation changes, as longer trachea has been found to lower the frequency of calls and raise amplitude (Fitch, 1999; Gaunt et al., 1987). The presence of striated muscle in the tongue also presents the possibility of tongue movements altering the calls as these movements will change space in the oropharyngeal cavity. The resulting shifts in space have been shown to cause changes to call frequency and amplitude in songbirds so this may be the case for kiwi as well (Beckers et al., 2004; Suthers et al., 2016).

Bill length can contribute to sound characteristic, as larger bills have been found to produce calls of a lower frequency (Friis et al., 2022), similarly, larger body sizes are also known to produce lower-frequency calls (Martin et al., 2011). Combining the characteristics of female kiwi (larger weight, longer bill, and longer trachea), it would be expected that females produce a lower frequency call and males a higher frequency call as is observed in the species (Corfield, 2004).

Future work could focus on a sex-based comparison of the two major components of vocal production, the medial and lateral syringeal labia, in addition to the pressure produced by contributing air sacs. Additionally, kiwi tongue movements should be investigated to find the degree to which kiwi move their tongues during calling and whether this accounts for any aspects or changes in spectral variables.

2.6 Conclusion

I found that brown kiwi vocal tract anatomy closely matches other paleognathous birds, only deviating in minor features, emphasizing the morphological link to the taxonomy of paleognaths. Features like the spoon-like tongue of the kiwi and the two sets of pharyngeal folds present as unique amongst paleognathous birds, with most having reduced tongues. Sexual dimorphism was consistent with vocalisations with bill size and the area (mm^2) of the syrinx's lateral labia prominent differences. Bill size was disproportionately larger in females, as was the syrinx itself. However, male brown kiwi on average had larger lateral labia than females but this result was not significant with the current sample size. Overall, the anatomical evidence supports the observation that females produce calls of lower frequency compared to males.

The primary limitation of this study was the availability of specimens. This limitation resulted in a small sample size which could have been remedied by extending the duration of the study This would also improve the statistical analyses, as the small data set contained a considerable range of variability between the sexes with no way to determine outliers.

Future work on brown kiwi vocal anatomy could focus on tongue movements during calling to investigate their impact on call structure and spectral variables. Additionally, studies could also include how the syrinx produces sound as this may explain the variable size of lateral labia in kiwi, and how the lack of a well-developed pessulus impacts call production. Lastly, studies of the pharyngeal folds of the kiwi are needed as their function is not understood.

3 Investigation into Vocal Behaviour of the North Island Brown kiwi (*Apteryx mantelli*)

3.1 Abstract

Understanding the vocal behaviour of brown kiwi is important for conservation as kiwi are commonly monitored using call surveys. A better understanding of calling behaviours could refine this method by helping turn the number of calls into approximate numbers of birds. This study has two aims: to investigate whether brown kiwis exhibit vocal individuality, and whether kiwi choose a calling location or altitude to optimally broadcast calls. To achieve these aims, passive and active acoustic monitoring was carried out over a 50-day period from August to mid-October 2023. Manually recorded calls of known individuals and broad 12-hour sound samples were recorded and analysed using a ranking system to rank call quality. Spectral variables for each call were also extracted.

The spectral variables were reduced to six principal components and clustered using k-means to evaluate vocal individuality across the calls recorded from the periphery of six nesting sites. The results of the k-means clustering were of low accuracy (9%) and thus was deemed unreliable and thus failed to identify individual calls.

The location of the calling bird was determined by identifying matching calls on multiple recorders and then using triangulation with call quality ranks indicating the relative distance to a recorder, thus providing estimated locations of callers. These estimated call locations were then analysed using a negative binomial generalised linear model to see if altitude was correlated with bird calling location. I found that altitude was a poor predictor of a bird's calling location, which suggests that wide scale broadcast is not the primary aim of calls during the incubation season, at least in a high-density population.

3.2 Introduction & Literature review

Vocal communication is an important component of many animals' behaviour as it allows for the transmission of information in environments when visual and chemical signals are ineffective (Diggins, 2021; Hauser, 1996). Vocalisations excel in various situations, especially when other methods of communication fail or are less effective, such as visually challenging environments (Diggins, 2021; Hauser, 1996). Vocalisations are particularly important at night, as sounds may reach further than other communication methods, particularly in the dark when things are quieter (Hauser, 1996). Some nocturnal species also benefit from vocalisations as they can be used for echolocation (Brinkløv et al., 2013; Konishi & Knudsen, 1979), aiding in cooperation and organisation of conspecifics (Gursky & Nekaris, 2019). Birds call for a variety of reasons related to all aspects of their life, territory maintenance, courtship, navigation, and predator avoidance to name a few (Brinkløv et al., 2013; Colbourne & Kleinpaste, 1984; Hollen & Radford, 2009). In this study we focus on the vocalisations and vocal behaviours of the North Island brown kiwi (*Apteryx mantelli*). Brown kiwi are a cryptic species of nocturnal, flightless bird, with a low reliance on vision at night (Corfield et al., 2015) but well-developed sense of smell (Castro et al., 2010; Corfield et al., 2014; Cunningham et al., 2009; Jenkins, 2001), touch (Cunningham et al., 2007; Cunningham et al., 2011) and hearing (Corfield et al., 2011). There are five recognised species of Kiwi (*Apteryx*) that belong to a basal group of birds known as paleognaths (Mitchell et al., 2014; Widrig & Field, 2022; Yonezawa et al., 2017). This group of mostly flightless birds have a range of vocalisations from long-ranging booms to high-pitched trills and whistles (Chiappone et al., 2024; Corfield et al., 2008; Mack & Jones, 2003; Pérez-Granados & Schuchmann, 2021; Pérez-Granados et al., 2020).

3.2.1 Kiwi conservation: the problem

Mammalian predators introduced to New Zealand subjected a variety of native species to selective pressures they did not evolve to deal with (Craig et al., 2000). This has resulted in the decline of a multitude of native and endemic species for reasons such as predation and competition (O'Donnell et al., 2017). Introduced mammalian predators required trapping and poisoning to minimise their impact on native species (Leathwick & Byrom, 2023). Despite these management actions, some native species were impacted to the point where they may only recover with assistance, with their conservation status representing how at risk they were (IUCN, 2017). The conservation status of *Apteryx* genus (IUCN, 2017) highlighted the need for optimal management measures informed by accurate monitoring. As a cryptic, nocturnal, burrow-inhabiting species, they can be tricky to monitor. Kiwi can be difficult to locate, sometimes in hard-to-reach areas, with labour-intensive efforts required to account for all the difficulties they present when monitoring. To aid in the recovery of kiwi, it is imperative to improve monitoring and management techniques, when possible, to provide the best chance for their future success.

3.2.2 Call surveys and limitations

Population monitoring of kiwi is commonly done via call surveys, meaning that call counts are the primary metric for kiwi population density estimates (Colbourne & Kleinpaste, 1984). Call surveys are limited by variations in call rates, (how often an individual will call) and the inability to account for juveniles and chicks since they do not call until after they are a year old (Robson & Gibbings, 1947). Factors such as weather, listener experience, call rate fluctuations, and call timing affect the results of kiwi call surveys (Colbourne & Kleinpaste, 1984; Digby, Towsey, et al., 2014).

Bird calls in general can contain information about the caller that is relevant to conspecifics but also to researchers as call information can provide insights into the animal's body condition (Bowling et al., 2017; Reber et al., 2017) and identity (Dent & Molles, 2016). This knowledge can then be used to gain a better understanding of population sizes through vocal surveys using the identification of individuals where possible.

3.2.3 Using individual identification of calls and call location in surveys

Call counts are not invasive as they do not require handling of the animals. Capturing animals can also be challenging for researchers as it can require getting into hard-to-reach locations, which can be expensive and present health risks. The challenge with acoustic recording, particularly passive field recordings with autonomous recording units (ARUs), is turning call rates into population estimates.

If there are individual variations in the way an animal sounds, then it is hoped that measurements taken from the calls could be used to identify the calling animals. Other research has reported that individual identification of sounds is possible (Clapperton, 1987; Dhondt & Lambrechts, 1992; Hutchison et al., 1968; Lambrechts & Dhondt, 1995; Marler, 1958). Utilising call individuality provides an opportunity to maintain less invasive monitoring of individuals, as their distinct call would be all that is needed to confirm an individual's presence which may be particularly useful during incubation periods, where interactions should be minimised. ARUs can be deployed to cover a whole study area and work almost entirely independent of human operators, as such, they provide considerable benefits to acoustic surveying (Castro et al. 2019; Shonfield & Bayne, 2017). ARUs are impacted by weather effects, however, ARUs can operate regardless of temperature, rain, and wind, the latter of which can be filtered out in audio analysis programs such as AviaNZ (Marsland et al., 2019). ARUs almost eliminate the need for workers in the field, other than to change batteries and replace SD cards. Lastly, ARUs record the calls which allows for

cataloguing and for analysis later, eliminating the issue of observer error as multiple observers can analyse the same call (Castro et al. 2019; Shonfield & Bayne, 2017).

If animals preferentially choose call locations, this could be used to better select locations of passive acoustic recorders (and human listeners). Many bird species choose specific sites to vocalise with specific locations chosen based on the purpose of the call. For example, Campos et al. (2009) studied the relationship between singing behaviour and song perch selection in East African Passerines. They found that birds often choose perches that balance the need for effective communication with the risk of predation. Selecting exposed perches may enhance song transmission but also increase visibility to predators. Other authors have found similar results: chaffinches (*Fringilla coelebs*) preferred perches that offer a better view of their surroundings, allowing them to detect potential predators more effectively while vocalising (Krams, 2001), and Pied Trillers (*Lalage nigra*) selected specific perch heights for singing in suburban areas, choosing sites that were safe from predators (Ramji & Mah, 2020). Predators are not the only reason to choose particular sites for calling. Male birds of paradise often use different perches specifically for vocalising before engaging in visual displays. This behaviour suggests a strategic selection of vocalisation sites to enhance mating success related to optimising sound transmission and reducing predation risk (Miles & Fuxjager, 2018). Identifying popular calling locations may also reveal seasonal trends of calls caused by shifts in behaviour (Jacobs et al., 1993; Jourjine et al., 2024; Pérez-Granados & Schuchmann, 2023; Vokurková et al., 2018; Yoo et al., 2020), as the intended audience of calls may change from ones of long-distance broadcasting to short. If unaccounted for, this could result in the under-representation of individuals by count as calls could be missed due to the shift in desired audience. Call location identification could also improve call surveys by reducing monitoring costs. By knowing the sites where birds are likely to call, surveys could be concentrated on these locations, minimizing the need for extensive location

coverage in monitoring (Frommolt & Tauchert, 2014; Rhinehart et al., 2020; Tseng et al., 2024). Lastly, by knowing the preferred call locations, monitoring in rough terrain or remote locations can be carried out effectively with less operator effort due to the ideal placement of listening stations or recording equipment (Frommolt & Tauchert, 2014; Rhinehart et al., 2020; Tseng et al., 2024).

3.3 Literature on Individual Identification of calls

3.3.1 How individual identification of calls is investigated

To investigate the vocal identification of individuals through calls, first unique characteristics representative of an individual must be identified. Such characteristics include spectral features of calls (Corfield et al., 2008; Digby, Bell, et al., 2014b), the production of which being linked to morphological characteristics of the vocal tract (Fant, 1960; Fox et al., 2008). Fant (1960) introduced the source-filter theory of speech production. The theory proposed that vocalisations are the result of vibrations from the source (in the case of birds, the syrinx) which then travel through the vocal tract (the trachea and oropharynx) which acts as a filter, modifying the resulting vocalisation. Thus, the morphological characteristics of the vocal tract impact the resulting vocalisation, with variations in morphology between individuals resulting in individually unique calls. The morphological characteristics may be reflected through individually distinct calls, thus could allow for individual identification via calls if they are distinct enough.

The calls of known individuals can be identified using call structural variables and there are some statistical procedures commonly used to analyse the data. For example, Corfield (2004) utilised a discriminant function analysis and a one-way repeated measures ANOVA to search for individual identification in brown kiwi using syllable duration, syllable gap duration,

frequency with the most amplitude, high frequency, and low frequency. Other authors have used neural networks to identify individuals (Bedoya & Molles, 2021; Fox et al., 2008; Stowell et al., 2019). The neural networks are trained on the relevant call data to form a feature set of call variables that is then used to classify individuals via their calls. Notably, using a type of neural network called a convolutional deep clustering network, Bedoya and Molles (2021) were able to accurately identify calls of known and unknown individuals in great spotted kiwi (*Apteryx maxima*). However, this is a black box approach that cannot be

3.3.2 Use of robust song characteristics

Studies investigating vocal individuality have used call elements such as fundamental frequency (the lowest harmonic bar in a syllable on a spectrogram), frequency ranges, amplitude, and time intervals between syllables, to identify individually unique calls (Corfield, 2004; Digby, Bell, et al., 2014b; Li et al., 2017). These characteristics are known as 'robust' because they are consistent, reliable, and functionally significant traits in bird vocalizations and are relatively stable across different environmental conditions, recording contexts, or individual variations. These characteristics are often resistant to noise, degradation, or variation due to external influences, making them valuable for species recognition, individual identification, or behavioural studies.

Vocalisations can provide information about an individual's body size through analysis of formants, fundamental frequency, and the shape of the vocal tract (Fitch, 1997; Fox et al., 2008; Pfefferle & Fischer, 2006; Reber et al., 2017). Amplitude is the intensity or volume of a call (measured in decibels (dB)), and frequency is the pitch of a call (measured in a scale of hertz (Hz)). Formants are sounds that are identified by peaks of amplitude centred around specific frequencies. They originate from vocal tract resonances (Fox et al., 2008). This amplitude peak results in a sound that may be unique to the individual (Wright et al., 1997). They are produced by changes in the length and shape of the resonance chambers in the vocal

tract (Wright et al., 1997), in birds' case, the syrinx, oropharyngeal cavity, and the trachea (Gaunt & Gaunt, 1985; Riede et al., 2006; Suthers, 1994). If the shape of the vocal tract is unique to an individual, then formants can be used to identify individuals as they are created by the unique features of an individual's vocal tract and thus, are representative.

3.3.3 Vocal individuality in Kiwi

Vocal studies on kiwi currently show that there is some evidence for vocal individuality in the species that have been studied. These species are the great spotted kiwi (*Apteryx maxima*: Dent (2013)), little spotted kiwi (*Apteryx owenii*: Digby, Bell, et al. (2014b)), and North Island brown kiwi (*Apteryx mantelli*: (Corfield, 2004)). These studies utilised areas of low population densities with Dent (2013), citing an estimated population density of one kiwi per 2-3km^2 in their study (McLennan & McCann, 2002), Digby et al. used a population with a density of 0.7/ha, and Corfield (2004) used a known population of 21 individuals in an area of 60 ha with Colbourne (2002), reporting a population of one pair per 3 ha for this site.

Dent (2013) investigated evidence of vocal individuality in great spotted kiwi by analysing the spectral variables recorded for the whole, start, middle, or end of a call. The spectral variables utilised were minimum, maximum, and peak frequency, call length, syllable duration, syllable rate, and bandwidth. Of these variables, they found that the potential for individuality coding differed based on which segment of the call they were extracted from. Variables from the middle, beginning, and end were utilised with the variables from the middle section contributing frequently (four out of seven variables). They were able to successfully classify individual males with a high rate of success (95.7%), improving the rates further by reducing the numbers of predictor variables. Corfield (2004) also investigated evidence of vocal individuality in brown kiwi. The variables utilised differed from Dent (2013) which were: syllable duration, syllable gap duration, frequency with the most amplitude, high frequency, low frequency, start frequency, and end frequency. Utilising a

discriminant function analysis with a PCA to reduce dimensionality, they were able to successfully identify males by using syllable variables 68% of the time, improving this to 85.4% by utilising syllable means with call variables. Digby (2013), investigating the vocal individuality of little spotted kiwi, utilised a range of variables with syllables being measured via bandwidth, various percentages of frequency, and the gaps between syllables. These variables were then averaged to produce mean syllable variables. Call variables were also utilised: mean 5% frequency, syllable rate, call duration, and duty cycle (sum of syllable durations divided by sum of syllable durations and gaps). Multiple methods of classifying individuals were utilised with no significant differences in their classification performances reported, resulting in an unbalanced accuracy of 57% for identifying individual males. A universal issue faced by these three studies was the variability of calls throughout their duration, called intra-call variability. Intra-call variability was dealt with via differing methods across the literature analysing vocal individuality in kiwi. Dent (2013) utilised the stepwise model of the discriminant function analysis to remove noise from intra-call variation allowing use of the full call. Corfield (2004) addressed variability by averaging the syllables across calls. Digby (2013) only utilised syllables between the 15th and 35th syllable to minimise variability, reinforced by Corfield (2004), who noted the low level of variability in the middle of a call. The ability to identify individuals by sound reduces as the density of individuals increases (Bristow et al., 2023; Digby, 2013; Průchová, 2024; Terry et al., 2005) and it often varies with time (Berryman, 2003; Saunders & Wooller, 1988; Terry et al., 2005). To date, no study has investigated the potential for vocal individuality in a dense kiwi population. This study investigates the presence of vocal individuality, and does so by testing a new method that does not rely on calls of known individuals, although these will be used to supplement data when possible. Developing a method that does not rely on known individuals will prove beneficial in improving population estimates where it may be difficult

to track and mark every individual. Such a study would provide an understanding of the call structure of kiwi that live close to each other, as it may be less distinct than that of birds from isolated populations, reducing their usefulness for monitoring purposes.

3.4 Literature on call location selection in birds

3.4.1 Environmental factors influencing calling location

Any study looking to investigate call location selection, and by extension vocalisations, must consider environmental variables and how they impact how the sound travels and how it is received. The main consideration for call recording is the attenuation of calls, which is how the call degrades over distance (Mack & Jones, 2003). Calls can degrade over distance but can also travel less efficiently with variations in humidity, air pressure, temperature, and foliage density (Bohn, 1987; Priyadarshani et al., 2018). Geographical features such as gullies, streams, rivers, and natural depressions can also impact sound travel as solid surfaces will change the sound path and waterways will escalate background noise making discerning specific calls difficult depending on volume (Gibb et al., 2019). Call detectability can be impacted by wind direction, with calls upwind of a recorder being detected less than calls downwind (Priyadarshani et al., 2018; Thomas et al., 2020). Calls originating from elevated positions travel further and thus can be detected at longer distances, however, too high and the call risks being missed entirely by recorders (Castro et al., 2019; Höbel & Barta, 2014; Parris, 2002; Schwartz et al., 2016).

Considerations must also be made to factor in environmental effects that influence call rates through their effect on detectability, particularly when the study focuses on abundance. Breeding seasons, rainfall, and wind have an impact on calling rates, sometimes not evenly between sexes (Digby, Towsey, et al., 2014). Female kiwi calls were detected less during high wind speeds but were less affected by rainfall compared to male call rates (Digby, Towsey, et al., 2014). Rainfall and wind increase ambient noise levels and thus reduce the

number of calls detected, impacting the perceived call rate. Female calls may be detected less during high wind speeds as the low frequency calls of females overlap with the frequency of wind (Digby, Towsey, et al., 2014).With so many environmental factors affecting sound quality, it is not surprising that many species of birds choose locations to broadcast their vocalisations depending on their intended purpose and specific environmental conditions (Ey & Fischer, 2009; Hunter, 1980; Jilka & Leisler, 1974).

3.4.2 Behavioural influences on call location selection

As calls convey information to adjust behaviour, it is not unlikely that behaviour becomes a significant factor in call location selection. An example of a behaviour influencing call location selection comes from mating displays. The vocal component of the display can be broadcast from anywhere, but the addition of a visually based mating display requires an adequately visible position to broadcast from (Williams, 2004). Other birds are influenced by predation risk, as advantageous singing spots may produce greater risk but also stand a better chance of attracting a mate (Krams, 2001).

As for brown kiwi, current literature suggests that brown kiwi call to maintain territory (Colbourne & Kleinpaste, 1983) instead of fighting (Thomson, 1964), as they are reported to be highly territorial birds (Colbourne & Kleinpaste, 1984). This idea conflicts with the population of brown kiwi on Ponui Island, where density has been estimated at 1 bird per ha (Cunningham et al., 2007), as calling for territory maintenance on such a densely populated island seems futile. Calling to maintain a small territory may result in more conflict between individuals as they are more densely distributed than they would be on the mainland. This may result in the density of birds altering the vocal behaviours of individuals to better adjust to this new, smaller habitat. If brown kiwi called for territory maintenance, it would not be unreasonable to assume that they may do this either from central locations in their territory, or elevated positions where their calls broadcast effectively. However, as of the time of

writing, there is no literature that investigates call location selection in brown kiwi, providing a significant gap in knowledge surrounding the calling behaviours of brown kiwi. One way to investigate the calling behaviours of Ponui Island brown kiwi would be to study call location selection, as if territories are maintained, distinct patterns of calling locations may be identifiable. Potential patterns of calling that may indicate territory maintenance could be the use of elevated positions to broadcast calls more effectively (Parris, 2002; Schwartz et al., 2016), to maintain a territory from an optimal or central location relative to nest sites. Brown kiwi calls become less frequent during incubation as call purpose may shift. The full breeding cycle for brown kiwi lasts for roughly 85 days, with two breeding seasons a year for a bird (Cockrem et al., 1992). This means that for almost half the year the call purpose may differ and thus change where males call, as territory defence and mate location may have differing broadcasting requirements.

3.4.3 Hypothesis

This study aims to test two hypotheses: (1) that male brown kiwi calls are individually distinct and can be identified via call variables of their vocalisations, (2) and that male brown kiwi select elevated positions to call to maximise the transmission range of the call and thus the effectiveness of the call. The second hypothesis relies on two assumptions. One is that the information communicated in the call is intended for a wide audience thus long-distance transmission is required. The other assumption is that the population density of brown kiwi on Ponui Island does not affect calling behaviour, thus the results are applicable to mainland populations.

3.5 Materials and Methods

3.5.1 Study species

Brown kiwi (*Apteryx mantelli*) were chosen for this study as they are a suitable model for animals that are hard to access or are cryptic. Conservation efforts focusing on similarly obscure animals are likely to experience similar, if not the same issues. Brown kiwi are a nocturnal species making it difficult to assess their behaviours visually without specialised equipment. However, they have sexually dimorphic calls that provide an opportunity to monitor them using call surveys and autonomous recording units. Previously identified patterns of behaviour make brown kiwi a suitable study species as these patterns provide opportunities that aid in monitoring.

One such factor is the consistency of nest sites. Male brown kiwi can maintain a nesting location for periods of up to 84 days (Colbourne, 2002) during the incubation period of their eggs. During this period, male brown kiwi maintain calling throughout the incubation and post hatching (Ellis & Marsland, 2022). This provided a fixed location for individuals to be located and subsequently, for recorders to be set up in the periphery of and utilised for up to three months. A fixed nesting location supplemented by literature on calls (Priyadarshani et al., 2018) and calling behaviours (Ellis & Marsland, 2022) allowed recorders to be strategically placed in areas likely to capture the calls of a known individual, maximising data accuracy. Additionally, consistency in nest sites means that fewer manipulations of recording equipment are required, further reducing any intrusion into nest sites, minimizing disturbances.

The predictability of call times was a considerable advantage brown kiwi posed as a study species. Brown kiwi have been documented to call within 120m of their nest and within 10 minutes of leaving their burrow (Ellis & Marsland, 2022). Combined with activity data from

known individuals, trends can be followed of their time of activity and thus a rough time frame in which a call is likely to occur. This provides researchers with predictable periods to conduct manual call recordings and can allow for better coordination concerning the selection of which individuals to record.

Call rate variations in brown kiwi calls, if consistent with call rate patterns in little spotted kiwi (Digby, Towsey, et al., 2014), make them a good candidate for a study that utilises ARUs and manual call recordings. Current literature suggests that the call rate of North Island brown kiwi peaks from autumn till the end of spring, and during incubation the average call time tends to be later at night (Miles, 1995). Environmental conditions influence call rates frequently, as they accounted for 44% of between night variations (Miles, 1995). This variation can make it difficult for human observers to maintain presence for observational studies, as low temperatures and unfavourable weather all reduce how long a researcher can stay in the field. Thus, utilising ARUs would negate the negative effects of varied calling times.

Lastly, Ponui Island has a population of brown kiwi that have been tagged, and as such, are easy to locate using radio telemetry equipment. This allows for easy tracking of individuals, their incubation status, time of emergence, and other information about their activity, through the information sent from their tracking tags. The population on Ponui Island also has many individuals nesting within a series of gullies, condensing the study area and reducing the amount of labour required in monitoring, and recorder upkeep. This makes the brown kiwi of Ponui Island prime candidates for this type of research. Predictable patterns of activity, accessible nesting areas, and consistency in calling behaviour all factor in to contribute to research that will improve the ease and accuracy of monitoring.

3.5.2 Study site

Ponui Island:

The study was conducted on the southern end of Ponui Island, located in the Hauraki Gulf of the North Island, New Zealand (WGS84: -36.86687327, 175.18394120; LINZ, 2020). The island is made up of a mix of pasture, wetlands, streams, and native forest. The forest includes a mixture of kanuka (*Kunzea ericoides*), kauri (*Agathis australis*), various tree ferns, broadleaf species, and other less prominent plants (Cameron & de Lange, 2005). The area used in the study was composed of three gullies called Pohutukawa Gully (PHKG), Red Stoney Hill Gully (RSHG), and Pipe Gully (PG) (Fig. 3-1).

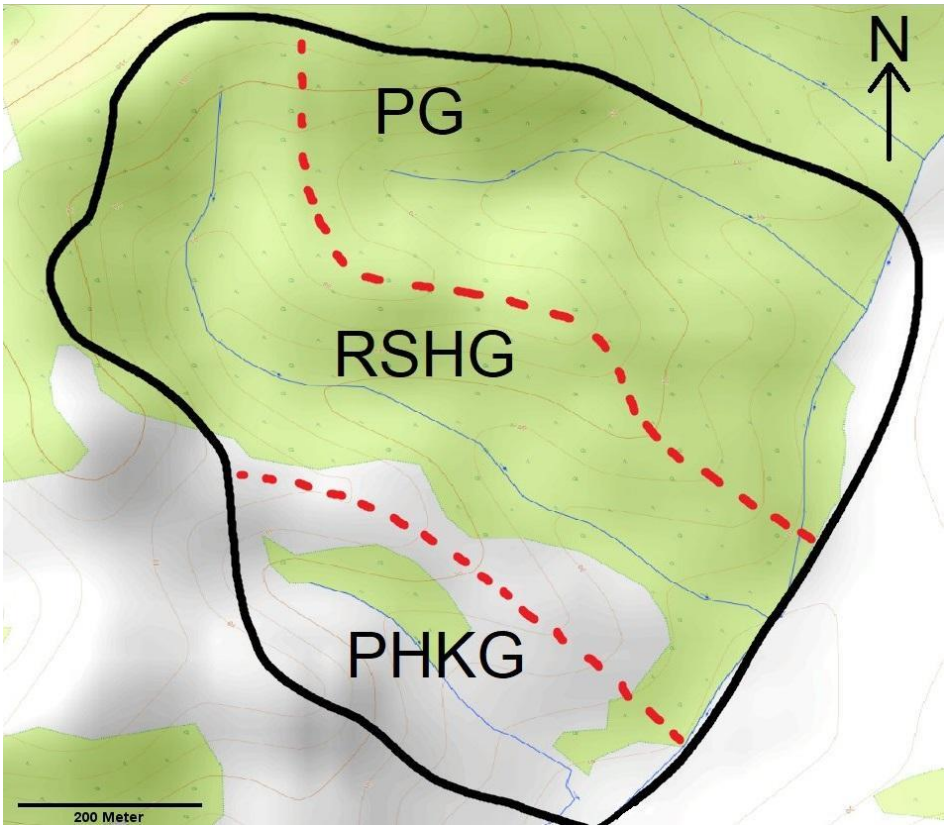

Figure 3-1) A map of the Ponui Island gullies relevant to the study and divided by the dotted red line. Green denotes forest or scrub areas while white indicates farmland pasture.

The gullies featured a variety of vegetation, small streams, and at the ends of the gully, wetlands. The burrows of kiwi were often found on either side of the gully, either in burrows that ran into the ground or in tree holes, all of which were marked. The forest had near-constant canopy cover with few clearings resulting from the dense vegetation which would likely impact recording quality (Priyadarshani et al., 2018) (Fig. 3-2).

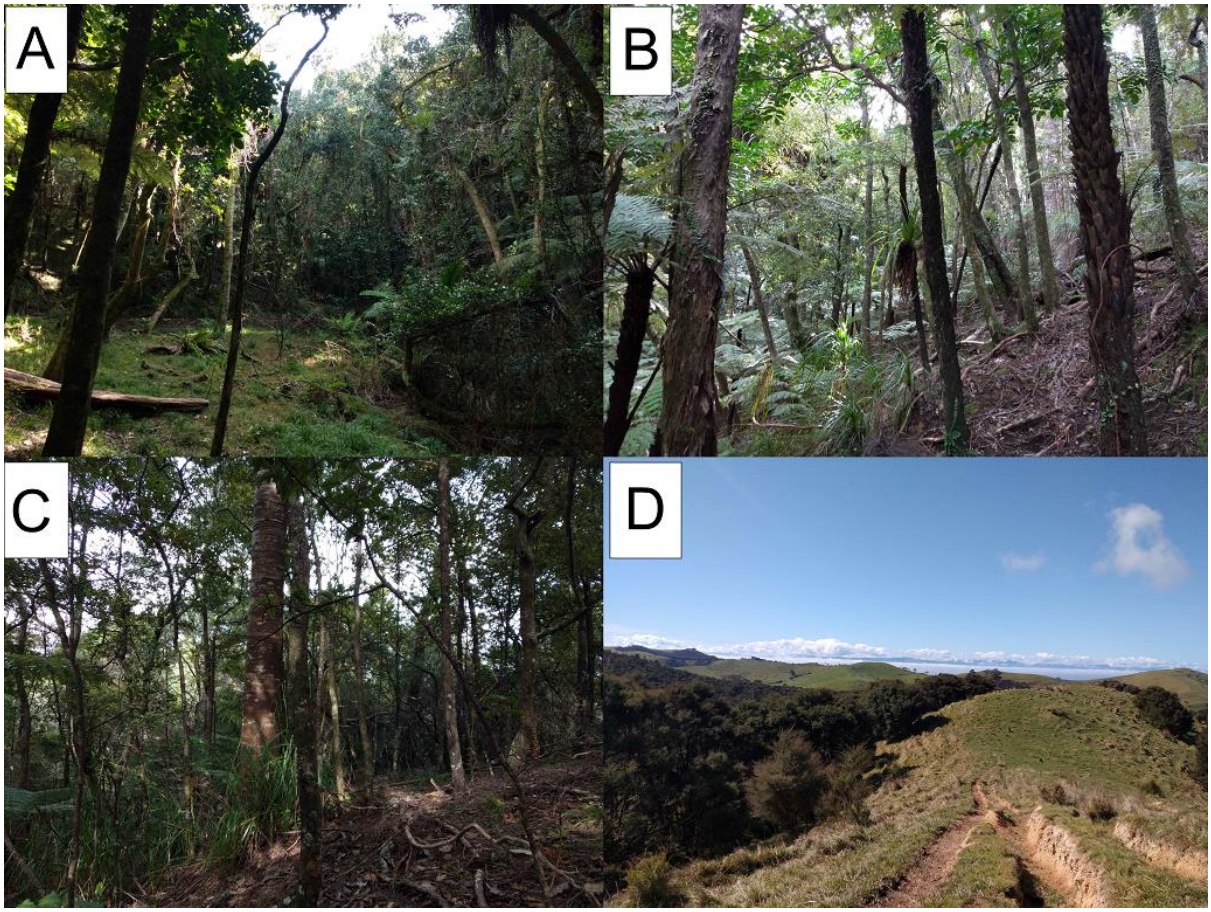

Figure 3-2) (A) An example of the forest in the lower Red Stoney Hill gully. **(B)** An example of the forest in the upper reaches of Red Stoney Hill gully. **(C)** An example of the forest on the upper ridge that divided Red Stoney Hill gully and Pipe gully. **(D)** The ridge that divided Pohutukawa gully (right) and Red Stoney hill gully (left).

3.5.3 Experimental design

To test hypothesis one (that the calls are unique to individuals), I took advantage of the known calling behaviour (they call soon after leaving the nest each night) and our current knowledge of the type of bird brown kiwi are (they are non-learners). Thus, I established four

recorders at each nest location, one at the nest and the other three 60 m away, forming a triangle with its corners equidistant to the nest. I chose birds nesting close to each other to maximise the known number of birds in an area with overlapping sound range, I then recorded them manually and with the ARUs. After the manual call recording was made, the individual's identity was verified by using the radio telemetry equipment and cross-referenced with the time of activity data also gathered via the radio telemetry monitoring. This would ensure that the manually recorded call and the call recorded by the ARUs would be from the targeted individual and thus a 'known' call to represent the individual. The call was then analysed to identify spectral variables that would be characteristic of the individual calling, such as frequency, duration, and trill presence. The variables could then be compared to all other calls of known and unknown birds to identify if clusters of variables would form to highlight individuals, thus showing an individually distinct call.

3.5.4 Site selection

The locations of nests in use by an incubating male were marked using a Garmin handheld GPS and physically marked with flagging tape. This provided a known location for the male that would be reliable and monitored via radio telemetry. Kiwi radio transmitters have a technology called Chick Timers (CT), which periodically transmit information about the activity of the bird in the last 24 hours and time of emergence for the previous night, amongst other behaviours (Wildtech, 2014). The information gathered by daily CT's provided consistent times when target kiwi would be active, as well as information on their partners and other nestmates to identify as many callers as possible. This information was collated onto an Excel spreadsheet to maintain consistent records, used to plan manual call recording sessions.

Birds were selected based on the remaining duration of incubation and distance between other incubating males to find males at the earliest stages of incubation, and to highlight any overlap of potential recorder ranges.

3.5.5 Automatic recorders

The recorders were affixed to tree trunks or branches at approximately eye level (1.8m, Fig. 3-3).

Figure 3-3) A Cornell SwiftOne recorder with pink flagging tape to mark recorders, affixed to a tree uphill from a nesting site on Ponui island.

A variety of recorders were used including 10 Cornell SwiftOnes (Marcot, 2022), 14 AudioMoths (Hill et al., 2019), and 5 DOC AR3/4 recorders (Department of Conservation, 2024). The chosen distance for the recording units was 60m as at this distance calls still had important vocal signatures but further away these signatures became harder to detect (Priyadarshani et al., 2018). Additionally, Ellis and Marsland (2022) found that North Island brown kiwi moved a maximum of 120m before their first calls for the 23 nights of a calibration experiment, so the triangular pattern for recordings covered the most available ground while minimizing the equipment needed. The first round of automatic recorders was set up on the 10th of August 2023 and ran until the 18th of September 2023. The second round of recorders was set up from the 19th to the 22nd of October 2023. The recorders were all set

to record from 18:30 to 06:30 every night with a sample rate of 48khz for the Cornell SwiftOnes and AudioMoths, and 32khz for the DOC AR3/4's.

3.5.6 Manual call recording

Manual recordings were conducted using a Marantz PMD661 MII solid-state recorder (48khz sample rate, 1058kbps bitrate) in conjunction with a Sennheiser MKE 600 shotgun microphone (20khz sample rate). The manual recordings were collected as close to 20m away from the nest site as possible as this was the only consistent location the target kiwi would be at. Every call recording included additional information such as location, time, date, and who recorded the call. This was to ensure accurate time logs were kept, enabling call matching with the ARUs. Once the call was confirmed, the site was marked with flagging tape and a GPS waypoint to provide a consistent location to conduct repeat recordings from. Recording continued for half an hour after the manual recording of the target bird was taken to ensure any extra calls were incorporated in case of operator error, such as mistaken ID of the individual recorded. CT data (activity information provided in the telemetry output) were also used the next day to verify that the target bird had already been active when the call was recorded. Manual recording of calls was carried out from the 7th of August 2023 to the 3rd of September 2023, and once again from the 20th to the 23rd of October 2023.

3.5.7 Call records

Calls were organised by date, recorder, and bird ID to keep consistent records. The calls were then processed using AviaNZ version 3.2 (Marsland et al., 2019) to detect kiwi calls within the automated recordings. All detected calls were then listed in Microsoft Excel (Microsoft Corporation, 2023) with spectral variables such as frequency range, duration, syllables etc.

3.5.8 Data analysis methods for individual identification

Calls recorded within seven days of the date of the manual recording were examined by visually comparing the spectrogram of the manual recording to spectrograms produced by recordings from the ARUs. The timing of the call was then matched to the time of activity for the target kiwi obtained through the transmitter to identify any calls from the target kiwi. This

made a dataset consisting of several automatically recorded calls, with some of the calls being very likely to come from a particular known bird. From this database of calls, spectral variables were measured (fig 3-4) and recorded into a spreadsheet.

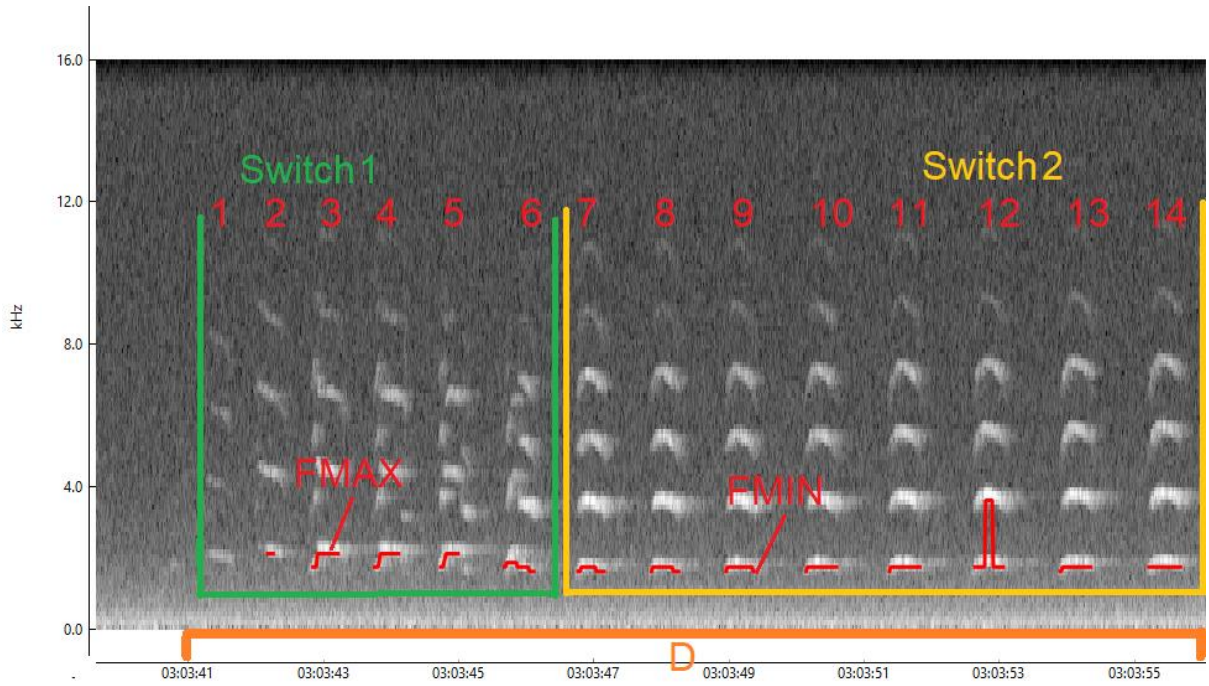

Figure 3-4) Exemplar spectrogram showing how call variables were recorded. D represents duration, FMAX and FMIN represent frequency maximum and minimum respectively, switch 1 and 2 represent two syllable types and thus one switch of syllable type, and the numbers 1 to 14 represent the number of syllables of the call.

A principal component analysis (PCA) was completed via R Studio (R Core Team, 2022), using the packages readxl (Wickham & Byran, 2023), factoextra (Kassambara & Mundt, 2020), ggplot2 (Wickham, 2016), and caret (Kuhn, 2008). The PCA was used to transform the original variables into a new set of uncorrelated variables (principal components). This reduction in dimensions allowed me to focus on the most significant features of the calls, making the clustering process more efficient and interpretable. I assumed that if there were individual differences in the males' calling, the features could be separated into clusters.

The dataset that the PCA and subsequent k-means clustering utilised was of all bird calls recorded within a week of the manual call recording for each bird. This resulted in call data from six out of ten brown kiwi in this study being utilised in the analysis. The dataset consisted of 445 observations with a subset of six bird call variables, including frequency minimum and maximum, syllable count, trill count, number of switches, and duration. The data were then scaled to have a mean of zero and a standard deviation of one.

The PCA reduced the call variables into six principal components. A scree plot was then produced to visualise the proportion of variance explained by each principal component, with the first four being selected for analysis, accounting for 92% of the variance. Next, a PCA biplot was generated to visualise relationships between the variables and the call data, followed by a PCA individual plot to show the spread and clustering of the points based on the first four principal components.

The principal components were then used by k-means clustering to identify any underlying patterns within the variables ultimately to highlight individuals. K-means clustering was applied to the scores of the first four principal components, then again separately with all six principal components. The number of clusters was set to six to represent each group of recordings produced by the recorders placed around the nest sites of the six individuals. Next, two confusion matrices were conducted to evaluate the clustering performance of the four and six components with the recording groups labelled from each bird and to assess the accuracy of the clustering. The confusion matrices were carried out using the cluster plugin for R studio (Maechler et al., 2023).

3.5.9 Call locations of brown kiwi

For hypothesis two, I used the calls from manual call recordings and the ARUs to identify an estimated calling location. To do this, I selected the period in which the highest number of

recorders were operating to eliminate any variation that could be provided by environmental factors such as wind and rain. This resulted in a consistency of environmental conditions.

3.5.10 Data analysis for call location

The calls were then graded from rank one to rank three based on the maximum number of harmonics visible on a spectrogram while keeping the visualisation parameters the same to maintain consistency of visibility (Fig-3-5) following the methods from Priyadarshani et al. (2019). Rank one calls (six or more harmonics) were high-quality calls, rank two calls (three to five harmonics) were medium-quality calls, and rank three calls (two or less harmonics) were low-quality calls.

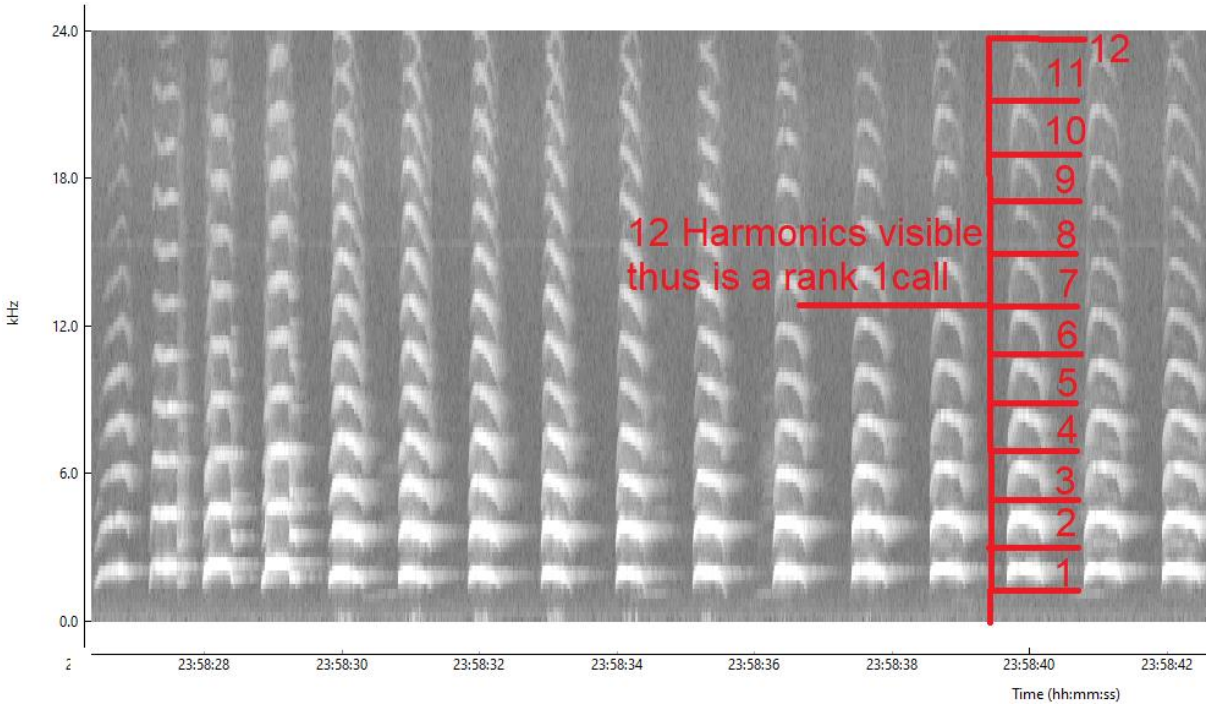

Figure 3-5) An exemplar spectrogram showing how the ranks of calls were determined by counting the number of visible harmonics in a call.

The number of harmonics visible correlates to a distance range that the call could be produced from, thus the call ranked across multiple recorders could provide an estimate of

location via triangulation (Priyadarshani et al. 2019). Rank one calls were estimated to be approximately 20m from the recorder, rank two were likely within 60m, and rank three were likely greater than 100m.

Two groups of calling data were made with one encompassing every call known as the ‘all’ group, and the calls that were detected on three or more recorders were allocated to the group known as the ‘shared’ group. Within both groups, each call was represented only once to prevent pseudo-replication. The nest sites and ARU locations were recorded via a handheld GPS, the resulting coordinates were mapped to acquire a height above sea level.

Once all the call locations were established on a map made using QGIS (QGIS Development Team, 2024), a heatmap (Hamilton, 2024) was made to visualise the pattern of selected calling locations. The areas with the highest density of calls were marked and the altitude was estimated to then compare to the elevation of the closest known male’s nest site to ascertain whether the hotspot was higher or lower than the nest site.

Relative recorder altitude will refer to the altitude of the recorder in relation to the altitude of the nest site. A recorder higher than the nest will have a positive relative recorder altitude, and a recorder lower will therefore have a negative relative recorder altitude. This was combined with the location and altitude of the other call hotspots to show the trend of call location selection. Elevation was the only factor tested, as this part of the study arose later due to limitations with the data. Elevation became the most accessible and apparent factor to test for when it came to calling behaviours, given the data available as a clear measure of potential effort when selecting calling locations. Comparing the altitude of commonly used calling sites with that of the nearest nest sites could reveal a pattern of altitude preference, with higher relative calling locations suggesting a deliberate choice despite the increased effort required to reach them., Distance from the nest when calling occurred could also have

been utilised, but this may only prove informative if we knew the individual calling, thus running into the same issue with limited manual call recordings.

Calls of all the study birds were collated together, covering a common time frame from 12/08/2023 to 19/08/2023 to provide the same environmental conditions for all recorders. I assumed that weather and temperature remained consistent across the study site, aside from small differences due to unknown variables.

The data from 'all' calls (n = 3468) were compiled into a spreadsheet to count the total number of each call per rank. The 'shared' spreadsheet listed all calls (n = 1325) that were shared between a minimum of three recorders, as this allowed for location estimation. Lastly, the ranking of manual calls and the ARUs that recorded them were logged into another spreadsheet. Locations of the studied birds' nests and the recorders surrounding them were compiled onto a topographic map made using QGIS (QGIS Development Team, 2024). The 'shared' data group was then plotted onto the topographic map by using the distance estimations of each rank across multiple recorders to triangulate the potential location of the calling kiwi. The plotted points were then used to generate a heatmap using the Density Analysis plugin (Hamilton, 2024) to highlight calling hotspots using the Open Street maps plugin (Nextgis, 2024) and the map from OpenTopoMap database (OpenTopoMap, 2024). The elevation of call hotspots, nest sites, and recorders was included in the analysis to provide information on elevation differences and the distances to the calling hotspots.

The 'all' dataset and the 'shared' dataset were used separately in two Negative Binomial Generalised Linear Model (NB GLM) analyses to counteract overdispersion in the data set, conducted using R studio (R version 4.2.2 (2022-10-31: R Core Team (2022) with the packages MASS (Venables, 2002), mgcv (Wood, 2004, 2011, 2017; Wood et al., 2016), and readxl (Wickham & Bryan, 2019). A NB GLM was selected instead of a Poisson GLM to

account for overdispersion in the data. The analysis was carried out using the predictor variables of recorder altitude and relative recorder altitude against the response variable of % rank either one, two, or three of calls for the ‘all’ and ‘shared’ datasets. This analysis was conducted to uncover any trend of altitude or relative altitude with call quality recorded from each nest site. Relative recorder altitude was measured by subtracting a recorder's altitude from the altitude of the nest site it belonged to. Predictions were made using the *predict()* function in R and made on the log scale then exponentiated to transform them back to the original scale. The results were then visualised using a fitted values plot with 95% confidence intervals with a solid line to represent the predicted values and a dotted line to represent the confidence intervals.

3.6 Results

3.6.1 Individual Identification

All principal components were utilised during this analysis (Table 3-1) as PC1 and PC2 alone did not provide a sufficient cumulative proportion.

Table 3-1: Summary statistics of the principal components.

Importance of components

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	1.4186	1.2631	0.9772	0.9703	0.61723	0.33866
Proportion of Variance	0.3354	0.2659	0.1592	0.1569	0.06349	0.01911
Cumulative Proportion	0.3354	0.6013	0.7605	0.9174	0.98089	1

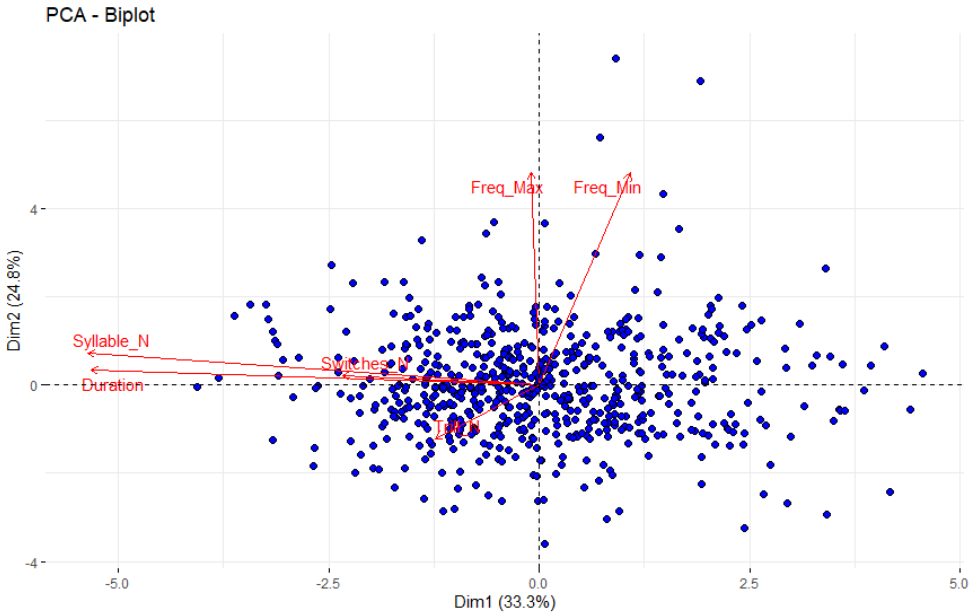

Figure 3-6) Biplot of PC1 versus PC2 of the PCA, with arrow length showing the loading strength of the variable, and the arrow direction showing the correlation of a variable to the others. These variables were sampled from the brown kiwi calls to show correlations between them.

PC2 represented frequency minimum and maximum as these two variables were correlated (Fig. 3-6). This was likely due to the relationship between call pitch and body mass of individuals, thus producing a pitch range tied to mass and distinct to an individual (Martin et al., 2011). Principal component one (PC1) was influenced by ‘number of syllables’ and ‘duration’, both exhibiting strong negative loadings (-0.6638 and -0.6563, respectively; Table 3-2) as longer calls are likely to have a greater number of syllables than shorter calls. Principal Component 2 (PC2) is mainly associated with 'Frequency min' and 'Frequency max', both showing substantial positive loadings (0.69306 and 0.67827, respectively; Table 3-2), indicating that PC2 differentiates calls based on their frequency range. Principal component three (PC3) was influenced by ‘Number of trills’, with a significant negative loading (-0.9411; Table 3-2), highlighting its role in distinguishing calls with varying trill counts. Principal component four (PC4) was influenced primarily by ‘Number of switches’, with a significant negative loading (-0.9113; Table 3-2), accentuating its role in differentiating calls by the number of switches. Together these four principal components collectively capture 91% of the variance in calls (Table 3-1), resulting in clusters of individuals based on their unique vocal signatures. The fifth and sixth principal components contributed significantly less than the others to the explanation of variance likely as they consisted of variables used previously.

Table 3-2: Results of the PCA analysis using call variables to form clusters for individual identification.

PCA Results	PC1	PC2	PC3	PC4	PC5	PC6
Frequency min	0.11839	0.69306	-0.0842	0.12456	0.695	-0.0045
Frequency max	-0.0751	0.67827	-0.2499	-0.1685	-0.664	-0.0506
Duration	-0.6563	0.02885	0.11928	0.25577	0.04707	-0.6975
Number of Syllables	-0.6638	0.08883	0.14198	0.15753	0.01811	0.71149
Number of Switches	-0.2982	-0.0525	-0.1017	-0.9113	0.25382	-0.056
Number of Trills	-0.1418	-0.2194	-0.9411	0.18825	0.09542	0.03883

Thus, we plotted the k-means clusters using the first four principal components (Fig. 3-7), then again with all six principal components to see if the accuracy of the clustering improved (Fig. 3-7). Bird names were included in Figure 3-7 as a representation of the k-means clustering to their corresponding recorder group. This was then compared to the true groupings of the calls recorded by these recorders in Figure 3-8.

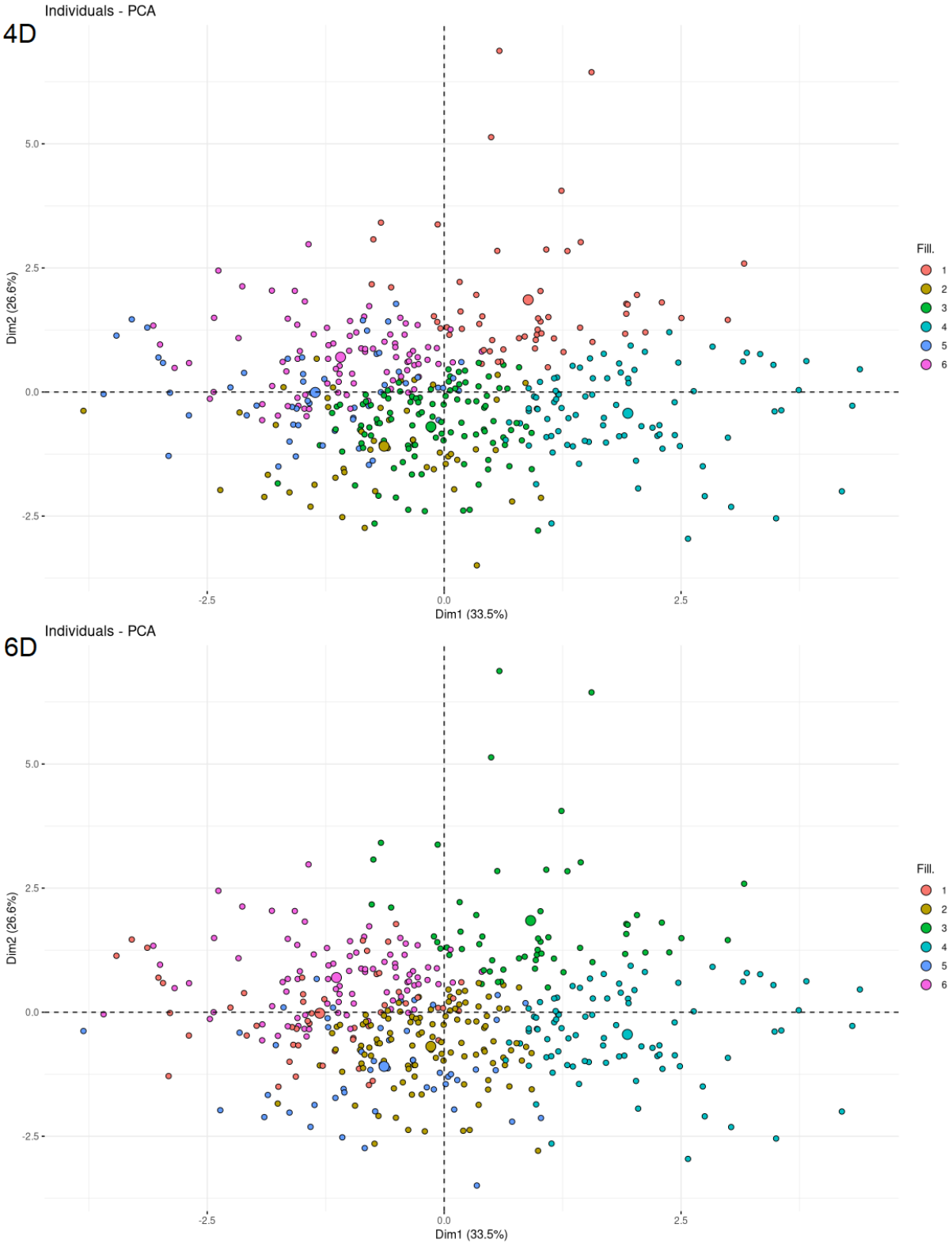

Figure 3-7) Plots of k-means clustering of four (**4D**) and six (**6D**) principal components to identify individual birds . The fill numbers 1 to 6 each represent the calls recorded by the recorders allocated to the nest site of a particular bird but are not recordings of one specific bird, rather, all birds within the recording radius. 1 represents Andre, 2 represents Jaeden, 3 represents Marc, 4 represents Martin, 5 represents Pippe, and 6 represents Shaun.

The plots (Fig. 3-7) show little difference in the clustering of call variables and show no evidence of distinct calls resulting from the clusters, regardless of whether four or all principal components are utilised. The k-means clustering failed to cluster together the groups of calls around a particular nest site that matches the bird calls to the correct recorder group. This result was reinforced when the k-means clustering was compared to the true identity of the calls (Fig. 3-8).

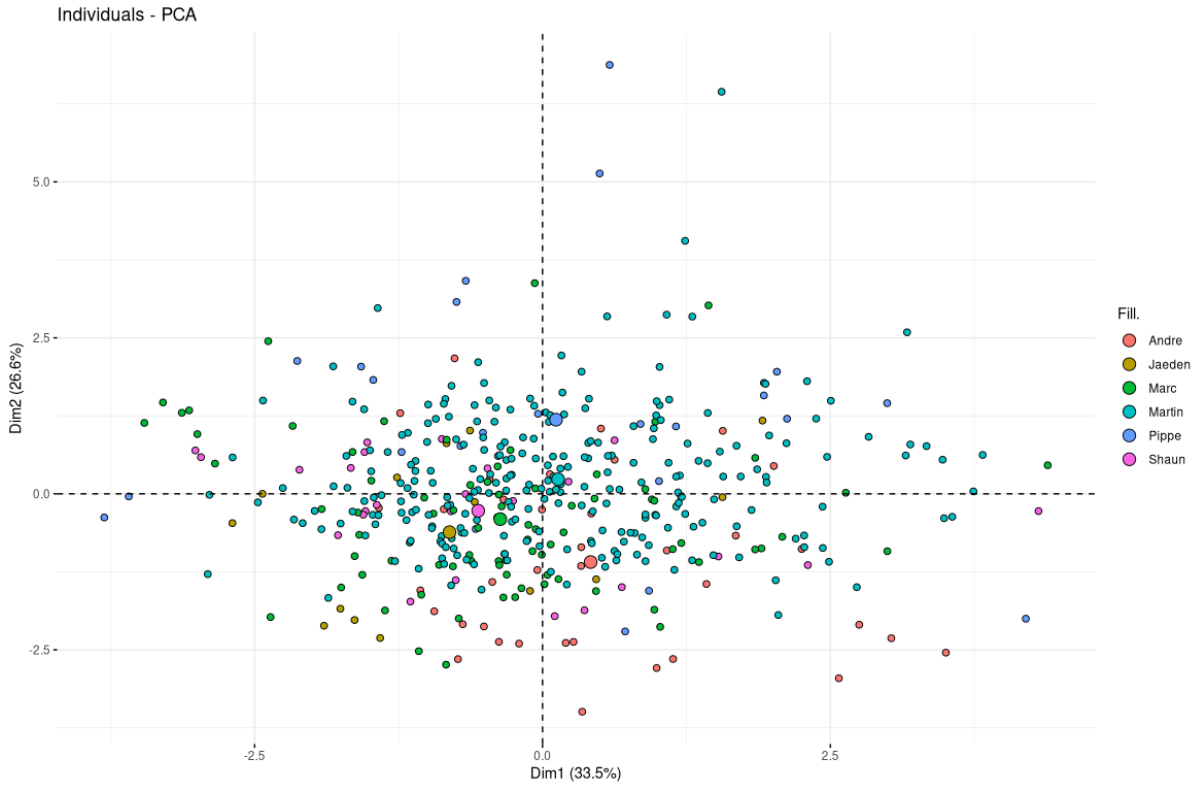

Figure 3-8) Plot showing the calls in relation to one another based on their spectral variables and coloured by what nest site the recorders were located around, showing the true identity of each call.

Increasing the number of principal components from four to six to increase the explanation of variance was unable to accurately identify the calls' identity using k-means clustering. The groupings of Figure 3-7 do not show any resemblance to the true groupings of Figure 3-8, which shows that increasing the number of principal components utilised does not increase the accuracy of the groupings. To test the accuracy of the k-means clustering when utilising four and then all principal components, two confusion matrices were conducted (Fig.3-9).

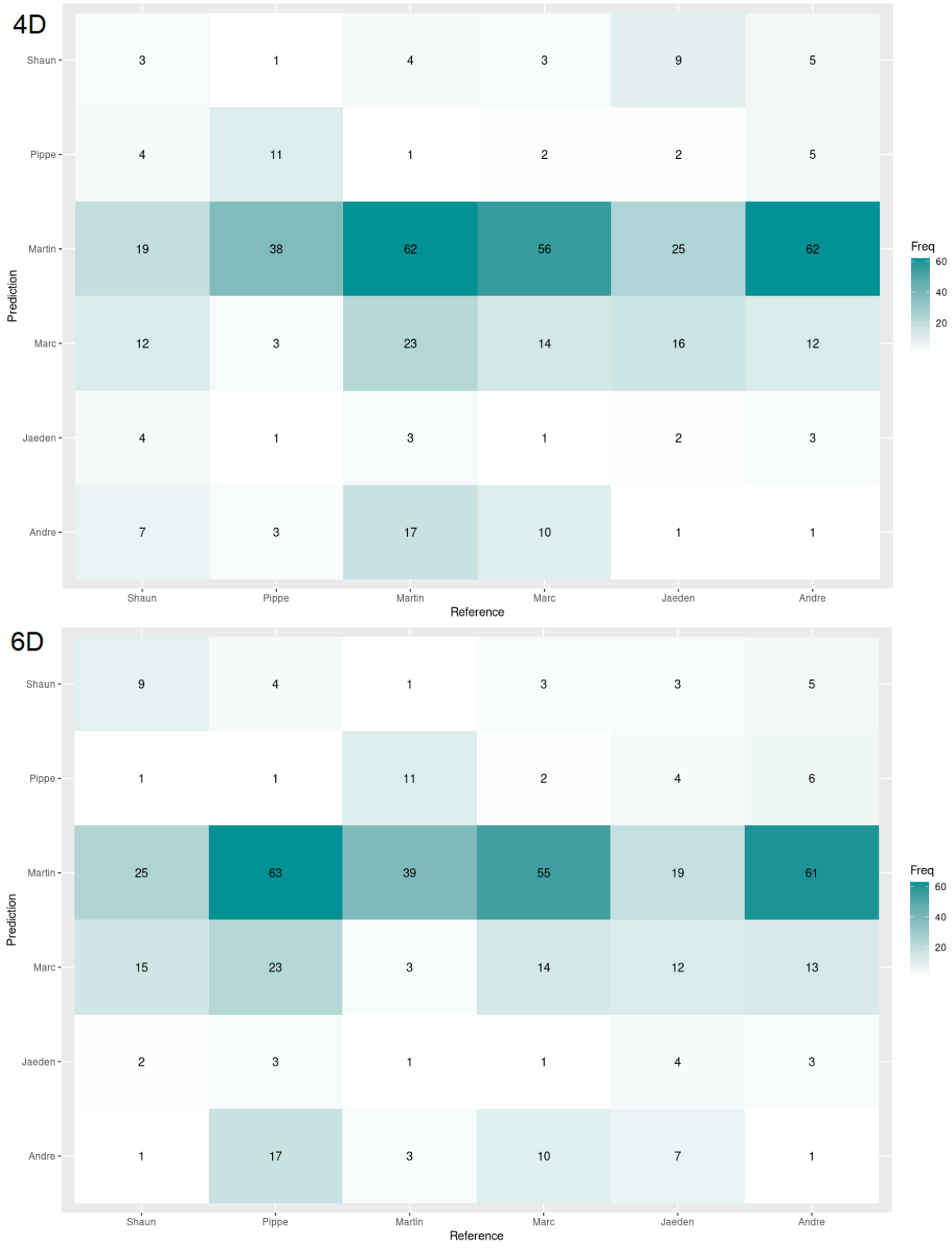

Figure 3-9) Plot of the two confusion matrices using four principal components to identify individual calls (4D), and with six principal components (6D). The reference row shows the true identity of the calls, and the prediction row shows who the model assigned each call to.

Results of the confusion matrices showed that the k-means clustering was more likely to mislabel calls than it was to correctly identify them. This result remains the same regardless of whether four principal components or six are utilised in clustering, with six even performing worse when identifying calls belonging to Martin's recorder group. This showed that even when using all the call variables provided (freq. min/max, duration, number of syllables, switches, and trills) the k-means clustering was not able to reliably identify the calls. Analysis of the confusion matrix results showed varying levels of classification performance. Recorder groups from birds such as Martin had higher balanced accuracies (0.504) while others such as Pippe were less accurate (0.413) and thus more likely to be misclassified.

The accuracy of the k-means clustering is further illustrated by the summary statistics of the confusion matrix, which reported that the clustering made correct identifications only 9% of the time. As a result, the identification of individual callers was not able to be obtained via these methods.

3.6.2 Call location estimation

Call location analysis showed that the relationship of call quality and altitude is primarily weakly negative (Fig. 3-10, Table 3-3). Across both 'All' and 'Shared' data sets, the percentage of rank 1 calls has a weak negative relationship with altitude, gradually decreasing as altitude increases (Fig. 3-10A, D). Rank 2 calls also share this trend, with the 'shared' group showing a strong negative relationship with altitude (Fig. 3-10B, E). The percentage of rank 3 calls followed a different trend, with a moderately strong positive relationship between altitude, and the percentage of rank 3 calls detected (Fig. 3-10C, F).

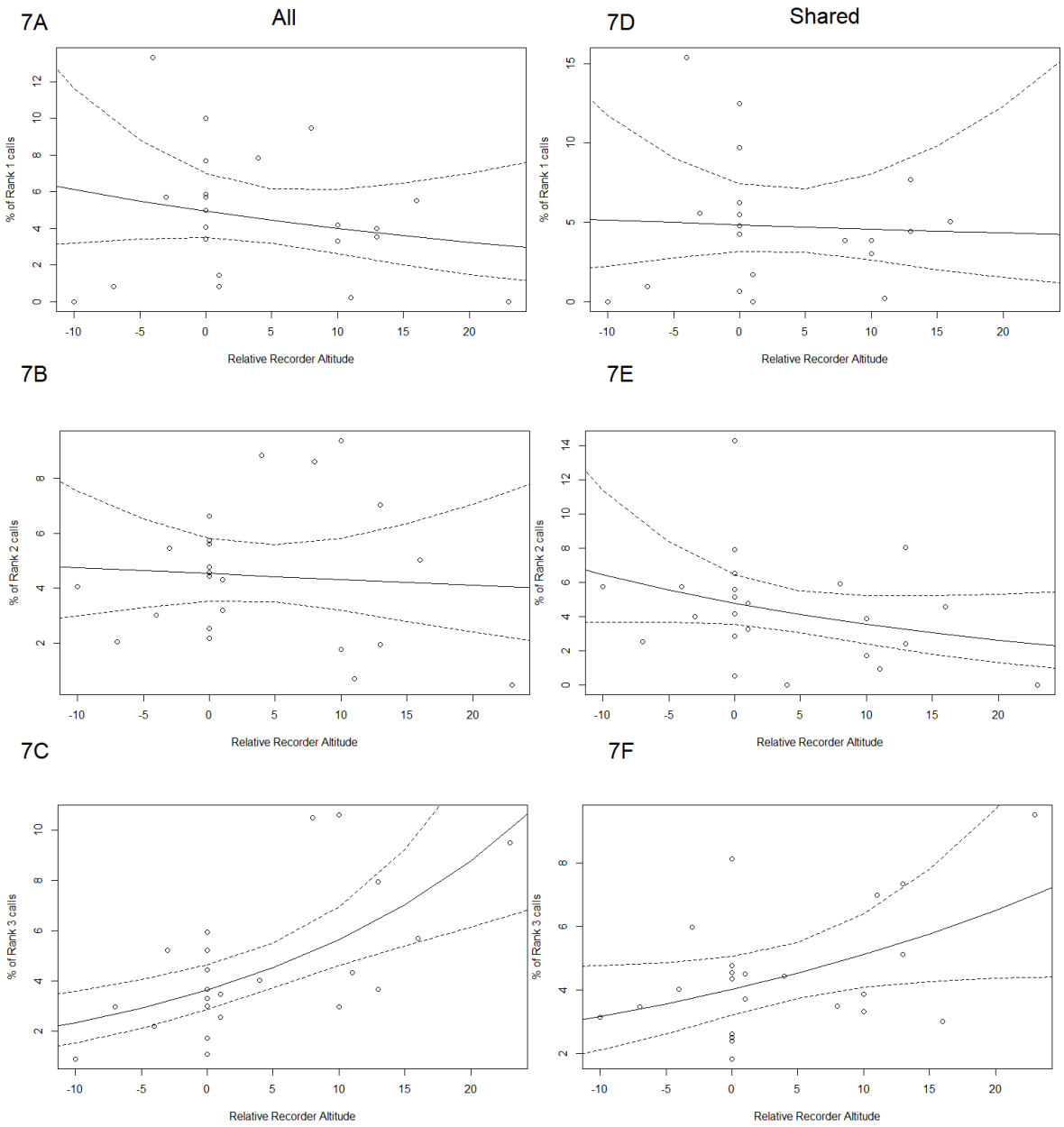

Figure 3-10) Trends of the percentage of rank 1, 2, and 3 calls vs relative recorder altitude using the all-inclusive dataset and the shared dataset.

Of these relationships, only the altitude against the percentage of rank 3 calls is significant (Table 3-3). This shows that altitude is a suitable predictor for rank 3 calls and thus having recorders in a high location allows the detection of distant calls. My results show that kiwi do not select to call at any relative altitude and other factors likely play a role in call location selection that were not investigated. This is shown as an increase in altitude for a calling

location relative to the nest site would indicate a preference for higher calling locations as effort would need to be expended to call from these sites, if they were advantageous to call from.

Table 3-3: Summary of the results of the negative binomial generalised linear model. The All dataset utilised the percentage of rank 1,2,3 calls per day against the relative recorder altitude to see if higher ranked calls occur more often at higher altitudes, with rank 1 being the highest rank. **SE** = standard error; **df** = degrees of freedom. RRA = relative recorder altitude (altitude of recorder in relation to the nest site its situated around); AIC = Akaki Information Criterion; * Indicates a significant p-value.

Rank	Dataset	Dependent variable	Predictor	Estimate	SE	p-value	AIC	Null df	Residual Deviance	Residual df
1	All	% rank 1 per day	RRA	-0.02123	0.02154	0.324	122.73	22	28.349	21
			Intercept	1.59744	0.17791	<2e-16*				
2	All	% rank 2 per day	RRA	-0.004873	0.015204	0.749	111.19	22	25.803	21
			Intercept	1.510181	0.12847	<2e-16 *				
3	All	% rank 3 per day	RRA	0.04411	0.0116	0.000143*	101.14	22	21.102	21
			Intercept	1.29045	0.425533	0.000514*				
1	Shared	% rank 1 per day	RRA	-0.005726	0.028845	0.843	111.16	19	24.375	18
			Intercept	1.577784	0.21814	4.73e-1*				
2	Shared	% rank 2 per day	RRA	-0.0302	0.15466	0.12	116.7	22	27.63	21
			Intercept	1.56343	0.15466	<2e-16*				
3	Shared	% rank 3 per day	RRA	0.02402	0.01209	0.0469*	95.254	22	13.365	21
			Intercept	1.39266	0.1172	<2e-16*				

The relationships highlighted between the NB GLM statistics and plots combined with the mapping of call hotspots (Fig. 3-11) indicated that the call quality rank is not predicted by altitude. This is shown by the spread of call locations throughout the gullies either highlighting a lack of optimal calling location, or the information conveyed via the call may not be intended for a broad audience. The only consistent trend of the data is that positions of higher elevations can detect calls of lower quality more often, suggesting that high-altitude locations provide good listening opportunities.

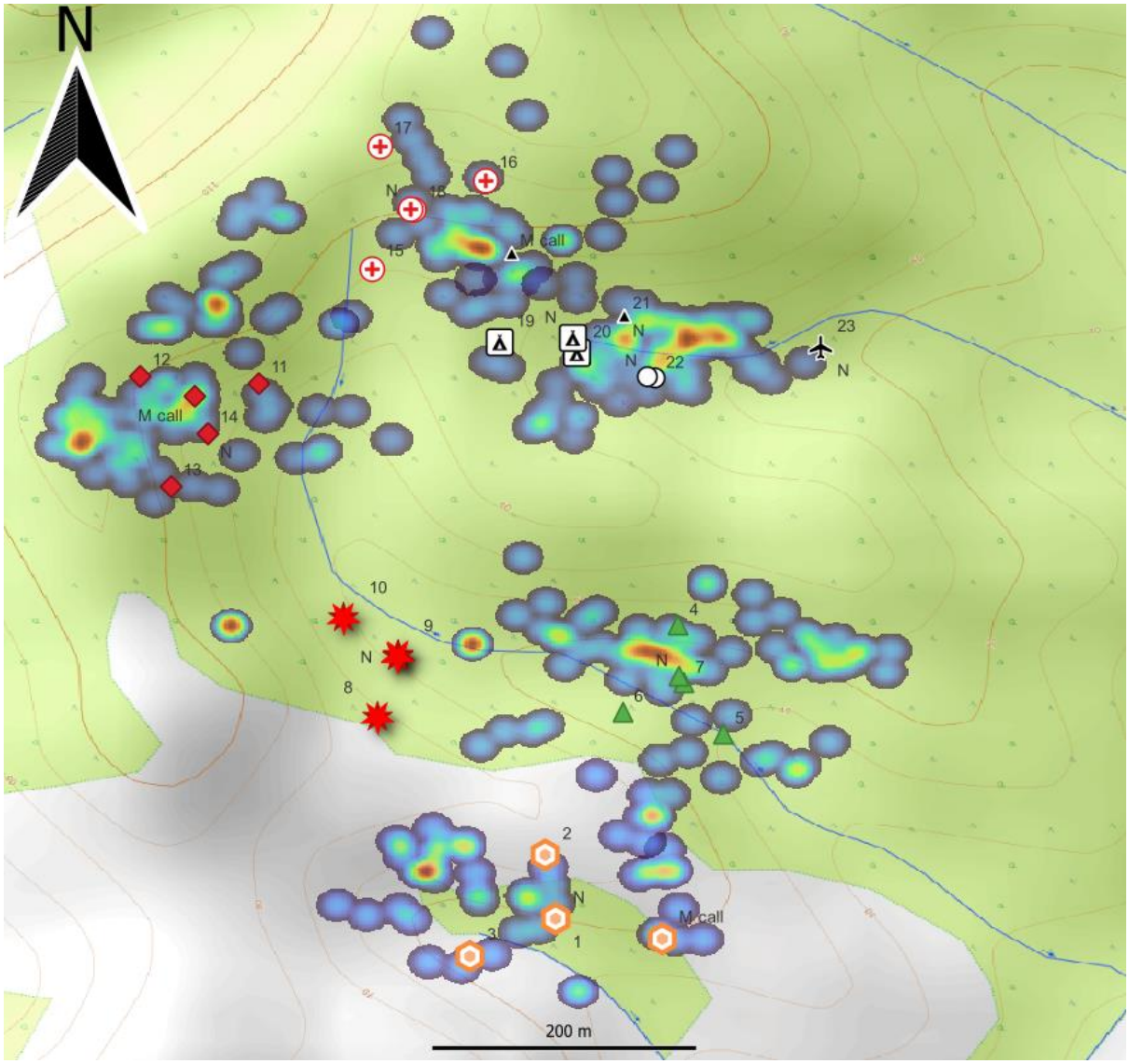

Figure 3-11) Map of calls recorded across multiple recorders per site, colour-coded to indicate which bird they belong to. Numbers one through 23 indicate recorders, N indicates nest sites, and M call indicates the estimated location of calls recorded manually. The different icons for each marker indicates a different nesting bird that the site is set up to monitor. The darker the red colour the higher the number of calls originating from roughly that location.

3.7 Discussion

Understanding the vocal behaviours of brown kiwi is important for conservation as methods of population surveying such as call surveys can be improved upon. This study aimed to test whether a small number of measurements from male brown kiwi calls could identify individual variation, and to see if kiwi seek higher ground before calling to better propagate their calls.

3.7.1 Individual ID

The results of this study propose that there may be elements of the brown kiwi call that could be individually distinct but when using all principal components and thus all call variables, the k-means clustering was not able to illustrate this. The results do not support the hypothesis that calls can be used for individual ID in brown kiwi. The rejection of the hypothesis may be the result of multiple factors, either independently, or compounding together. Such possibilities include: the utilisation of uninformative call variables, not accounting for intra-call variation, misidentification of the birds, differences in call type, and not utilising syllable variables either individually or in conjunction with call variables.

Using k-means clustering to group calls by comparing a set of spectral variables to highlight the clustering of calls of unknown individuals failed to find a significant pattern using these variables. Plotting calls from the recorders of known individuals produced a degree of overlap in the spectral variables. One possibility for the overlap in call variables (in this case frequency min/max), could be the result of similar body size, as body size negatively correlates with frequency in some birds (Martin et al., 2011). With regards to vocal individuality, birds displaying similar call characteristics may be difficult, if not impossible to identify based on calls alone, as no call stands out as particularly unique based on the degree of overlap in PC1 to PC4.

The lack of discernible pattern of call variables for the brown kiwi of Ponui Island could be the result of multiple possibilities. One such possibility is the movement of brown kiwi, as literature suggests they do not call more than 120m away from their nest site (Ellis & Marsland, 2022), and calls being audible from the 120m (Priyadarshani et al., 2018). This could provide variation in where calls are detected and thus mixing of calls from individuals that may move around within the gullies or even potentially in between gullies. This could result in recorders picking up a variety of calls and thus discerning any pattern from them, difficult if not impossible. If territoriality is a strong driver of calling behaviours, individuals may be limited to small zones around the periphery of their nest site and thus may not be able to move to optimal call locations. However, Ziesemann (2011) highlighted that brown kiwi within Ponui Island have considerable overlap in their home ranges which would likely allow for them to seek high ground for calling, despite what limitations may seem imposed by territory size.

The genetics of Ponui Island brown kiwi would likely impact call production, as genetics vary the structural components of the vocal tract, and thus change the resulting call (Corfield, 2008) . The brown kiwi population on Ponui Island was founded from brown kiwi that were translocated from Waipoua Forest, and Little Barrier Island (Undin, 2021). As the signalling of an individual has a strong genetic basis (Beecher, 2015; Dale et al., 2001; Levréro et al., 2009), one would assume this would make the brown kiwi's call distinct, however our results do not reflect this. The degree of relatedness to surrounding kiwi may also influence the resulting call, and the degree to which they are distinct. Closely related individuals may sound similar due to anatomical similarities. This could be influenced by dispersal, as family members may stay close, or move far from other family members to lessen the effects of competition on each other.

An additional factor is time. Jaeden's recorders ran exclusively from the 21st of October till the 22nd, opposed to the other calls which were recorded throughout August. This could result in kiwi calling for different purposes as individuals that may have been incubating in August, may not be incubating in October. This is also likely to be a factor in the purpose of calls, as this study utilises calls exclusively from the incubating periods of males. By extension this means that the calls analysed are likely to be representative of brown kiwi calls for approximately five to six months as this includes two clutches (Cockrem et al., 1992).

Other studies on kiwi species acknowledge the presence of vocal individuality in three out of five kiwi species, namely brown kiwi (*Apteryx mantelli*), the great spotted (*Apteryx maxima*), and little spotted kiwi (*Apteryx owenii*) (Corfield, 2004; Dent & Molles, 2016; Digby, Bell, et al., 2014b) with the variability of the individuality of calls being noted within the *Apteryx* genus. One of the main differences between this study and others investigating vocal individuality is the method. This study primarily uses spectral variables from the whole call of an individual, measured using visual analysis of spectrograms with no focus on any part of a call. Other literature used differing elements of the call, some being broken up into syllable groups either to cover the entirety of the call in three groups as in Dent and Molles (2016), others use amplitude and frequency ranges of the fundamental harmonic of every syllable to categorise calls (Corfield, 2004). Additional to the differences in the sampling method of the call variables is the difference in analysis method, with discriminant function analysis being a common method used for the analysis of calls (Corfield, 2004; Dent & Molles, 2016; McGregor et al., 1993). The main reason for not using a discriminant function analysis in this study was because it requires calls to be catalogued from known individuals (Corfield, 2004), which while it was attempted during this study, insufficient known individual calls were recorded.

Other literature has sampled distinct segments of calls, with some sampling theorised signatures, and others sampling syllables from the middle of a call (Corfield, 2004; Puglisi & Adamo, 2004). This method may be more appropriate however, it requires multiple recordings of known individuals which we were unable to collect during the short duration of this study.

To improve the study, longer durations of monitoring would be required with multiple recordings of calls from known individuals. Once the manual call recordings were acquired, they could be catalogued and compared to other individuals within Ponui Island to test whether individuals could be identified even in high-density kiwi populations.

If brown kiwi have individually distinct calls with an individual signature of low variability (Terry et al., 2005), in addition to being stable throughout an individual's repertoire then accurate classification via calls alone would be possible. This could be incorporated into call surveys to improve population estimation accuracy. It would also be useful in areas of high population densities, cryptic species, and for species that inhabit densely foliated (Peake & McGregor, 2001) or otherwise difficult-to-approach areas to reduce the effort needed for monitoring. Provided evidence of other unstudied kiwi species possessing vocal individuality, this method of monitoring could be applied to the *Apteryx* genus, providing a standardised monitoring technique for the group.

Future work should focus on developing a method that utilises vocal individuality to successfully monitor cryptic, nocturnal, or hard-to-reach species. The resulting study should aim to be long-term to capture potential shifts in vocal repertoire and account for unforeseen difficulties that arise from developing a new monitoring method. This new method could also be tested on vocal non-avian species to see if broader applications would be appropriate for other endangered species.

3.7.2 Call location

We found that the calling location of brown kiwi was not determined by relative altitude from the nest as shown by the results of the NB GLM in conjunction with the approximation of calling locations shown via a heatmap. The results of the NB GLM show that despite the relationships between call quality and relative altitude, in general, being weakly negative (excluding rank 3 quality), there is no significant effect of relative recorder altitude on call rank quality. The intercepts of the NB GLM show that there is a relationship to call quality, but altitude is not the appropriate explanatory variable. The heatmaps of calls from the shared dataset show that there are hotspots that in some cases tend to be of high-altitude locations thus potentially better for call transmission. This trend is not found throughout all call hotspots suggesting altitude is not the main call location predictor but instead likely results of multiple compounding factors.

One consideration when it comes to bird call recordings is the environmental factors interacting with call transmission. Weather, foliage presence, and the shape of the surrounding terrain interact with the way a call travels and thus is received by a recorder or potential listener (Gibb et al., 2019; Priyadarshani et al., 2018). To mitigate the impacts of environmental factors, all recordings were taken from the same period to maximise the number of functional recorders and keep the weather conditions as consistent as possible. Naturally, there was still likely to be variation due to the differences in foliage density and type in addition to the differing geography of the gullies and consequently, the recorders' location in gullies (Gibb et al., 2019; Priyadarshani et al., 2018). Variations in location resulted in recorders being placed on the gully floor for some and others being located around the periphery of the gully wall just below the ridgeline. All these environmental variables variations can result in differing detection rates for calls which was accounted for by utilising

three different gullies with different environmental variables with the dataset being compared across every site instead of individually.

When the results of this study are compared with other literature, there is a trend of calls from an elevated position, travelling further, naturally implying less attenuation (Parris, 2002; Schwartz et al., 2016). This is important to consider regarding this study, as the hypothesis is that brown kiwi call at an optimal location in the form of an elevated position. Thus, elevated positions would likely be the optimal calling location based on the assumption that brown kiwi want to broadcast calls as far as possible, which in a densely populated habitat like the habitat on Ponui island, may not be necessary. Call location selection in other literature considers the trade-off between call projection and the risk of predation (Krams, 2001; Miles & Fuxjager, 2018; Ramji & Mah, 2020). When brown kiwi behaviour is thought of in this context there are two groups of predators to consider, extinct past predators (other birds) and the current predators (mammals). The shift in predator presence may cause a shift in the brown kiwi's calling behaviour as calling locations now face different pressures.

Lastly, another potential driver of call location is temperature. Temperature affects how song travels through a soundscape (Bohn, 1987), alters call rates (Braga & Motta-Junior, 2009; Digby, Towsey, et al., 2014), and alters metabolic efficiency in some animals (Höbel & Barta, 2014).

As the results of this study show no pattern in call location, this presents multiple possibilities as to why this may be the case. The alternative reasoning that is indicated by the data is that male brown kiwi call at random locations within their home range shown by the lack of relationship between call quality and relative altitude. The heatmap of calling locations shows this as well, as there are locations with greater numbers of calls than others but there is no distinct pattern to determining this location such as altitude, or even position within the gully.

Utilising recorders distant from an individual's nest such as the case in Pipe gully, may have blurred the true calling patterns of a male. This would make it difficult to identify the use of the high ground as calls from distant males may skew the most utilised location.

Calling from altitudes greater than the nest site could cause a negligible impact on call distance thus changing altitude may be more costly for little to no gain. Another possibility is that the narrow environment of the gullies may not require long-reaching calls, as the information communicated via calls may only be useful/intended for other kiwi within the gully. The calls utilised in this study were recorded during the breeding season, so it is not unlikely that this influenced the function of the calls, and potentially the calling behaviours associated. The costs and benefits associated with communicating relevant information during the breeding season are likely factors influencing the calling behaviours. If the calls were for the males to communicate that they have left the nest, they may not need to broadcast them far if the female is close by, even being disadvantageous to do so, as it may advertise an empty nest. The male's nests on Ponui Island are often close to each other, so to signal their territory, they may not need to broadcast very far, thus seeking good broadcasting locations redundant or detrimental.

If an environmental or geographical factor was found that adequately explained call location selection, this could be tested in mainland environments where individuals are sparsely distributed and compared to island habitats. This would provide a useful comparison to investigate whether call location selection is impacted by differing population sizes of the respective habitats. This information could then be utilised to help infer the purpose of brown kiwi calls as the current understanding is that kiwi call for territory maintenance but this conflicts with the multiple kiwi living within close proximity on Ponui island.

This side of the study could be improved by better categorising and cataloguing the environmental variables that affect calling, and thus potentially affect call behaviours.

Additionally, limiting the calls used to a 120m radius from the nest may improve the accuracy of identifying call locations, as covering more area may obscure true call location patterns. A better understanding of brown kiwi call behaviours would allow for better management in a variety of environments and population densities to contribute towards more effective conservation of the *Apteryx* genus.

While the data from this study had the potential to provide a basis for understanding brown kiwi behavioural ecology, it was limited by various factors. The short overall duration of the study was a limiting factor and this itself was caused by the difficulties of logistics and the availability of funding. The experience of the researcher as equipment knowledge and experience resulted in issues at times. This resulted in malfunctions and user error causing data loss and contributing to the lack of manual call recordings that were available to acquire during the short window of research. Lastly, the weather of the study period was a severe limitation as the telemetry equipment was not waterproof and thus significantly reduced the availability of suitable manual call recording sessions. While these limitations did hamper research, they are not impossible to overcome and can be mitigated in future. This could be done by allowing a longer study period and increasing the familiarity of the equipment as these are the two main solvable limitations within this study.

Future work should be conducted on call location selection across several endangered species as knowing the habitat and calling preferences of vocal species can contribute significantly to conservation. Knowing preferred calling locations allows for the improvement of habitat management which then can be used to tailor conservation efforts specifically to the species being managed. Kiwi could be studied further to investigate if there are broadcast location preferences in other populations, across a range of locations to capture potential behavioural variation due to geographic differences. Future work could also investigate the potential for changes in call structure or type over time, through different seasons and over years, to

account for any behavioural changes caused by environmental variables, and breeding seasons.

3.8 Conclusion

This study aimed to explore if brown kiwi displayed vocal individuality, and if they call from an optimal position at a greater elevation than the nest. We found that we could not provide evidence for vocal individuality, possibly due to using uninformative call variables and having no repeated manual call recordings. In the future, the study would ideally be carried out over multiple years to observe the impact of multiple breeding seasons on brown kiwi calls to capture more of an individual's vocal repertoire. A discriminant function analysis would also be used in conjunction with a greater library of manually recorded calls with the identity of the bird verified post-recording. These changes would deal with most of the limitations of this study and provide better insights into the identification of vocal individuality in a densely populated brown kiwi habitat.

We also found that while there are minor patterns in call location selection, none are statistically significant. This shows that while there are patterns, they are not explained by differences in elevation as all call quality ranks have a relatively neutral relationship to relative elevation. Future studies should focus on other environmental factors impacting both calling behaviour, and the acoustic environment for passive acoustic monitoring. Estimations of population densities should be included to investigate the role population density has on calling behaviour as these may display plasticity because of density-dependent behaviours.

While both hypotheses have been answered, both can be improved upon and thus play a role in better filling the knowledge gaps surrounding brown kiwi vocalisations if the challenges presented by passive and active acoustic monitoring can be overcome, in a more robust, longer-term study. The potential gain for brown kiwi could come in the form of less labour-

intensive, minimally invasive, passive monitoring allowing better censusing of populations and their dynamics, with known individuals readily identified, and the relationships between individuals potentially being identified.

Overcoming these challenges contributes significantly to improving the knowledge surrounding a national icon, providing better ecological management of an ancient species while contributing to the field of conservation through proven utilisations of new methods to monitor cryptic, endangered species.

4 Concluding remarks

During this thesis, the vocal anatomy, vocalisations, and vocal behaviours of the North Island brown kiwi (*Apteryx mantelli*) were explored in a variety of manners. During this undertaking, there have been successes and shortcomings alike. The vocal anatomy of the brown kiwi was described, covering every aspect from the tongue and oropharynx, right through to the bronchi. Such a complete description has not been undertaken ever and will greatly contribute to our understanding of kiwi vocal production and its application in taxonomy. Additionally, I found differences in the vocal apparatus of male and female kiwi and between kiwi and other members of the ratite group.

Investigation into the vocal individuality of brown kiwi showed call overlap with little consistency to the patterns of overlap or distinctiveness. However, the reason why is currently unclear, as there may be more to the call repertoire of brown kiwi than what was captured. Calling location selection uncovered little preference for broadcasting locations, but instead showed that for optimal listening, positions along elevated ridgelines were preferable. The contributions of this study to our understanding of this national bird will be significant in multiple avenues. Improving our understanding also improves our management and knowledge of this species and the other members of the *Apteryx* genus.

4.1 Successes

The investigation into the vocal tract of brown kiwi, displayed clear differences between male and female kiwi, highlighting a likely source of origin for the sexually dimorphic calls. The investigation into call location selection did not provide support for the hypothesis that male brown kiwi select advantageous locations of increased altitude to call. However, trends were highlighted via the heatmap that showed patterns of bird calls being detected in greater

frequency at positions of high elevation, often near the top of ridges. This trend was supported by mapping the location of every confirmed call of known individuals which showed calls occurring at greater elevations than their nest sites. While evidence for vocal individuality in brown kiwi was lacking potentially due to our methods, the method for recorder placement proved effective as there were rarely times when calls were not detected on multiple recorders. This shows that the supporting literature was applicable and effective in their methods, during this study despite differing geographic features than that of the literature used. This can be used in future studies as it now provides a proven framework for monitoring nest sites of brown kiwi using ARUs, maximising coverage while minimising equipment requirements.

4.2 Limitations

Utilising the limited data available, we tested our hypothesis that individual male brown kiwi can be identified by robust characteristics of their call alone. We tested this utilising a PCA which failed to provide adequate variance explanation over the two principal components used. This resulted in low accuracy of the PCA and consequently provided little evidence for vocal individuality. The differences in male and female brown kiwi vocal anatomy were present but often were not statistically significant. This was likely not due to any fault of the methods, but simply due to the availability of specimens. Carcasses of an endangered species in usable condition were present, but not in sufficient numbers. Often, distinct features were difficult to identify due to the inexperience of the author and the varying conditions of the specimens, with damaged and decaying tissue frequently obscuring features. One of the more significant limitations faced during the study was the time frame of fieldwork, as the total fieldwork was carried out over one and a half months. This may have contributed to the result's lack of significance, as user error and equipment failures were all concentrated within

the timeframe used. The duration of fieldwork also meant contending with poor weather conditions present as the bulk of fieldwork was undertaken during the last month of winter. This contributed to the small database of manual call recordings from known individuals, hampering results further.

4.3 Refining the study

The anatomical investigation and description of the brown kiwi vocal tract could be improved upon in a couple of ways. Additional fresh specimens of male and female kiwi would contribute greatly to highlighting the significance of the variation found between the sexes. With more male specimens, the degree of individual variation could be investigated with the role of testosterone being considered as well. If represented by other paleognaths, the development of the vocal tract could be observed in emu (*Dromaius novaehollandiae*) as this species has been farmed in Australia. As they are farmed, individuals could be chosen at specific times during development to show changes in the vocal tract over time, with the supply of specimens not being limited due to conservation status or availability. Additionally, the impacts of testosterone on vocal tract development in juvenile kiwi could be investigated during the first breeding season, as testosterone is known to increase during this period in males and females (Jensen et al., 2019; Malecki et al., 1998; Potter, 1989). Emu would also be an ideal study specimen as the rest of the individual can be used commercially minimising the waste generated through dissections, as only small portions of the animal would be required.

The investigation for evidence of individual variation in brown kiwi calls could also be improved upon. Longer recording periods, ideally up to four years to account for variations in call repertoires, environmental changes, changes in bird location, and provide ample time to record multiple manual call recordings of known individuals. This could provide stronger

patterns of call variables while highlighting the consistency or lack thereof, of brown kiwi calls over time. Longer recording periods would also allow for remedying user errors and equipment failures, as equipment can take long times to repair if repair is possible at all.

To identify patterns in call location selection, longer recording periods could also be utilised to improve the pattern-detecting ability, granted by the data. However, greater collation of environmental variables could also improve the study. The only way this thesis accounted for weather effects, was by using the same recording period for all calls utilised, thus providing consistency of weather patterns, moon phase, and temperature. Naturally, this limited the amount of data available significantly. More attention could be given to the acoustic properties of the environment of Ponui Island. Testing call detection by using an array of recorders like that of Priyadarshani et al. (2018) prior to setting up recordings in the study site would be useful to show how calls are transmitted and are received in a highly variable environment.

4.4 Future considerations

As this study focused on a dense population of brown kiwi, it would be advantageous for future work to be carried out on a population of similar density. What we currently know of brown kiwi vocal behaviour is largely derived from areas of low population density and is unlikely to uncover potential differences arising from density-dependent behaviours. How territory is maintained in dense populations should also be of interest. While the current population of kiwi species remains reduced in their historical ranges, it would be beneficial to know how they may act once populations rise to greater densities to better inform management decisions.

As the goal of this thesis was to improve current monitoring techniques of brown kiwi, it would be important to investigate the fundamental components of call surveys. I would suggest repeating this study on vocal individuality but with accommodations made to reduce the limitations faced and with improvements made on the methods. Brown kiwi have no fixed call rate (De Rosa, 2021), which leaves a couple options for monitoring, either utilising vocal individuality or utilising a custom spatial capture-mark-resight model for population density estimations (De Rosa, 2021; Efford & Hunter, 2018). Changes would be made to the methods of another study, including the use of animal-borne acoustic recorders (ABARs) to remove the need for manual call recordings which were heavily impeded by weather. Changes to the call analysis would also be needed to minimise the impacts of intra-call variation as Corfield (2004), Dent (2013), and Digby (2013), noted high levels of variation at the beginning and end of a call. Minimising the impacts of intra-call variation can be done by utilising calls with a select number of variables or averaging the syllable variables to make for a more informative data set. Including syllable variables additional to the call variables would be an important step for the future study as it is a common trend in other studies analysing calls for vocal individuality in other kiwi species (Corfield, 2004; Dent, (2013); Digby, (2013), and may provide more informative variables than the call variables we used alone. Recording calls over a longer duration would also be important to capture a wide variety of calls representative of the brown kiwi vocal repertoire. Recording over a longer time would also provide a larger library of data to work with in discriminating individual calls. Additionally, the longer recording time would also cover variations caused by seasonal changes in call purpose.

Future anatomical studies could pick up where this thesis ends, providing multiple opportunities for investigations into brown kiwi anatomy. One such study could be investigating the role of the two pairs of pharyngeal folds found in the brown kiwi oropharyngeal cavity, as similar structures in ostrich (*Struthio camelus*) and emu (*Dromaius novaehollandiae*) have been found and are functionally similar to true tonsils in birds.

Neurological examination of the vocal control mechanisms of male and female brown kiwi would be beneficial. We have identified structural differences in vocal anatomy, thus uncovering the degree of control individuals have over these anatomical features would further illustrate the significance of the sources of dimorphic vocalisations.

A study into the variation of brown kiwi vocal tract features could also be beneficial, as this thesis has provided evidence of sexual variation but lacks information on individual variation. Such a study may provide support for individually distinct vocalisations as unique vocal tracts would produce unique calls.

Lastly, research on the efficacy of utilising vocal individuality data should be undertaken as to be of any benefit to monitoring efforts, it must be feasible to utilise the data this vocal feature may provide. The ease of use must outweigh the associated costs of using information-dense data as time and finances may limit its practicality. Testing potential applications would be important as the goal is for vocal individuality to be used in improving current monitoring methods, thus improving management actions for conservation.

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