Sequencing the New Zealand dawn chorus: can song playback alter the timing of song initiation?

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Abstract

The dawn chorus of songbirds is a behavioural phenomenon occurring prior to sunrise; birds of many different species sing simultaneously at rapid rates. Avian physiology, social behaviours and local environment all influence the onset of dawn song. The influence of social cues on dawn chorus singing is poorly delineated relative to the effect of environmental or physiological factors; in particular, our knowledge of the role of heterospecific cues is limited. In this study, I aimed to determine if New Zealand songbirds would chorus in a distinct order, like those seen in other countries. I investigated whether the timing of song onset relative to sunrise would change as the breeding season progressed. I also assessed if conspecific and heterospecific acoustic cues influence a species' start time. Finally, I explored the influence of acoustic cues from an early singer, the Tui (*Prosthemadera novaeseelandiae*) and a late singer, the Riroriro (Grey Warbler; *Gerygone igata*) on start time. I recorded the dawn chorus at nine sites at the Maungatautari reserve between September and November 2016, using arrays of time-synchronised autonomous recording devices. I broadcast different playback stimuli at three arrays per morning; an early singer, a late singer, and noise. My results suggest that New Zealand dawn choruses follow an order and that the timing of chorus start time changes over time as the breeding season progresses. Tui began singing earliest, and their start time shifted much earlier as the breeding season progressed. Most species joined the chorus in a highly interchangeable order within the same 12 minute window, while Pōpokatea (Whitehead; *Mohoua albicilla*)

sang last. Start time was not found to shift in response to any playback stimuli for any species. The onset of Tui or Riroriro song is unlikely to be used as a cue by either con- or heterospecific neighbours to initiate their own dawn song.

Acknowledgements

And finally, I'd like to thank the birds for what was nothing less than a stellar performance. Here's to many bigger and bolder ones in years to come.

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Chapter 1

General Introduction

1.1 The dawn chorus

"Why do birds sing?" is a question that has surely crossed the mind of many a bleary-eyed person woken by the raucous singing of birds in the early morning. Songbirds possess a unique vocal organ, the syrinx, which allows them to produce complex acoustic signals that can be easily modulated (Larson & Goller 1999). These signals, which we describe as "songs" are a complex form of vocalisation that requires learning from conspecifics in the Oscine songbirds, and serve many different functions (Catchpole & Slater 2008). Mate attraction and territory defence are the chief functions of birdsong, though it is also important for social stimulation of the reproductive state and conspecific and sex recognition (Catchpole & Slater 2008; Marler & Peters 1977). Most songbirds sing during daylight hours (Catchpole & Slater 2008), and day song is the most studied and well understood of their diel singing patterns.

Less well understood are the singing behaviours of birds at dawn. The distinctive singing of many individuals at once at high song outputs is known as the "dawn chorus" (Burt & Vehrencamp 2005). Starting 30-60 minutes before dawn, typically in the breeding season, males from different species join in a cacophony of song, which then recedes after day breaks (Staicer et al. 1996). Due to its complexity the ultimate and proximate causes of the dawn chorus remain controversial (Farina et al. 2015), and various hypotheses on its causes and functions have been put

forward, many of which are not mutually exclusive (Staicer et al. 1996). Factors influencing dawn chorus song are broadly categorised into three groups: intrinsic factors, environmental factors and social factors (Staicer et al. 1996; Dabelsteen and Mathevon 2002). Intrinsic factors are aspects of the bird's anatomy and physiology that influence dawn song; for example, dawn chorus song output in Blue Tits (*Parus caerulus*) is positively correlated with testosterone levels (Foerster et al. 2002). Environmental factors describe influences from the bird's environment on its singing. Temperature is one such example, with increased temperatures having been shown to result in earlier singing in White-Cheeked Bulbuls (*Pycnonotus leucotis*) (Hasan & Badri 2015). Social factors describe aspects of the dawn chorus related to communication; Black-Capped Chickadees (*Poecile atricapillus*) for example will increase their dawn song output in response to aggressive song with high levels of frequency matching and song overlapping compared with more submissive song that lacks these qualities (Foote et al. 2008).

Historically, the dawn chorus has been difficult to study due to the logistical challenges of surveying large numbers of birds in the field at dawn (Foote et al. 2008). However, the development of new techniques such as the use of remote microphone arrays has made studying dawn chorusing much easier than before, particularly when it comes to interactions at the community level (Burt & Vehrencamp 2005).

1.2 Intrinsic factors

Circadian cycles have been proposed as one of the key factors explaining why songbirds sing so intensely at dawn. Staicer et al. (1996)

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proposed that elevated levels of certain hormones at dawn may be the cause for such high song outputs. Goodson et al. (1998) found that elevated levels of arginine vasotocin, a hormone that controls reproductive and aggressive behaviours in most vertebrates, resulted in more vigorous dawn singing in Field Sparrows (*Spizella pusilla*). In their 2010 study Helm & Visser found that the circadian free running period of Great Tits (*Parus major*) exhibited great variation, and that these variations were highly heritable. If deviations from the standard free running period conferred a fitness benefit, they could be selected for and alter singing behaviour within the population (Helm & Visser 2010).

1.3 Environmental factors

Several aspects of a bird's environment can influence its singing behaviour at dawn, and environmental conditions at dawn play a part in why dawn may be the optimal time for an energetic bout of high song output (Dabelsteen & Mathevon 2002). Ambient light is one such factor, as many songbird species will alter their singing behaviour to naturally track the changing times of sunrise and twilight (Allard 1930; Fisler 1962), marking it as an important cue for song onset. The influence of artificial night lighting on dawn singing is well documented, with light pollution being shown to alter song timing and behaviour in many species, such as American Robins (*Turdus migratorius*) (Miller 2006) and Northern Mockingbirds (Hill et al. 2005).

The acoustic environment naturally has a significant impact on behaviours involving the propagation of acoustic signals (Brumm & Slabbekoorn 2005). One reason proposed for why birds sing at dawn is

that impediments to acoustic transmission are minimal (Henwood & Fabrick 1979). Atmospheric heterogenies are lower at dawn than during the day, resulting in less variable signal quality (Brown & Handford 2003). As signal masking has fitness consequences, songbirds exhibit adaptations to minimise the effect of ambient noise, be it from environmental, anthropogenic, conspecific or heterospecific sources (Brumm 2005). Some birds respond to noise by increasing the amplitude of their song (Brumm 2004), however in particularly noisy environments shifts in song timing and frequency may be more effective at minimising signal masking.

Environmental effects are particularly important from a conservation standpoint, as both anthropogenic noise and light have been shown to have a significant impact on dawn singing in songbirds (Arroyo-Solís et al. 2013), which could then have knock-on effects for breeding behaviour and breeding success (Kempaeners et al. 2010).

1.4 Social factors

Much like day song, there is much evidence to suggest territory defence and mate attraction are significant functions of dawn song (Staicer et al. 1996). As a behaviour strongly tied with breeding, sexual selection likely plays a key role in dawn singing. Otter et al. (1997) found that song output in Black-Capped Chickadees served as a reliable indicator of a male's dominance rank, and that females were actively assessing the quality of males through their song output. Displays such as dawn chorus singing are particularly useful male quality indicators because their expression depends on the performer's immediate condition

(Murphy et al. 2008). The ability to pitch shift during the dawn chorus in Black-Capped Chickadees has been also been shown to function as a reliable indicator of male quality (Christie et al. 2004), as does the start time of dawn singing in Eastern Kingbirds (*Tyrannus tyrannus*) (Murphy et al. 2008). Improvement of male's physical condition through increased food intake has been shown to increase song output, as shown in a study of Eurasian Blackbirds *(Turdus merula*) where the birds were found to increase the duration, peak song rate and start time of their dawn chorus after their body condition improved as a result of supplementary feeding (Cuthill & MacDonald 1990).

Patterns of female fertility and brooding across the breeding season can also affect dawn singing behaviour in males (Welling et al. 1995). Male Great Tits will increase their dawn song output as the fertility of females increases prior to the egg laying period, and this elevated output will drop off again once eggs have been laid and female fertility drops (Mace 1981). In their 2014 study, Bruni & Foote found that male Eastern Phoebes (*Sayornis phoebes*) show a similar pattern of increased song output in periods of high female fertility, and that brood number also had an effect, with males singing less vigorously during the fertile period of the second brood than of the first. Such studies show that dawn singing in males is intimately tied to female fertility.

In many species, rates of dawn singing remain high during the breeding season after territories are established and most males have already formed pair bonds, suggesting it has social functions in addition to mate attraction (Slagsvold et al. 1994). One such function is interactive

communication between males; when all males are singing simultaneously a male individual can easily assess its neighbours, their place in the dominance hierarchy and the boundaries of their territories (Foote et al. 2011). Stacier (1996) believed this "social dynamics hypothesis" best explained many of the qualities of the dawn chorus, and several studies since have established the importance of the dawn chorus as an interactive communication network. Burt and Vehrencamp (2005) noted that during the dawn chorus, Banded Wrens (*Thryophilus pleurostictus*) did not seem to be interacting with any one neighbour in particular, rather they directed their song at a range of different individuals. In their 2008 study of Black-Capped Chickadees, Foote et al. found that Black-Capped Chickadees frequency-matched the singing of neighbours during the dawn chorus, and that the amount of matching was related to both flock membership and rank disparity, suggesting communication between males is an important function of dawn song. A study of Black-Capped Chickadee choruses found that males were engaged in song matching with other males for 40% of their dawn chorus, solidifying the importance of communication between males in the dawn chorus (Foote et al. 2010).

While there are distinct benefits associated with attending to conspecific cues, they are not the only auditory cues available to songbirds in the early morning (Stanley et al. 2016). A typical dawn chorus consists of a multitude of different species singing at once, often joining the cacophony in a predictable, stereotyped sequence (Allard 1930; Leopold & Eynon 1962). Individuals therefore have access to signals from many different heterospecific neighbours at dawn. Heterospecific cues can

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contain important information; for example, the Collared Pika (*Ochotona collaris*) eavesdrops on the alarm calls of both conspecifics and heterospecifics, and increases its vigilance towards predators in response to both (Trefy & Hik 2009). A similar type of response has been observed in songbirds as well; Forsman and Mönkkönen (2001) found that foraging aggregations of birds attend to heterospecific song, and may be using it as a cue for predator absence. It is possible that there may be benefits to attending to heterospecific cues during dawn singing as well, though very little work has been done in this area, so the extent to which species use and respond to these cues is not known.

1.5 The New Zealand dawn chorus

"And in the morning we were awakened by the singing of the birds. The number was incredible, and they seemed to strain their throats in emulation of each other. This wild melody was infinitely superior to any that we had ever heard of the same kind: it seemed to be like small bells, most exquisitely tuned; and perhaps the distance and the water between might be no small advantage to the sound."

Captain James Cook, hearing the dawn chorus for the first time in 1770

Cook's reaction conveys the wonder many people have upon hearing New Zealand's dawn chorus for the first time. New Zealand's songbird communities are highly endemic (Brockie 2012), resulting in a chorus unlike that heard anywhere else in the world. With the complex, varied warbles of the Tui (*Prosthemadera novaeseelandiae*), which possesses two synringes (Hill 2011), the liquid bell-like notes of the Korimako

(Bellbird; *Anthornis melanura*) and the sonorous, organ-like tones of the North Island Kokako (*Callaeas wilsoni*), it is unsurprising that the New Zealand chorus has found many admirers (Soper 1976).

Long before Cook had even set sail, Māori had been attentive to the intricacies of New Zealand's dawn chorus for hundreds of years (Orbell & Lagahetau 2003). Songbirds have long been integral to Māori culture and legend; as the children of the forest god Tane it was believed that their song served as his voice (Gordon 1938). To Māori, the dawn chorus was an affirmation of life that came with the breaking dawn (Orbell & Lagahetau 2003). One story likens the dawn chorus to a haka, with the different birds joining the performance at a different cue, with the Tui and Toutouwai (North Island Robin; *Petroica longipes*) leading and the Piwakawaka (New Zealand Fantail; *Rhipidura fuliginosa*) and Pīpīwharauroa (Shining Cuckoo; *Chrysococcyx lucidus*) joining later on (Gordon 1938). But other than these oral traditions and anecdotal evidence from bush-goers, there is little systematic information on the specific timing and order in which New Zealand birds join the dawn chorus.

The chorus of today is thought to pale in comparison to those from days past (Gordon 1938). Since pre-European times, native bird populations have been ravaged by deforestation and the introduction of mammalian pests, leading to decreased numbers of singing birds and widespread local extinction of many chorusing species (Fleet 1984; Spurr & Anderson 2004; Innes et al. 2009). "Bringing back the dawn chorus" is thus a common goal of many conservation projects (Wallace 2002; Butler

et al. 2014). A strong foundation of knowledge on the dawn chorus in New Zealand, which is currently lacking, can only help in this endeavour.

1.6 Aims

The purpose of this study was to lay a foundation for our understanding of the dawn chorus in New Zealand songbirds, and address knowledge gaps in our understanding of the use of acoustic cues by songbirds during the dawn chorus. While there have been some studies of responses of songbirds to conspecific acoustic cues during the dawn chorus (Foote et al. 2008; Foote et al. 2011) very little work has been done involving heterospecific cues. In an observational study of dawn chorus singing, I aimed to systematically establish the order in which New Zealand songbirds join the dawn chorus for the first time. In a playback experiment, I attempted to experimentally manipulate the dawn chorus through playback of an early singing species, the Tui, and a late singing species, the Riroriro (Grey Warbler; *Gergone igata*), before the chorus would normally begin. Here I investigated the role of both conspecific and heterospecific song during the dawn chorus, and whether New Zealand songbirds use the songs of neighbours as cues to modify the timing of their dawn song onset. The research was undertaken at Maungatautari, a fenced sanctuary free of mammalian predators. I hoped to produce findings that would be useful and interesting for researchers planning future projects on New Zealand's dawn chorus, conservationists working with songbirds both at Maungatautari and elsewhere, and those interested in the cultural and natural history value of our dawn chorus.

1.7 Thesis structure

This thesis is organised into four chapters. Chapter 2 covers my observational study of dawn chorus timing, while Chapter 3 covers the playback experiment. Chapter 4 is a Conclusions and Recommendations section that consolidates my findings from both chapters and makes suggestions for further study. I will be using the Māori names for all native species, a list of English equivalents can be found in the Appendix. As chapters two and three were written to be published as individual papers, there may be some repetition between them.

Chapter 2

Observational study of dawn chorus timing in New Zealand songbirds

2.1 Introduction

Chorusing is a distinctive type of signalling behaviour where individuals aggregate and produce acoustic signals simultaneously; chorusing has been documented in a wide range of species including anurans, insects, and birds (Ryan et al. 1981). The avian dawn chorus is a particularly spectacular event, where various bird species sing together before sunrise at rapid rates (Burt & Vehrencamp 2005). In their review of the avian dawn chorus, Staicer et al. (1996) identified a host of explanations for the phenomenon, and the factors that influence its characteristics. The factors generally fall into three groups: intrinsic, environmental, and social (Staicer et al. 1996). Intrinsic factors controlling dawn singing include physiological and morphological features, for example the elevated production of septal neuropeptides leads to increased dawn singing in field sparrows (*Spizella pusilla*) (Goodson et al. 1998). Environmental factors such as ambient light (Kempaeners et al. 2010), noise (Dorrado-Correa et al. 2016) and temperature (Farina et al. 2015) also influence dawn singing. Social factors include behaviours such as mate guarding (Poesel et al. 2006) and adjusting social relationships between territorial males (Foote et al. 2010).

Timing of song onset is a key characteristic of dawn singing. Most of what is known about chorus timing is based on studies of intraspecific

factors. The two main established functions of bird song, mate attraction and territory defence (Mace 1987), are among the best studied. Mace (1987) found that male Great Tits (*Parus maj*or) sang earlier and longer as egg laying approached, and that dawn song was often followed by copulation with mates, suggesting dawn singing is important for protecting paternity and inducing mating. Extra-pair paternity may be another factor influencing timing, as the incidence of extra-pair paternity in monogamous songbirds is highest at dawn when visibility is low (Greives et al. 2015). Earlier singers have been found to be more successful at defending mates from extra-pair copulation, while increasing their own rates of extra-pair paternity (Greives et al. 2015). Male Blue Tits (*Cyanistes caeruleus*) that started singing earlier were found to have more mating partners and were more likely to gain extra-pair paternity than those which sang later (Poesel et al. 2006). Dawn chorus start times have also been found to vary significantly as the breeding season progresses in certain species; Eastern Phoebes (*Sayornis phoebes*) were found to sing earlier during the egg laying period and later during the incubation period (Bruni & Foote, 2014). They were also found to sing earlier and more intensely during their first brood compared with their second, suggesting brood numbers influence dawn singing (Bruni & Foote, 2014).

Dawn chorus start time varies considerably between species (Planque & Slabbekoorn 2008), however compared with factors that influence timing at the intraspecific level, much less is known about forces that structure timing differences at the interspecific level. The different relative influence of intrinsic, environmental and social factors results in

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staggered start times observed across different species each morning (Staicer et al. 1996). Differences in morphology such as eye size and other factors influencing the ability to detect light at dawn can affect song timing among species (McNeil et al. 2005). A phylogenetic analysis of start times across species found that songbirds with larger eyes start singing earlier than those with smaller eyes (Thomas et al. 2002). Linked closely is the effect of differing foraging habits: the 'inefficient foraging hypothesis' proposes that birds sing at dawn because foraging at low light levels is inefficient, meaning the net cost of singing instead of foraging is lower (Staicer et al. 1996). Since the time at which foraging becomes efficient varies among species, the optimal time to start singing will vary as well (Thomas et al. 2002). In tropical Ecuadorian forests, birds that forage high in the canopy start singing earlier than species that feed on the forest floor (Berg et al. 2006). Body size and available energy reserves can also have an effect on start time; Thomas et al. (2002) found that body size was a good predictor of start time, and supplementary feeding has been found to increase song output in both Tauhou (Silvereye, *Zosterops lateralis*) (Barnett & Briskie 2007) and Black-Capped Chickadees (Grava et al. 2009). Many species sing earliest during the egg laying period when female fertility is at its peak, such as Great Tits (*Parus major*) (Naguib et al. 2016) and Eastern Phoebes (*Sayornis phoebes*) (Bruni & Foote 2014). Therefore variation in the timing of egg laying cycles and female fertility between different species will also lead to different start times across species (Welling et al. 1995).

The acoustic transmission hypothesis posits that birds will alter their singing behaviour to maximise successful transmission of signals and signal to noise ratios (Staicer et al. 1996). Partitioning of "acoustic space" to avoid spectral overlap with heterospecifics is therefore also thought to be an important mechanism that structures the timing of different species (Stanley et al. 2016). As the optimal transmission window will vary depending on the amplitude and spectral profile of a species' song, favourable conditions to initiate dawn singing will vary in time across different species (Planque and Slabbekoorn, 2008). Songbirds have been shown to alter the timing of their song in response to anthropogenic noise such as urban (Dorrado-Correa 2016) and airplane noise (Gil et al. 2015), and to heterospecific sources of noise such as insects (Stanley et al. 2016), suggesting that maximising signal transmission plays an important role in timing.

Differences in social behaviour such as the importance of communication between males and advertising to extra-pair partners may also give rise to different start times across species. Rates of extra-pair paternity vary considerably by species (Cramer et al. 2011) which given the established significance of extra-pair paternity to dawn chorus start time (Dalziell & Cockburn 2008; Suter et al. 2009; Sexton et al. 2007), could influence the variation in start time between species.

A significant characteristic of dawn choruses is the way in which different species initiate singing at different times, often in a predictable order (Staicer et al. 1996; Allard 1930). In Welsh woodlands, Common Redstarts (*Phoenicurus phoenicurus*) are first to sing, followed by

European Robins (*Erithacus rubecula*), Common Blackbirds (*Turdus merula*), Song Thrushes (*Turdus philomenos*) and Pied Flycatchers (*Ficedula hypoleuca*) (Thomas et al. 2002). Allard's (1930) foundational study of the dawn chorus order in Washington D.C. found that while some species' start times track the changing times of twilight and sunrise closely, others vary considerably over the course of the breeding season, shifting up and down in the singing order. Similar patterns have been observed in assemblages in Wisconsin (Leopold & Eyval 1961) and Michigan (Fisler 1962), suggesting the singing order of the dawn chorus is not "set" and certain species are more predisposed to drifting earlier or later in their singing times depending on the time of year.

The New Zealand dawn chorus is widely known and renowned for being pleasing to the ear; however, there has been no systematic study of the singing order in the dawn chorus. Anecdotal evidence and Māori oral tradition suggests that New Zealand songbird choruses do follow a particular order, with Tui (*Prosthemadera novaeseelandiae*), Toutouwai (North Island Robin; *Petroica longipes*) and Korimako (Bellbird; *Anthornis melanura*) being suggested as particularly early singers (Orbell & Lagahetau 2003; Gordon 1938). In Pre-European times Māori watchmen also used dawn chorus singing to estimate the time until dawn (Orbell & Lagahetau 2003), suggesting some degree of predictability in its order. New Zealand species vary considerably in aspects of their life history, which could in turn affect variation in song timing, such as fertile periods and brood numbers (Soper 1970; Higgins & Peter 2001; Higgins et al. 2003; Higgins et al. 2006). Therefore, it is likely that New Zealand

choruses will also display fluctuations in the order and timing of song across species as the breeding season progresses.

I investigated whether the New Zealand dawn chorus follows a distinctive sequence like those observed in avian communities in other parts of the world. I also investigated variability in the timing of song initiation across New Zealand species and how this may change in response to progression of the breeding season. Given that birds have been observed to join the chorus in a distinct order in other assemblages (Allard et al. 1930; Thomas et al. 2002), I predict that New Zealand species will also initiate singing in a predictable sequence. Based on Māori oral tradition I would also expect to see Tui, Toutouwai and Korimako initiate singing earliest (Orbell & Lagahetau 2003; Gordon 1938). As factors that influence start time such as food availability (Barnett & Briskie 2007), fertility cycles (Naguib et al. 2016), and territory boundaries (Molles & Vehrencamp 2001) undergo significant changes as the breeding season progresses in other species, I expect that start times might show some variation across the breeding season in New Zealand species as well.

2.2 Methods

2.2.1 Study site and recording methods

My study was conducted from 29 September 2016 to 26 November 2016 at the Mount Maungatautari reserve. I used the "Over the Mountain" track (beginning at 38°03'18.8"S 175°33'40.1"E) on the mountain's southern side to access my study sites. The track is within a podocarp-

broadleaf forest with a Tawa (*Beilschmiedia tawa*) dominated canopy, surrounded by a pest-proof fence (Fig. 1). With the exception of Mice (*Mus musculus*), no introduced mammalian pests are present on the mountain (Butler et al. 2014). The mountain is home to a wide range of bird species, including native species both endemic to the mountain and translocated, along with several introduced European species. Species endemic to the mountain include Tui, Piwakawaka (New Zealand Fantail; *Rhipidura fuliginosa*), Riroriro (Grey Warbler; *Gerygone igata*), Miromiro (New Zealand Tomtit; *Petroica macrocephala*), Korimako, Tauhou and Pīpīwharauroa (Shining Cuckoo; *Chrysococcyx lucidus*). Introduced species present on the mountain include Eurasian Blackbird (*Turdus merula*), European Chaffinch (*Fringilla coelebs*) and European Greenfinch (*Carduelis chloris*). Several translocated native species that are either non-endemic or were previously extirpated on the mountain are present as well, including: Toutouwai, Pōpokatea (Whitehead, *Mohoua albicilla*), Tieke (North Island Saddleback, *Philesturnus rufusater*), Hihi (Stitchbird, *Notiomystis cincta*) and North Island Kokako (*Callaeas wilsoni*).
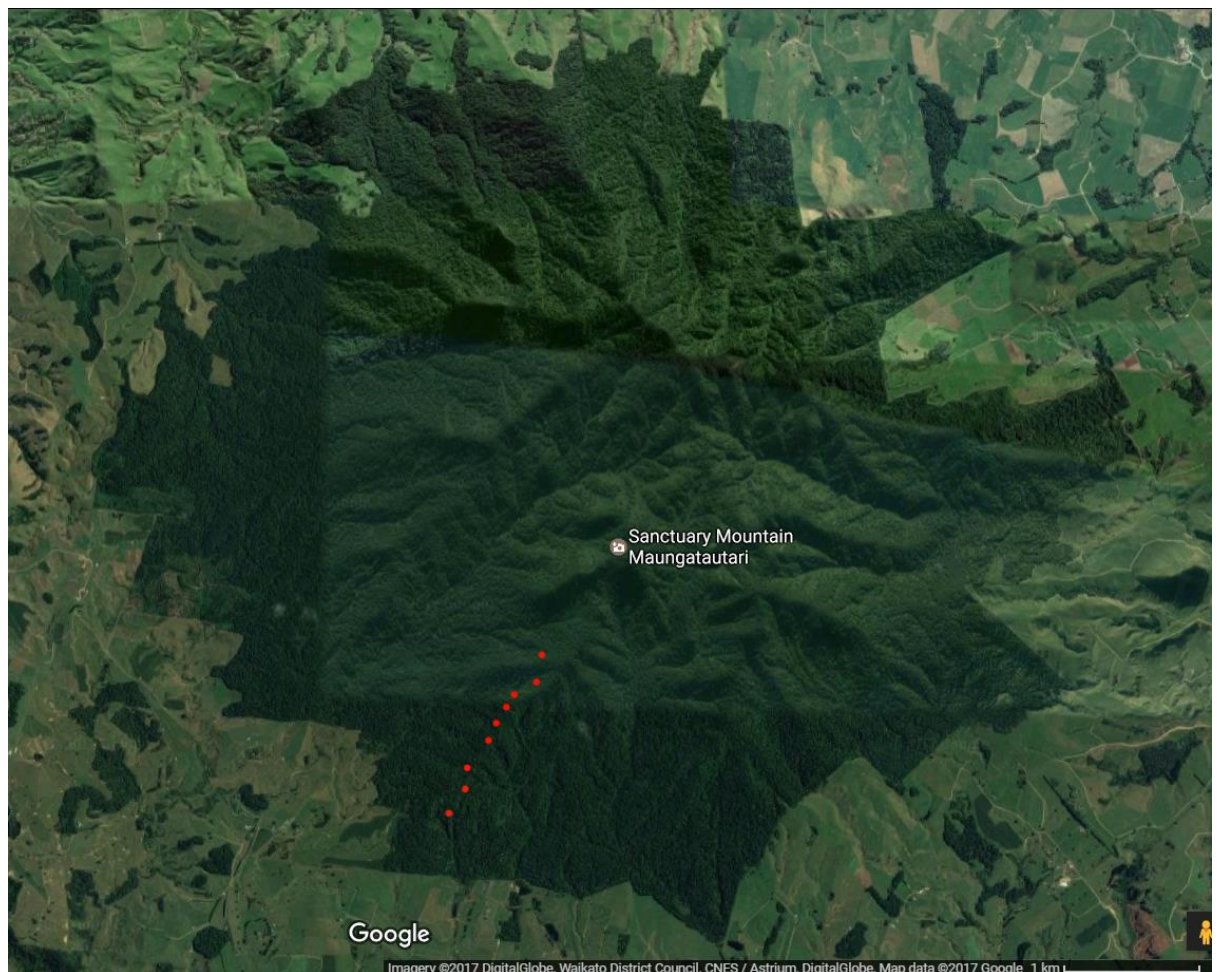
Figure 1: Map of Maungatautari reserve, with nine recording sites marked using red circles (Source: Google maps)

I selected nine recording sites along a 1.8km stretch of the track (all on trust-owned land); these sites were spread at 200m intervals (Fig. 1). At each site, I set up three Song Meter SM2+GPS autonomous recorders (Wildlife Acoustics, Inc., Maynard, MA, USA) 75m apart in an equilateral triangle to form a microphone array (Fig. 1). When later analysing the recordings, this allowed me to exclude birdsong from outside the target area by discounting faint song that was picked up by just one recorder. By comparing the amplitude of song between the three recordings taken by each device, I could determine which birds were outside the target area, to

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exclude them. This setup also allowed me to sample the same fixed area at each recording site. I strapped the recording devices to trees 1.5-2m above the ground in order to reduce ground attenuation while still being easily accessible to change batteries and memory cards. I selected trees with a maximum diameter of 50cm so that the microphones stuck out on either side of the tree and were not placed in a sound shadow on one side of the tree. The 200m separation of recorders ensured that each location included different individuals of each species.
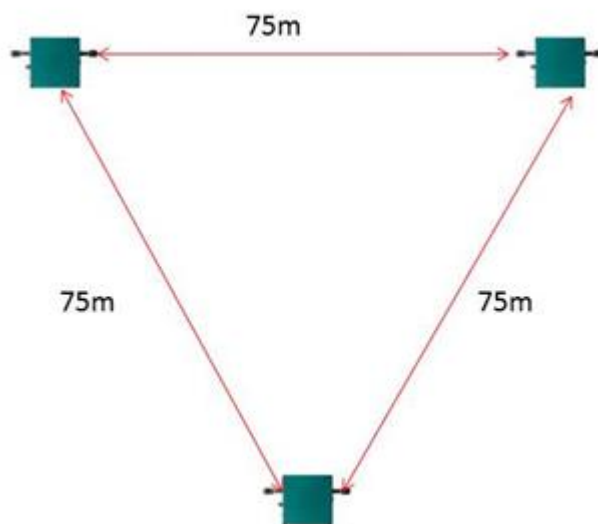
Figure 2: The recording setup at each sampling station

Array 1 was set 200m from the southern edge of the publicly owned land and Array 8 200m from the northern border of the public land. As I ran out of space at the end of the 1.8km of track for array 9, I placed this array between arrays 5 and 6. This site maintained acoustic independence from the other arrays I ran at the same time, being more than 400m away from them.

2.2.2 Protocol for data collection

The nine arrays were divided into three blocks such that concurrently running arrays on a given sampling day were at least 400m apart to ensure for acoustic independence. Arrays were set up at three sites at a time (Table 1).

Table 1: Details of recording locations and dates for nine dawn choruses

Array	Recording dates	Date analyzed	GPS Co-ordinates
Array 1	30 Sept- 13 Oct	1 Oct	38° 3' 0.3521'' S 175° 33' 41.7575'' E
Array 2	31 Oct - 6 Nov	31 Oct	38° 2' 57.2464'' S 175° 33' 34.5564'' E
Array 3	14 Nov - 25 Nov	20 Nov	38° 2' 51.8176'' S 175° 33' 31.0111'' E
Array 4	30 Sept- 13 Oct	1 Oct	38° 2' 45.6389'' S 175° 33' 35.1529'' E
Array 5	31 Oct - 6 Nov	31 Oct	38° 2' 40.6457'' S 175° 33' 40.707'' E
Array 6	30 Sept- 13 Oct	1 Oct	38° 2' 35.4534'' S 175° 33' 45.8957'' E
Array 7	31 Oct - 6 Nov	31 Oct	38° 2' 31.4714'' S 175° 33' 51.9221'' E
Array 8	14 Nov - 25 Nov	20 Nov	38° 2' 24.9306'' S 175° 33' 55.6189'' E
Array 9	14 Nov - 25 Nov	20 Nov	38° 2' 37.9212'' S 175° 33' 43.1388'' E

The Song Meters were set to record for 6 hours each day, recordings were taken for 59 minutes each hour with the recorders pausing for 1 minute at the end of each hour to write files. Sound files were written in WAV format. Recording was set to begin 1 hour before astronomical twilight, which was determined to be two hours before the onset of dawn singing in our pilot study. At the end of the sampling period for each block of arrays, the SD cards containing the recordings were obtained from the Song Meters, and the arrays packed up and moved to the next block of sites.

2.2.3 Analysis

From each site, the first date with clear weather that was not a playback date (see Chapter 3) was selected for analysis (Table 1). Using Syrinx PC (John Burt, Seattle, WA, USA), I determined the 'start time' for each species in each of the nine recordings. I defined start time as the first song detected for each species that was followed by another song from that species within five minutes. I excluded potential nocturnal song from the analysis by discounting very early singers which paused singing for more than 10 minutes. This ensured I was annotating continuous dawn song and not errant, infrequent night song (Bruni et al. 2014). I annotated the first five songs for each species using the time and frequency cursors in Syrinx; if fewer than five songs were annotated that species was excluded from the analysis for that morning. Additionally, I annotated the time of sunrise in each recording using sunrise times for Maungatautari (Edwards 2016). I then calculated the start times in minutes before sunrise.

To test for differences in start time across species I used a linear model with species and date (days from the start of recording, 1 Oct 2016) as independent variables. I also included an interaction between species and date in the model. I then used a Tukey's multiple comparisons post-test to identify species that differed significantly in start time. Results were considered significant at $\alpha \leq 0.05$. Species that did not sing before sunrise in more than 50% of recordings were excluded from the analysis. This statistical analysis was run in JMP (SAS Institute Inc., Cary, NC, USA).

2.3 Results

Analysis of dawn chorus recordings taken at Maungatautari showed that there was a significant difference in dawn chorus start times among species (linear model: $r^2 = 0.94$, $F_{17,54} = 47.90$, $p < 0.0001$; Table 2).

Table 2: Results of effect tests from linear model investigating variation in chorus start time among nine species

Term	F	Df	P
Species	90.4272	8	<.0001
Date	2.5962	1	0.1130
Species x Date	11.2508	8	<.0001

Comparisons of start times using the Tukey post-hoc multiple comparison test reveal that Tui were the first birds to sing, beginning over 40 minutes earlier than any other species. Toutouwai and Korimako follow, then Blackbirds, Miromiro, Piwakawaka, Tauhou, Riroriro and finally Pōpokatea (Fig. 3). The curve of start times shows a sharp drop between Tui and Toutouwai, with the start times levelling off from Blackbirds to Riroriro and then dropping sharply in Pōpokatea.

After Tui, the start times for other species fall into three overlapping groups rather than a set order (Fig. 3). Toutouwai and Korimako form the second group, with the next sharpest drop in start time on the curve (Fig. 3). Blackbird, Miromiro, Piwakawaka, Touhou and Riroriro formed the third group of singers, with all birds in this group initiating singing on average within 12 minutes of one another. Pōpokatea were the last to sing, initiating song on average less than 10 minutes before dawn, though their start time was not found to be significantly different from Tauhou.
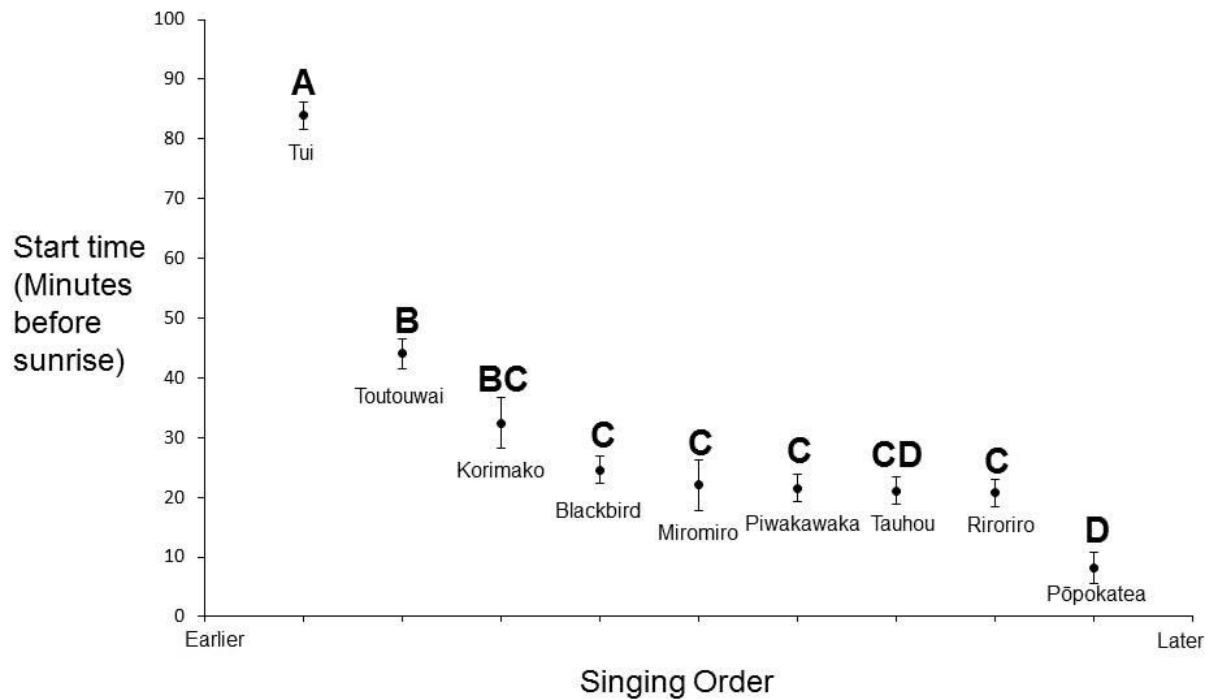
Figure 3: Start times in minutes before sunrise for each species, with standard errors shown. Start times for species that do not share letters were found to be significantly different in the Tukey Pairwise comparisons.
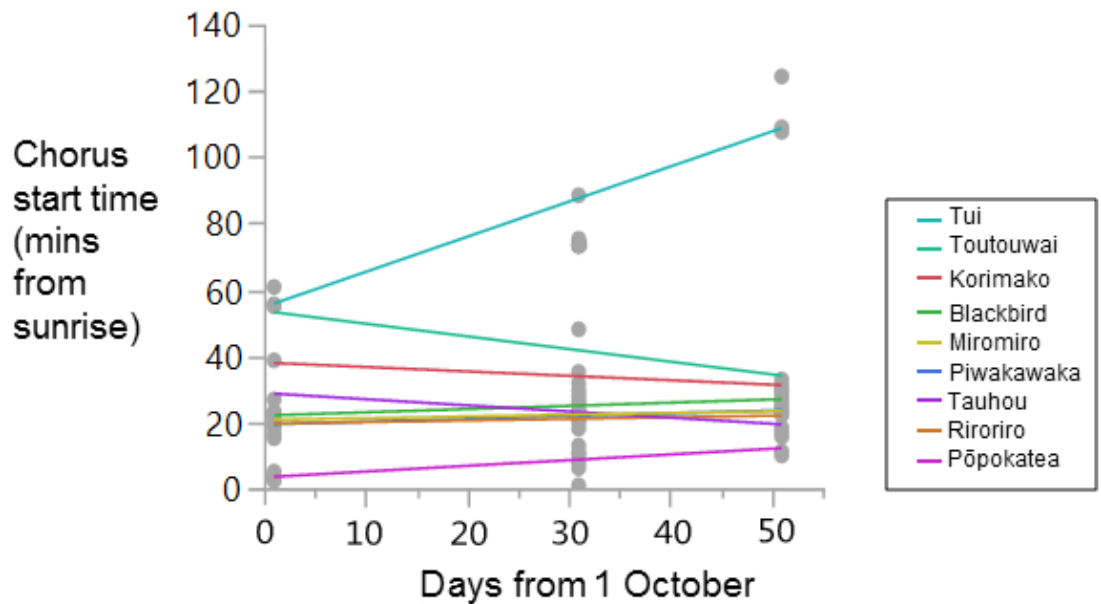
Figure 4: Linear regression from the linear model showing start time for each species against date (in days from the start of study)

Date did not significantly predict start time on its own (Table 2), however the species-date interaction was significant (p < 0.0001; Table 2); thus, date was related to start time for some species but not others. Tui started singing much earlier as the breeding season progressed (Fig. 4), with birds from recordings near the end of the study initiating singing approximately twice as early relative to sunrise compared with recordings from the start of the study. Other species showed less variation in start time and may have either showed an earlier start time, a later start time, or no change in start time as the season progressed (Fig. 4).

2.4 Discussion

Observations of dawn chorus timing in New Zealand songbirds revealed that they follow a particular start order. Interestingly, my results corroborate Māori oral traditions that suggest Tui, Toutouwai and Korimako are the first species to start singing (Gordon 1938). However with the exception of early and late singing species this order is neither "set" nor predictable. Most New Zealand species joined the chorus in quick succession of one another in a highly interchangeable order, within a 12 minute window; overlap in singing order such as this have been observed in other studies of chorus order such as Bruni et al.'s (2011) study.

Observing the order in terms of body size, it would appear that early singers follow a descending order of body size; with the large Tui (125g) singing first, followed by the smaller Toutouwai (35g) and Korimako (34g) (Higgins et al. 2001; Higgins et al. 2003). However Eurasian Blackbirds (90g) (Higgins et al. 2006) come in after the latter two species despite being much heavier, and Pōpokatea are also heavier than several species

that sing significantly earlier than them. Also the North Island Kokako, the heaviest New Zealand songbird (233g), is characterised as a late singer that initiates song very close to sunrise (though I did not detect any in my study) (Gordon, 1938; Higgins et al. 2006). Therefore body size limitations on start time are unlikely to be the main factor partitioning song initiation among species.

It is possible that different foraging habits could be structuring differences in start time between the species. The earliest singers are all nectar feeders or ground-feeders that forage in leaf litter, whilst species that sing later are predominantly insectivores or insect-feeding omnivores that forage by gleaning, sallying or catching prey on the wing (Higgins et al. 2001, Higgins et al. 2002, Higgins et al. 2006). Nectar feeders and ground-feeders may be more efficient at foraging at lower light levels than those which take mobile invertebrate prey (Hutchinson 2001), in which case the inefficient foraging hypothesis predicts they would initiate singing earlier to begin foraging as soon as light levels allow. Of the several species (Blackbird, Miromiro, Piwakawaka, Touhou and Riroriro) that started singing at a similar time however, not all are exclusively active insectivores. Tauhou also feed on nectar and fruit (Soper 1976), and Blackbirds feed in leaf litter in a similar manner to Toutouwai, so start time may not be constrained by feeding habits in all species. However it is important to note that many of the species in the middle-late singing group that initiated singing around the same time, such as Miromiro and Riroriro, form mixed-species foraging aggregations with each other (Higgins et al. 2003; Higgins et al. 2006). Piwakawaka in particular take advantage of other

insectivores by preying on insects flushed out by the foraging behaviour of heterospecifics (Higgins et al. 2006). Mönkkönen et al. (1996) demonstrated that birds that form mixed species foraging aggregations actively seek out heterospecifics with similar foraging habits. If birds profit from foraging as part of a mixed-species aggregation then it would benefit those species to initiate and end dawn singing around a similar time, so that they can begin foraging synchronously.

Partitioning of acoustic space and avoidance of signal masking may be an important factor structuring the timing differences across New Zealand species. Tui song is highly complex and the various vocalisations that constitute the song cover a wide range of frequencies (Hill et al. 2015). Tui song will therefore have a high degree of spectral overlap with song from almost every other species, and so it will benefit Tui to sing at a time when no other species is singing (Planque & Slabbekoorn 2008). For the same reasons it is also possible that heterospecifics may delay their song until Tui are no longer singing. Additionally, Tui sing in lengthy bouts with short pauses, making it difficult to avoid temporal overlap by singing in between the bouts of heterospecifics (Brumm 2006). While Toutouwai and Korimako songs do not share the range of frequencies that Tui song does, they also sing in relatively lengthy bouts (Higgins et al. 2001; Higgins et al. 2003). Comparing the songs of species in the middle-late singing group, their songs tend to cover a narrower range of frequencies (Higgins et al. 2003; Higgins et al. 2006), so there is comparatively less spectral overlap between species in this group compared with Tui. As they sing in shorter bouts with longer song intervals (Higgins et al. 2003; Higgins et al. 2006),

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they will also have a greater capacity to reduce signal masking by slotting song into the acoustic space between heterospecific bouts (Brumm 2006). As avoiding signal masking may be easier for these species, there would be less benefit for them to initiate dawn singing at substantially different times.

New Zealand birds vary in their territorial and sexual behaviours (Soper 1976). The three earliest singers are all highly territorial species that exhibit strong intrasexual competition between males (Higgins et al. 2001; Higgins eat al 2003). Under the 'social dynamics hypothesis', it may be important for males of these territorial species to be able to mediate their social relationships through dawn song (Staicer et al. 1996; Foote et al. 2010). Highly territorial species have been noted to have a more intense, lengthy chorus (Staicer et al. 1996). Conversely the very late singing Pōpokatea are co-operative breeders that are not strongly territorial (Higgins et al. 2003). Male Riroriro, as relatively late singers, do not exhibit particularly intense aggressive or territorial behaviour either (Higgins et al. 2003). As the re-evaluation of territory boundaries and dominance hierarchies among males is less important in these later-singing species, they may benefit less from singing earlier. The relative importance of extra-pair paternity may influence start time among New Zealand species as well (Poesel et al. 2006). Tui have some of the highest rates of extra-pair paternity of all monogamous songbirds; extra pair young occur in 72% of broods and account for 57% of all offspring (Wells et al. 2015). However extra-pair paternity is very rare in Toutouwai (Higgins et al.

2003), so obtaining extra-pair copulations is not likely to be a significant for song timing in all early singers.

Much like the North American choruses studied by Allard (1930) and Leopold and Eynon (1961), the position of New Zealand species within the chorus order and their start time relative to sunrise varies as the breeding season progresses. This is unsurprising given that New Zealand species vary in their brood numbers and fertile periods (Soper 1970). Korimako, which varied little in their start time, are unlikely to have completed rearing their first brood in late November, as their first fertile period is in late October/early November (Higgins et al. 2001). In contrast the Toutouwai, which demonstrated a shift to singing later, has its fertile period in late September, meaning recordings taken in November are likely to be occurring during the incubation and fledging periods, or during the second brood (Higgins et al. 2003). As dawn chorus singing had been found to start later during these periods compared with the first fertile period, I would expect to see such a shift over the season (Bruni & Foote 2014).

Another significant event occurring later in the breeding season is the arrival of migrant cuckoos; both the Pīpīwharauroa and Koekoeā (Long-tailed Cuckoo, *Eudynamys taitensis*) arrive later in the breeding season of their main host species (Higgins et al. 1999). Despite the fact that Pōpokatea often rear a second brood in late spring, they demonstrated a shift to singing earlier, and may be shifting their dawn song earlier to avoid being detected and parasitised by Koekoeā, which can sometimes be active before sunrise (Higgins et al. 1999). Pōpokatea

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have been known to alter their singing behaviour later in the season when cuckoos are present (Higgins et al. 2003), though whether this extends to dawn singing is not known. However no such change was seen in Riroriro, the Pīpīwharauroa's preferred host, although the Pīpīwharauroa is a late riser and may not be active at a time where it could use dawn song to locate nests anyway (Gordon 1938).

The drastic shift in start time seen in Tui as the breeding season progressed was extreme compared with all other species at Maungatautari; several aspects of Tui behaviour and ecology may explain this trend. One noteworthy difference between Tui and other species present on the mountain is that Tui are highly transient, and will fly over long distances to exploit new food sources when they become available (Higgins et al. 2001; Moon 1967). This marked seasonal migration has been observed in populations moving to the coast to exploit Pohutakawa (*Metrosideros excelsa*) (Moon 1967), and may also be taking place at Maungatautari in late spring as new food sources such as Rewarewa (*Knightia excelsa*) become abundant. Indeed, both radio tracking of birds and anecdotal evidence suggest that large numbers of Tui leave the satellite towns surrounding Maungatautari in late spring (J. Innes, personal communication, February 14, 2017; C. Smuts-Kennedy, personal communication, February 14, 2017), and that the mountain had a particularly heavy crop of Rewarewa blossoms in 2016 (K. Richardson, personal communication, February 15, 2017). The arrival of large numbers of new males would lead to elevated levels of male-male competition and the need to establish new territory boundaries and dominance hierarchies,

driving them to sing earlier as predicted by the "social dynamics hypothesis" (Foote & Mennil 2011; Staicer et al. 1996). Additionally, the increased abundance of nectar later in the season would increase the perceived value of established territories (Molles & Vehrencamp 2001), escalating the need for aggressive territory defence. Studies of Tauhou showed that increasing territory value through supplemental feeding resulted in earlier singing, and rich crops of Rewarewa nectar may induce a similar shift in Tui (Barnett & Briskie 2007). Finally, greater numbers of males would also result in increased competition for acoustic space to signal during the dawn chorus, resulting in the need for individuals to sing earlier to partition acoustic space to transmit signals efficiently without signal jamming from conspecifics (Wilson 2016).

Another possibility not unrelated to the arrival of new males, is a potential connection between Tui brood cycles and their extremely high rates of extra-pair copulation (Wells et al. 2015). Sexton et al. (2007) found that neighbourhood fertility and availability of extra-pair females were important factors driving earlier dawn song in Eastern Kingbirds; these factors may have important influences on Tui start time as well. Tui can have up to two broods per season, with the first fertile period occurring in late September and early October followed by a total incubation and fledging period of around 28 days (Higgins et al. 2001). It is therefore likely that many Tui females will be entering their second fertile period in late spring. A significant aspect of the second brood in Tui is that provisioning young falls to mated males, which leaves females with greater opportunities to pursue extra-pair copulations (Wells et al. 2015). It is

possible that the arrival of new males in late spring may create a "hidden lek", an aggregation of males from a socially monogamous species that is maintained by extra pair copulation behaviour (Wagner 1998). This may explain some aspects of Tui biology that previously seemed at odds with a socially monogamous breeding system, such as their extreme sexual size dimorphism that is more typical of a polygynous species (Wells et al. 2015). Similar rates of extra-pair paternity have been observed in Superb Fairy-Wrens (*Malurus cyaneus*), a socially monogamous breeder that exhibits hidden lek aggregations of unmated males in the breeding season (Cockburn et al. 2009). Unmated Tui that do not have to invest energy into territory defence and brood provisioning may be able to invest all their energy into dawn song to obtain paternity through extra-pair copulations alone (Wagner 1998). The role of dawn song in Tui mating systems is not well understood, but a potential connection between changes in song timing, male provisioning and high incidence of extra-pair mating is worth further investigation.

The results of my study establish the singing order of the New Zealand avian dawn chorus empirically for the first time. Like assemblages studied in other parts of the world, the New Zealand chorus follows a distinct order (Thomas et al. 2002; Bruni et al. 2014). A heterogeneous change in singing time across species as the season progressed suggests intrinsic, environmental and social factors influencing the behaviour of each species differently (Staicer et al. 1996). A greater understanding of the function and importance of dawn chorus behaviour for each individual species would help establish the relative influence these factors have on

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dawn singing. Establishing the singing position of the North Island Kokako will also be required to obtain a complete understanding of the New Zealand chorus order as it was in pre-European times.

Chapter 3

Experimental manipulation of dawn chorus start time through song playback

3.1   Introduction

Chorusing is a type of signalling behaviour in which many animals gather and produce a cacophony of acoustic signals simultaneously, and is most commonly observed in insects, anurans and birds (Ryan et al. 1981). The avian dawn chorus is a widely observed phenomenon among bird communities in the breeding season, where males of many different species exhibit a period of high song output before sunrise each morning (Staicer et al. 1996). Various non-mutually explanations for why birds sing at dawn currently exist; these include intrinsic factors such testosterone levels (Foerster et al. 2002), environmental pressures such as the increased ability of song to propagate at dawn (Brown & Handford 2003) and social factors such as mate guarding, territory defence (Catchpole & Slater 2008) and the adjustment of social dynamics among males (Foote et al. 2010).

One particularly noteworthy feature of the dawn chorus is the way various species join the chorus at different times in a staggered fashion (Staicer et al. 1996). Songbird assemblages in Ontario show this typical staggered starting order; Alder Flycatchers (*Empidonax alnorum*) sing first, followed by Song Sparrows (*Melospiza melodi*), White-throated Sparrows

(*Zonotrichia albicollis*), American Robins (*Turdus migratorius*), Eastern Phoebes (*Sayornis phoebe*) and finally Black-Capped Chickadees (*Poecile atricapillus*) (Bruni et al. 2014). A range of different factors influence the time a species initiates dawn singing, such as ambient light levels, eye size, the opportunity cost of singing rather than foraging at dawn and available energy reserves at dawn (Staicer et al. 1996; McNeil et al. 2005). While highly variable, the start times of different species in a particular avian community often follow a predictable order (Allard 1930), suggesting that there are factors partitioning chorus timing at the species level (Stanley et al. 2016).

The sensitivity of dawn chorus start times to auditory cues has been demonstrated in a number of studies. Foote et al. (2011) found that male Black-Capped Chickadees initiated dawn singing earlier in response to playback simulating a territorial insertion (i.e. territorial song playback) by an unfamiliar male, played earlier than the chorus would normally begin. This effect also extended to neighbouring males, indicating that shifts in song timing can also propagate though communication network effects. Birds have also been found to shift their start times in response to high levels of insect noise (Stanley et al. 2016), and the effect of anthropogenic noise on the start times of birds in urban areas has been well documented (Arroyo-Solís et al. 2013; Dorado-Correa 2016). In equatorial birds, artificial noise was found to have a greater effect of shifting the start times of birds than artificial light (Dorado-Correa 2016). As many birds rely on acoustic signals to defend territories and attract mates, acoustic masking will have significant consequences for fitness and reproductive success

(Dorado-Correa 2016). The findings of these studies suggest that social dynamics and avoiding acoustic masking are likely to play important roles in changing dawn chorus start times in response to auditory stimuli (Foote et al. 2014; Arroyo-Solís et al. 2013).

While the importance of intraspecific communication networks in dawn chorus singing are reasonably well understood, comparatively little work has been done on the significance of interspecific interactions. In the breeding season, birds compete with heterospecifics for many of the same resources that they compete with conspecifics for, such as nesting space, food and acoustic "space" for signalling (Møller 1992). Therefore we would expect a species being able to utilise the signals of heterospecifics. Being able to modify behaviour in response to heterospecific signals or generate new signals to influence the behaviour of heterospecifics would improve an individual's ability to compete with them, and thus its reproductive success (Kostan 2002). Møller (1992) found that playback of Black Wheatear (*Oenanthe leucura*) song resulted in increased numbers of both conspecific and heterospecific males singing at dawn. Many studies of interspecific responses to bird song focus on predation risk and the use of heterospecific vocalisations for predator avoidance (Forsman & Mönkkönen 2001; Møller 1992), while the role of interspecific communication in a dawn chorus context remains poorly understood.

One relatively unexplored possibility is that some bird species may use the song of heterospecifics as a cue to begin their own dawn song. Møller (1992) suggests that social facilitation of heterospecifics may influence dawn singing, based on the responses of several species to

Black Wheatear playback. Birds have been found to adjust their song timing predictively in anticipation of early morning urban noise, suggesting they are actively using urban noise as a cue (Dorrado-Correa 2016). As eavesdropping on conspecifics has been observed in many bird species (Forsman & Mönkkönen 2001; Mönkkönen, Forsman & Helle 1996), we could expect to see them using heterospecific song in a similar way.

New Zealand avian communities offer a fascinating opportunity to investigate the variability and sensitivity of dawn chorus start times in multiple species, and the role of interspecific communication in dawn singing. The New Zealand dawn chorus, while well known in cultural and tourism contexts (Orbell 2003), has not been studied in any significant detail. The fact that two of the most prominent dawn songsters, the Tui (*Prosthemadera novaeseelandiae*) and the Korimako (Bellbird; *Anthornis melanura*) mutually mimic one another (Higgins et al. 2001) gives credence to the possibility that New Zealand dawn chorus could function as a complex interspecific communication network (Kostan 2002).

Here, I investigate the effect of pre-chorus playback from a species that sings early in the dawn chorus, the Tui, and a species that sings late, the Riroriro (Grey Warbler; *Gerygone igata*; see Chapter 2) on the time that different species join the dawn chorus in a community of New Zealand songbirds. I also investigate whether New Zealand songbirds use the song of heterospecifics as a cue to begin their own song. Based on previous studies involving the effect of playback on conspecific start time (Foote et al. 2011), I predict that conspecifics will start singing earlier in response to playback of song from their own species. If birds do adjust their dawn

singing behaviour in response to the song of heterospecifics then I predict that playback of heterospecific song will result in a shift in start time for one or more heterospecific species. If we assume that birds actively use the song of heterospecifics as a cue to initiate their own dawn song at a specific time, I then expect this shift will be greater for early singing species in response to the early playback, and late singing species in response to the late playback.

3.2 Method

3.2.1 Study site and recording methods

The experiment was conducted at Mount Maungatautari Reserve from 4 October 2016 to 21 November 2016, on the southern section of the "Over the Mountain" track (38°03'18.8"S 175°33'40.1"E). The habitat is lowland podocarp-broadleaf forest with a canopy dominated by Tawa (*Beilschmiedia tawa*). Many native songbird species found in North Island podocarp forest have endemic populations on the mountain's southern side, most common among these are Tui, Piwakawaka (New Zealand Fantail; *Rhipidura fuliginosa*), Riroriro, Miromiro (New Zealand Tomtit; *Petroica macrocephala*) and Korimako. Common introduced species include Blackbird (*Turdus merula*), European Chaffinch (*Fringilla coelebs*) and European Greenfinch (*Carduelis chloris*). Translocated populations of Toutouwai (North Island Robin, *Petroica longipes*), Tieke (North Island Saddleback *Philesturnus rufusater*), Pōpokatea (Whitehead; *Mohoua albicilla*), Hihi (Stitchbird; *Notiomystis cincta*) and North Island Kokako (*Callaeas wilsoni*) are also present.

I identified nine recording locations at 200m intervals along a 1.8km stretch of the track (on trust-owned land; see Fig.1 in Chapter 2). At each site, I set up three Song Meter SM2+ GPS time-synchronised autonomous recording devices (Wildlife Acoustics, Inc., Maynard, MA, USA; Fig. 5). The Song Meters were arranged 75m apart in an equilateral triangle to create a microphone array (Fig. 5). Recording devices were strapped to trees 1.5-2m above the ground to reduce ground attenuation while still being easily accessible for changing batteries and memory cards. Trees of up to 50cm DBH were chosen to minimise sound shadows and limiting of the recorder range by the tree.
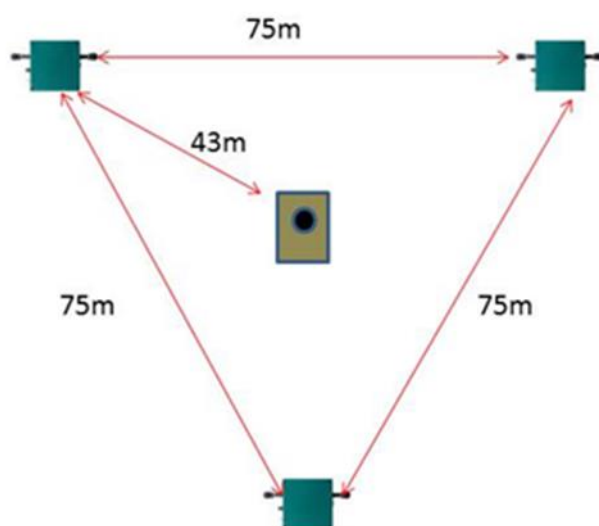
Figure 5: The playback speaker (centre) and surrounding recorders at each sampling station

The recording array allowed me to exclude birdsong from outside the target area when later analysing the recordings by ignoring faint song that was not picked up by more than one recorder. By comparing the amplitude of birdsong between recordings taken by each device, I could

identify individuals likely to be outside of the target area and exclude them. This configuration and approach also allowed me to sample the same fixed area at each recording site. The 200m interval between arrays ensured acoustic independence between sites. Array 1 was set 200m from the southern border of the publicly owned land and Array 8 within 200m of the northern edge of the public land. As I ran out of space at the end of the 1.8km of track for array 9, I positioned it between arrays 5 and 6. This site maintained acoustic independence from the other arrays I ran at the same time, being more than 400m away from them.

3.2.2 Experimental design

I assessed if early singing would trigger song initiation in con- and/or heterospecifics by conducting playback experiments using recordings of both early and late singing species, along with a white noise control. I analysed the start times of species in previous recordings taken at Maungatautari in February 2014 to determine the species used for the playback stimuli (Taipeti, C. & Waas, J.R., unpublished data, 2014). Tui and Riroriro were chosen as the early and late singing species respectively based on their start time relative to sunrise and their abundance in recordings. I used three treatments consisting of song playback from Tui (early), Riroriro (late), and a bandpass-filtered white noise control that matched the temporal and frequency properties of each species song (Figs. 6 and 7). This allowed me to present a white noise stimulus to the birds that emulates the timing and frequency of birdsong.
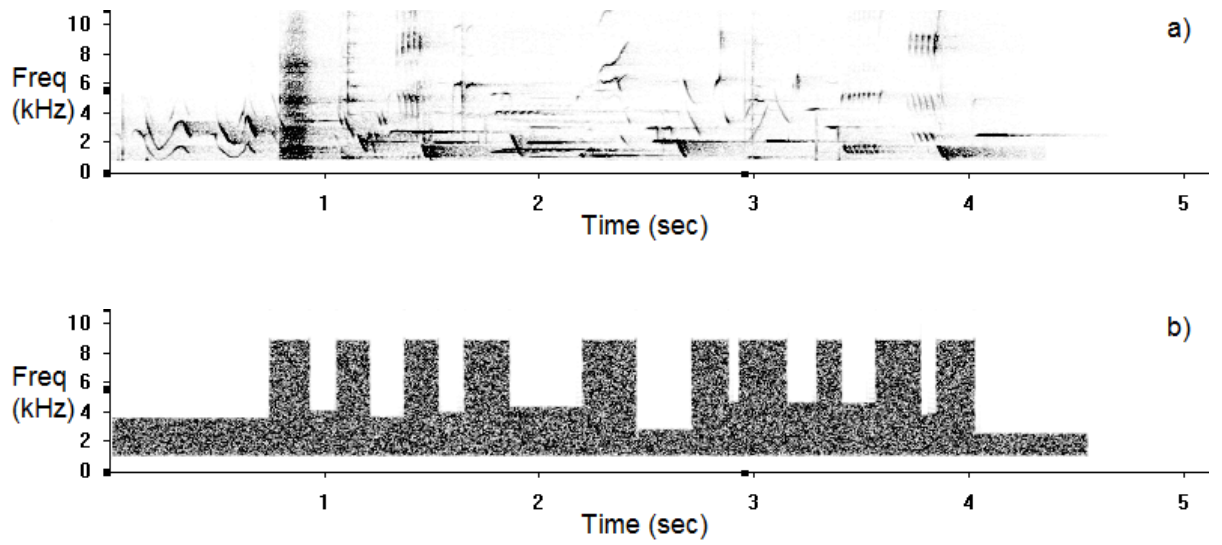
Figure 6: Spectrogram of a segment of Tui playback (a) compared with the noise control derived from Tui song (b)
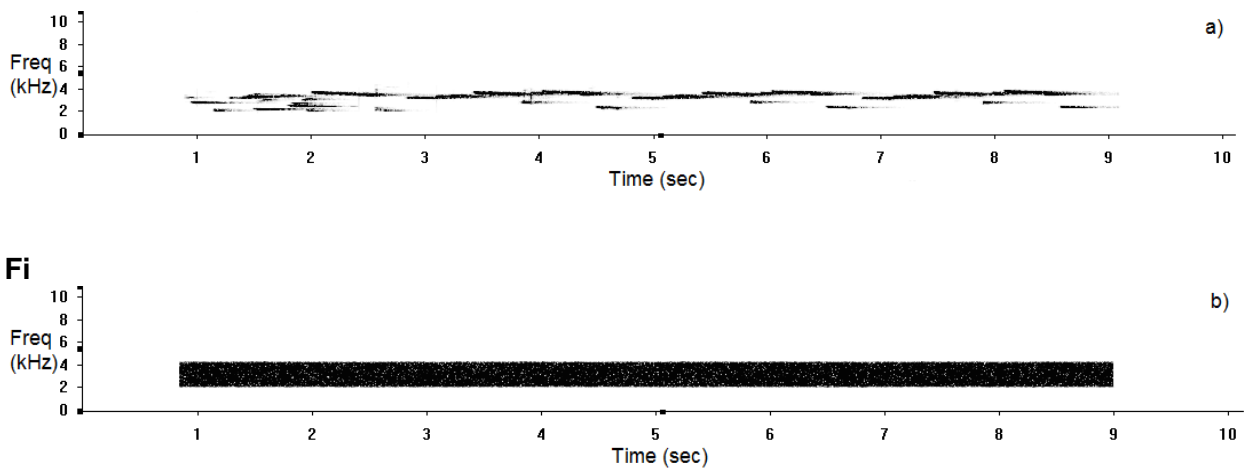

Figure 7: Spectrogram of Riroriro playback (a) with the noise control derived from it (b).

I made the playback stimuli using focal recordings taken with a Marantz digital recorder (model PMD 660, Marantz, Kawasaki, Kanagawa Prefecture, Japan) and an AKG directional microphone (model C460 B

CK68-ULS, AKG Acoustics, Vienna, Austria) at the entrance of the Over the Mountain track and at the Out in The Styx Guesthouse in Pukeatua between September and November 2016. These were supplemented with recordings taken with an omni-directional microphone (model C-3, Behringer, Willich, Germany) in February 2014 from both the study site and Maungatautari's northern enclosure. Each playback consisted of one minute of song or noise alternated with one minute of silence. I created playbacks that closely matched each species' natural singing behaviour. Tui typically sing in irregular bouts of relatively continuous song with short pauses (Higgins et al. 2001; Fig. 6a). Tui song playback was created at the natural singing interval from the source recording, about 6 irregular bouts per minute. Riroriro sing by repeating their single song type with a clear pause between songs (Higgins et al. 2002; Fig. 7a). Thus Riroriro playback was created at a rate of 4 songs/minute to match the song rate in my source recordings. Control playbacks matched the song rate of the species they were derived from. Each playback lasted for one hour, repeating the one minute of song or noise/one minute of silence sequence 30 times. The amplitude of playback was set to 90dB measured at 1m; this is a standard amplitude for bird song at the source used in playback experiments involving birds (Brumm 2004).

3.2.3 Protocol for data collection

The first three recording arrays were set up on 29 September 2016 and left to record without playback; these pre-experiment recordings were used to approximate the start time of the dawn chorus to determine my playback and recording start times. For the experiment the recording

devices were programmed in advance to record for 6 hours starting 1 hour before astronomical twilight, at least two hours before the onset of singing in the pre-experiment recordings. The Song Meters recorded for 59 minutes each hour, pausing for 1 minute to write files.

The nine arrays were divided into three blocks such that concurrently running arrays were at least 400m apart to ensure for acoustic independence (Table 3).

Table 3: The dates on which each array took recordings and sampling site GPS co-ordinates

Array	Recording dates	GPS Co-ordinates
Array 1	30 Sept- 13 Oct	38° 3' 0.3521" S 175° 33' 41.7575" E
Array 2	31 Oct - 6 Nov	38° 2' 57.2464" S 175° 33' 34.5564" E
Array 3	14 Nov - 25 Nov	38° 2' 51.8176" S 175° 33' 31.0111" E
Array 4	30 Sept- 13 Oct	38° 2' 45.6389" S 175° 33' 35.1529" E
Array 5	31 Oct - 6 Nov	38° 2' 40.6457" S 175° 33' 40.707" E
Array 6	30 Sept- 13 Oct	38° 2' 35.4534" S 175° 33' 45.8957" E
Array 7	31 Oct - 6 Nov	38° 2' 31.4714" S 175° 33' 51.9221" E
Array 8	14 Nov - 25 Nov	38° 2' 24.9306" S 175° 33' 55.6189" E
Array 9	14 Nov - 25 Nov	38° 2' 37.9212" S 175° 33' 43.1388" E

Playback experiments were run at the three arrays in each block with a single playback per morning using a randomised block design (Table 4). During each playback day, an early singer, late singer, and noise control were broadcast at the three sites. Scorpion FOXPRO speakers (FOXPRO Inc., Lewistown, PA, USA) were used to broadcast the playback stimuli. The noise control alternated between noise based on Riroriro and a Tui song such that I used 5 Riroriro noise controls and 4 Tui

noise controls across the 9 sites. Speakers (in plastic Ziploc bags to prevent water damage) were placed at the centre of each array the evening before scheduled playback. Dawn singing began close to nautical twilight in the pre-experimental recordings, so playback from the speakers was programmed to begin 30 minutes before nautical twilight (Edwards 2016). Each Playback day was followed by an "After", "Pause" and "Before" day (Table 3) with no playback to prevent habituation, with the next playback being run the morning after a Before day. However, the Pause days were eliminated after the first block of experiments due to time constraints. Playbacks were not run if forecasts predicted rain for the following morning. Once all three treatments had been run at each site, the equipment was moved and arrays set up at the next block of sites.

Table 4: Example of the playback schedule and block design using the first block of playbacks

Day	Array 1	Array 4	Array 6
1	Before	Before	Before
2	**Tui Playback 1**	**Noise Playback (Riroriro) 1**	**Riroriro playback 1**
3	After	After	After
4	Pause	Pause	Pause
5	Before	Before	Before
6	**Riroriro Playback 2**	**Tui Playback 2**	**Noise Playback (Tui) 1**
7	After	After	After
8	Pause	Pause	Pause
9	**Noise Playback (Riroriro) 2**	**Riroriro Playback 3**	**Tui Playback 3**

3.2.4 Analysis

I analysed sonograms of the recordings using Syrinx PC (John Burt, Seattle, WA, USA) to determine the start times for each species on the

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playback days. Start time of the dawn chorus for each species was defined as the time the first song that was followed by another song from the same species within five minutes. Discounting very early singers which paused singing for more than 10 minutes allowed me to exclude short bouts of non-continuous "night singing" from the analysis. The first five songs for each species were noted, and a species was excluded from the analysis if fewer than five songs were recorded. The start time of each species was then calculated in minutes before sunrise.

To investigate the effect of the playback stimuli on start time, I used a repeated measures ANOVA. As my experiment spanned a long period of time over the breeding season, I controlled for date by running the ANOVA using a linear mixed-effects model and including the number days from the start of the experiment as an additional fixed effect. Array location was included as a random effect (repeated measure). All analyses were run in JMP (SAS Institute Inc., Cary, NC, USA).

3.2.5 Ethical note

This study was granted full approval by the University of Waikato Ethics Committee and Waipa District Council. As a condition requested by Waipa District Council, I supervised the first day of playback experiments to monitor signs of disturbance such as suppressed singing behaviour or speaker mobbing. No evidence of disturbance was observed.

3.3 Results

Nine species were recorded singing before dawn on playback days including both of the playback species, Tui and Riroriro. My analysis of

dawn chorus start times under treatments of Tui playback, Riroriro playback, and noise playback showed no significant differences between treatments for any species (p>0.17; Table 3), including the two focal species, Tui (Fig. 8) and Riroriro (Fig. 9). No species changed start time significantly in response to playback of either conspecific or heterospecific song (Table 5).

Date from start of the experiment was found to have a significant influence on start time in four species (Table 6): Tui, Korimako, Blackbirds, and Mohua. Tui were found to start singing hours earlier in the later weeks of the experiment compared with early weeks; this shift was significant enough for them to start singing earlier than my playback stimuli were broadcast.

Table 5: Results of the fixed-effect test for playback type from the linear mixed model for nine species

Species	F	Df	P
Tui	0.1179	2	0.8896
Toutouwai	0.0252	2	0.9752
Korimako	0.1124	2	0.8945
Blackbird	1.9365	2	0.1793
Miromiro	0.3056	2	0.7409
Piwakawaka	0.2515	2	0.7807
Tauhou	1.1055	2	0.3693
Riroriro	0.1164	2	0.891
Pōpokatea	0.7244	2	0.5084
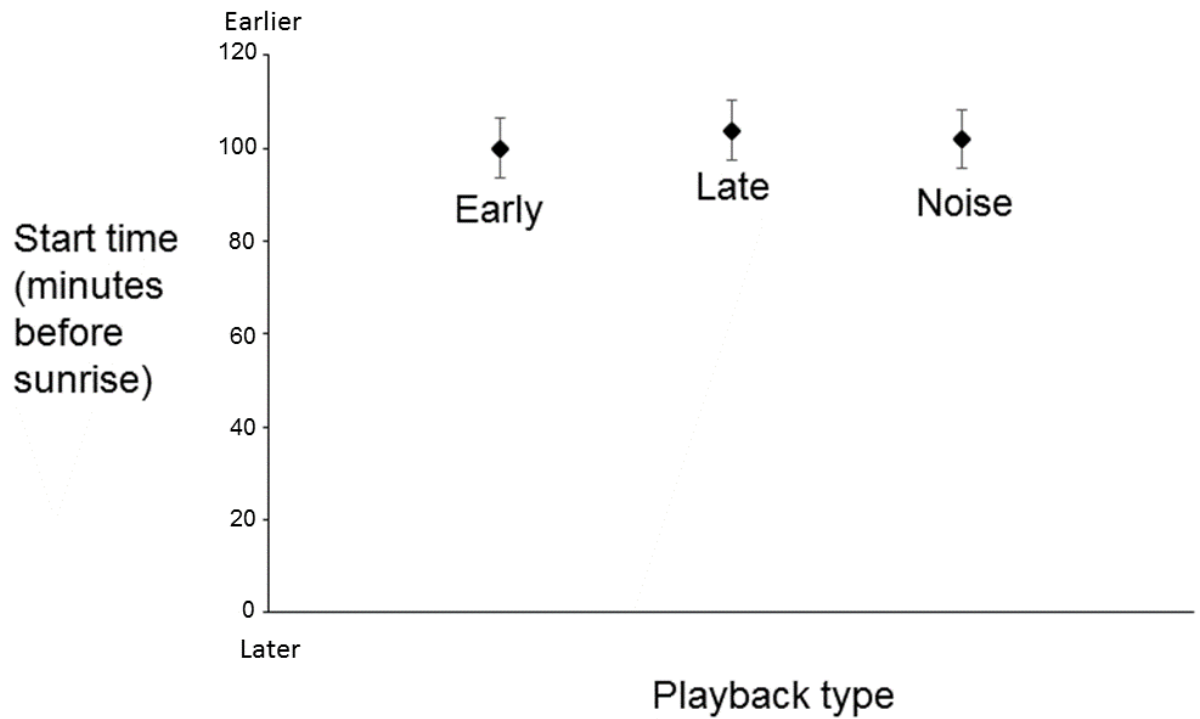
Figure 8: Mean Tui start times under the three different treatment types with standard error; Early = conspecific, Late = heterospecific
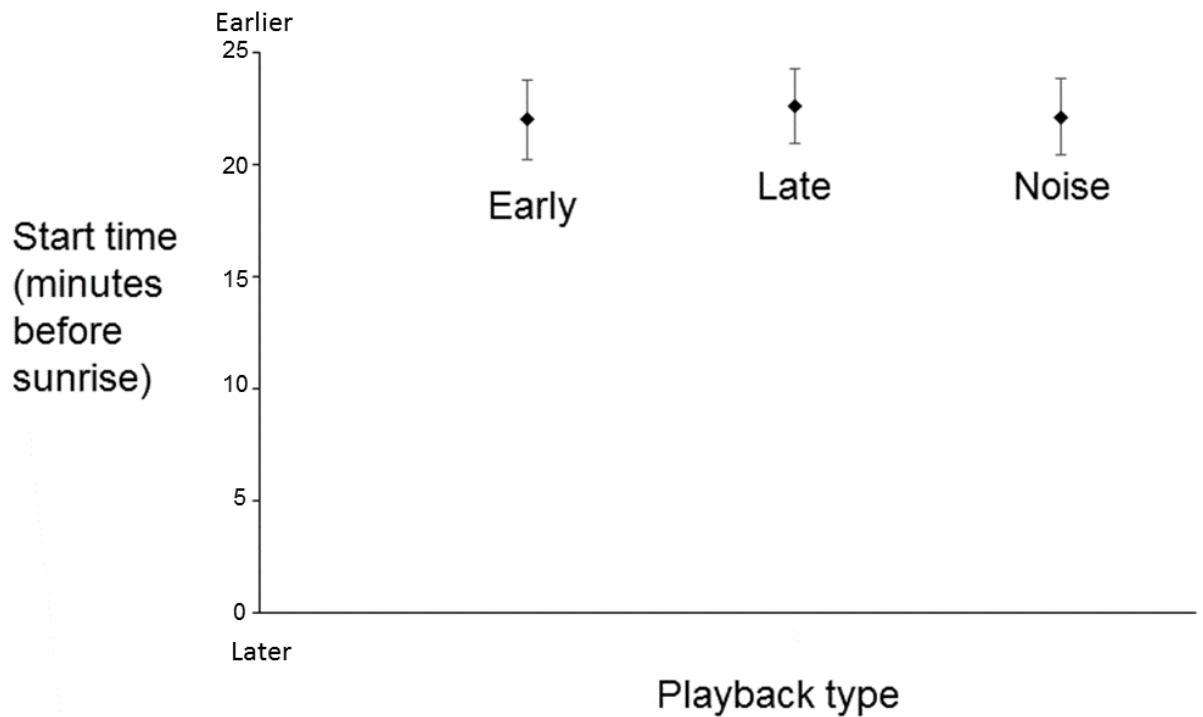
Figure 9: Mean Riroriro start times under the three treatment types with standard error

Table 6: Results of the fixed-effect test for day from start of recording (i.e. time progression of the breeding season) from the linear mixed model for nine different species

Species	F	Df	P
Tui	47.2289	1	0.0002*
Toutouwai	2.8176	1	0.1299
Korimako	35.3415	1	<.0001*
Blackbird	14.4257	1	0.0058*
Miromiro	1.106	1	0.323
Piwakawaka	0.0626	1	0.8087
Tauhou	2.3228	1	0.1832
Riroriro	0.0774	1	0.7859
Pōpokatea	7.5175	1	0.0248*

Tui start time did not change significantly in response to their own song compared with other treatments (Fig. 8), nor were Riroriro start times any earlier for the conspecific playback than for the Tui playback or control (Fig. 9).

3.4 Discussion

The results of my playback experiment demonstrate no evidence that New Zealand songbirds use song as a cue to initiate their own dawn song. There was no significant timing shift in response to conspecific playback in either Tui or Riroriro. Additionally, there was no significant response of any of the nine species to heterospecific song.

The lack of a time shift in response to conspecific song is surprising, as Foote et al.'s (2011) study of Black-Capped Chickadees found they chorused earlier in response to conspecific playback broadcast before

their usual start time, unlike the Tui and Riroriro. Hodgson (2017) also found that early but not late singing species shifted their timing earlier in response to conspecific playback. Aspects of Tui and Riroriro singing behaviour and the timing of my playback schedule may explain my result. As Tui began singing earlier than the playback stimuli for most of the recordings taken in November, my ability to gauge their response to the playback was limited. Tui are "night singers" that sing sporadic bouts of song before the dawn chorus begins (Higgins et al. 2001). For this reason, Tui may be desensitised to the presence of particularly early singing individuals, and not be attentive to their cues or attempt to match their timing. Due to the difficulty involved in obtaining focal recordings of dawn song with directional microphones, I used daytime territorial song for my Tui playback stimuli. While similar to dawn song, it may have spectral differences that could elicit a different response in conspecifics. Tui song is highly complex, and small differences such as the quantity of trills sends different signals about the sender's condition (Hill et al. 2015), and so Tui may have recognised that the playback is not dawn song and refrained from using it as a cue. Meanwhile Riroriro are known to become accustomed to a particular recording very quickly (Higgins et al. 2003), and may have simply ignored the playback stimuli after acclimating to it. As late singers, they may also be less sensitive to acoustic cues, as they must initiate their singing in a noisier environment than early singers (Hodgson, 2017).

Another possible explanation for the lack of response is that my playback stimuli were broadcast too early, which could inhibit response to

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the stimuli in several ways. First, birds will not wake to cues if they are still asleep, and even once awake may require a certain light level to initiate singing (Foote et al. 2011). Also timing shifts observed in response to playback in previous studies were only on the scale of a few minutes (Brumm 2006; Foote et al. 2011; Hodgson 2017). As a late singing species, Riroriro attempting to match the playback would be shifting their song forward by around ten minutes to more than an hour, which may represent an energetic cost that might not be worth the benefits associated with shifting start time earlier (Sexton et al. 2007). Most species other than Tui would have to make a shift on a similar scale, which may explain the lack of heterospecific response as well.

As shifts in chorus timing in response to heterospecific birdsong playback have not been studied in detail, I can make few direct comparisons. Nonetheless, Stanley et al.'s (2016) study of timing shifts in response to Emerald Cicada (*Zammara smaragdina*) playback found several species altered their song timing, in contrast with the results from my study of heterospecific birdsong playback.

If birds use the start time of heterospecifics as a cue to initiate their own song, then we would expect to see the start times of later singers "track" the start times of earlier singers as the season progresses (Leopold & Eynon, 1961). I did not observe such a trend, and found that while some species significantly altered their singing times as the season progressed, many either did not or shifted their start time in the opposite direction to the early singers. This is consistent with the findings of studies of chorus start time such as Allard (1930) and Leopold & Eynon (1961), where some

species varied considerably in their start time across the breeding season while others maintained more consistent timing relative to twilight and sunrise times. Because heterospecific start time has been demonstrated to be highly variable and influenced by numerous factors (Leopold & Eynon, 1961; Staicer et al. 1996), it may not be a particularly reliable cue. Birds are more likely to entrain their diel cycles to reliable stimuli that are significant to their morning activities, such as light levels (Thomas et al. 2001), and unless there is some direct benefit from matching their song timing to that of a heterospecific (Kostan 2002), there will be little to gain from the increased cost of singing earlier. Several New Zealand species sing sporadically throughout the night (Higgins et al. 2001; Higgins et al. 2003), making heterospecific song cues even less reliable as timing indicators.

My playback stimuli were broadcast over an hour, which largely coincided with the period where only Tui were singing. Tui song is spectrally complex and covers a wide range of frequencies (Hill et al. 2015; Higgins et al. 2001), and therefore has a high degree of spectral overlap with the songs of most other species. The bouts are also long, leaving very little in the way of "acoustic breaks" that heterospecifics could slot their song into (Brumm 2006). Tui are also highly aggressive towards heterospecifics (Soper 1976; Higgins et al. 2001), and the risk of territorial aggression from Tui may be constraining heterospecific response to playback. Forsman & Mönkkönen (2001) found that songbirds altered their singing behaviour in response to heterospecific playback, but only if predation risk was not a factor; it is possible that the risk of territorial

aggression from Tui may constrain singing behaviour in heterospecifics in a similar way.

While I did not observe any direct response to playback in terms of start time, it is entirely possible that given the evidence that some New Zealand birds do eavesdrop on each other (Higgins et al. 2001) that birds may respond to heterospecific song in other ways. Due to the large number of species involved in my experiment, I did not examine other aspects of dawn song such maximum song rate, average song rate, length of bout, song complexity or time to final song. All these aspects of dawn song have been found to change in response to conspecific playback in other species (Foote et al. 2011; Fitzsimmons et al. 2008), and may be altered in response to heterospecific playback as well. Heterospecific song may also influence more than just vocalisation; it may affect movement behaviour for example. Martin (1996) found that Least Flycatchers (*Empidonax minimus*) will more readily approach a playback speaker broadcasting American Redstart (*Setophaga ruticilla*) song, while Redstarts will make fewer flights during Flycatcher song. Agonistic behaviour between New Zealand birds is common, particularly between highly territorial honeyeaters such as Tui and Korimako (Higgins et al. 2001), and so heterospecific playback may lead to changes in movement behaviour in these species as well.

It is possible that birds do use heterospecific cues to initiate their dawn song, but this cue may be a quality other than start time. Rather, the attenuation or end of dawn singing in a heterospecific may be a cue songbirds use to initiate their dawn song; noise avoidance is the most

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common response to heterospecific signals (Brumm & Slabbekoorn 2005) and the energetic benefits of singing at a time where masking and interference are minimised could drive birds to eavesdrop on heterospecifics and initiate their dawn song as soon as acoustic breaks become available (Luther 2009). Brumm (2006) found that Nightingales (*Luscinia megarhynchos*) adjust their song timing to mimimise spectral and temporal overlap with heterospecific playback during daytime song, and a similar response may be occurring at dawn. Stanley et al. (2016) found songbirds with a high degree of spectral overlap with cicada calls delayed their song until playback of cidacas ended. Whether birds simply use the absence of overlapping heterospecific song to initiate their song or actively eavesdrop on heterospecifics in anticipation of an approaching acoustic break is an avenue for further study.

While I did not observe any shifts in timing in response to heterospecific playback, heterospecific interactions may still be important factors influencing the dawn chorus. The mutual mimicry of Korimako and Tui, and the lack of bell-like notes in Tui dawn song where Korimako are absent (Higgins et al. 2001), suggests eavesdropping is occurring and the use of heterospecific cues at dawn may be significant in New Zealand songbirds in ways I did not assess (Malavasi & Farina 2013). The acoustic recording array method I used is an effective way of studying dawn chorus singing that has been highly successful in previous studies of the dawn chorus (Mennil et al. 2006; Fitzsimmons et al. 2008; Foote & Mennil 2011; Bruni et al. 2014) and may still have merit in the study of dawn song in New Zealand species. In particular, the use of an acoustic locating system

to track movement in a similar way to Foote et al.'s (2008) study would shed light on the movement behaviour of New Zealand birds at dawn, and their interspecific interactions. More foundational work on the role of dawn song in each individual species needs to be done before we can truly understand the role of interspecific communication in dawn chorusing songbird assemblages in New Zealand.

Chapter 4

Conclusions and Recommendations

4.1 Conclusions

My study was the first investigation into dawn chorus start times in New Zealand songbird communities. Prior to this study, our knowledge of dawn chorus timing in New Zealand was limited, with no systematic study of its timing or sequence having been done. Additionally, very little work had been done on the influence of heterospecific cues on dawn chorus initiation in songbirds in general (Hodgson 2017). With nothing known about the cues that New Zealand songbirds use to initiate their dawn song, making any inferences about its function in New Zealand species was difficult.

The observational study (Chapter 2) revealed that Tui (*Prosthemadera novaeseelandiae*) always sang first during the dawn chorus, and were typically followed by Toutouwai (North Island Robin; *Petroica longipes*) and Korimako (Bellbird; *Anthornis melanura*), with Pōpokatea (Whitehead; *Mohoua albicilla*) usually singing last. The singing order had considerable variation and overlap among the mid- and late-singers (Chapter 2). Māori oral tradition (Gordon 1938; Orbell & Lagahetau 2003) accurately predicted the early singing order, positing it as a useful resource for informing behavioural studies in New Zealand birds. Like the chorusing assemblages of other countries (Allard 1930; Bruni et al. 2014), it is likely that the New Zealand chorus is structured by a complex interplay of several intrinsic, environmental and social factors. Body size is unlikely

to be a significant factor structuring the chorus order, due to the variable positions in the chorus of larger birds (Chapter 2). The foraging habits of the birds, which require differing light levels to be efficient (Thomas et al. 2002), may influence the optimal time for each bird to initiate singing. Partitioning of acoustic space between birds and the relative ability of each bird to avoid signal masking is also likely to be important for structuring the timing of song onset in each species (Brumm 2006), with birds that can partition space easily being more likely to sing at similar times. Further, territoriality and the degree of intrasexual competition between males may be leading to different start times (Foote et al. 2010), and species for which intrasexual communication is more important may benefit more from singing earlier. Rates of extra-pair paternity may also influence start time (Poesel et al. 2006), and species such as Tui that have high extra-pair copulation rates may also sing earlier.

I found that the order of New Zealand choruses was highly changeable over time (Chapter 2), much like choruses observed in other countries. Chorus timing changed relative to sunrise as the breeding season progressed, and Tui in particular shifted their song initiation much earlier. Differences in brood cycles and the fertile periods of females between species are likely to lead to species shifting their start times differently across the breeding season (Bruni & Foote 2014). The arrival of cuckoos in late spring may also be leading to changes in singing behaviour for their target species to avoid brood parasitism. The drastic shift in Tui start time may be related to seasonal migration to rich food sources in the spring (Moon 1967), and the increased population densities

in these areas. Increased population densities in these areas could be leading to elevated levels of male-male competition and higher rates of extra-pair paternity, which can drive dawn signing earlier (Sexton et al. 2007). The high rates of extra-pair paternity seen in Tui coupled with their seasonal migration patterns and established size dimorphism could be characteristic of a "hidden lek" mating system for which early dawn song is important (Wagner 1998).

I did not detect any shifts in song timing in any species in response to any of the playback stimuli (Chapter 3). Additionally, from early November onwards Tui began singing earlier than the playback stimuli. The lack of response to conspecific cues in Tui may have been due to their night singing behaviour (Higgins et al. 2001), which could desensitise them to particularly early singers. Also my playback stimuli consisted of daytime territorial song, and Tui may have recognised the subtle spectral differences and ignored it. The lack of conspecific response in Riroriro may have been due to acclimation to the playback, which Riroriro are prone to (Higgins et al. 2003).

The absence of any timing shift in response to heterospecific cues may be due to heterospecific song being an unreliable cue, as it is a highly variable stimulus that is subject to influence from numerous factors (Leopold & Eynon 1961; Fisler 1962). It is also possible that my playback stimuli being broadcast largely at a time when Tui were singing may have led to a lack of response. The high degree of spectral overlap Tui song has with other species and their aggression toward heterospecifics such as Korimako (Craig et al. 1981) may have deterred earlier singing in this

period. Considering evidence of eavesdropping exists between certain New Zealand species such as Tui and Korimako (Higgins et al. 2001), it is possible that they are attending to one another's cues but altering their behaviour in a way other than start time shifts. Increases to song output and movement behaviour are possible examples of such a change.

The order and timing of dawn chorus singing explored in the observational study (Chapter 2) may be related to the way birds attend to and use cues from neighbouring birds that I tested in the playback experiment (Chapter 3). It is possible that Tui always sing first because their song actively suppresses singing responses in heterospecific neighbours, rather than its start time serving as a cue. Their aggression toward heterospecifics and wide spectral profile that overlaps with a broad range of frequencies could act as a deterrent to initiating dawn song before they begin (Craig et al. 1981). If singing when Tui are not singing confers a fitness benefit, then we would expect heterospecifics to attend to Tui song (Brumm 2006). In this case, the cue to initiate singing would be the end or attenuation of Tui song, rather than its onset.

In the observational study I observed a clustering of start times around the same 12 minute window. If these species initiate singing close to one another because they benefit from synchronising their behaviours, such as if they formed a mixed-feeding aggregation, then we would expect species from this group to attend to each other's acoustic cues (Forsman & Mönkkönen 2001). Species from this group would therefore be unlikely to respond to the early Tui song, as seen in the playback experiment. Additionally, it is possible species in this group may be attending and

responding to multiple cues. From this group, Riroriro had the latest average song time, meaning that when they initiate singing many other species from this group have already started singing. It is possible a context dependent succession of cues, rather than any one individual cue may be key to eliciting a response in con and heterospecifics (Blumstein 2001).

An alternative possibility is that there is a specific "leader" species that birds in the later singing group use as a cue, which was a species that I did not broadcast playback stimuli from. The mixed feeding aggregations studied by Mönkkönen et al. (1996) for example, were structured around a specific "nuclear" species that all species responded to strongly (in their study this species was the Willow Tit; *Poecile montanus*). As a late singer that did not elicit any change in start time in the playback experiment, Riroriro are unlikely to be such a nuclear species that heterospecifics attend to closely during the dawn chorus and use as a cue to initiate singing. Whether such a species exists in New Zealand assemblages is an avenue for future research. Finally, the possibility that heterospecific cues are not important for structuring the order and timing of the dawn chorus must also be considered, as a shift in song timing in response to heterospecific birdsong has yet to be observed in any study (Hodgson 2017).

4.2 Recommendations

Due to the large number of species observed and the timeframe of my work, I did not investigate the influence con- and heterospecific cues had on aspects of the dawn chorus other than timing, such as song output.

Studies focused on the responses of an individual species might better elucidate the ways chorusing birds attend to neighbours and modify their songs in response. Additionally, studies investigating whether songbirds attend to the end times of neighbours' dawn song might aid in our understanding of what cues songbirds use to initiate singing and the ways they might partition acoustic space. Playback of Tui song later in the chorus may also reveal whether species actively supress singing around Tui to avoid aggression and spectral overlap. If this is occurring we might expect to see playback of Tui song leading to reduced song output and delayed start times if broadcast at this time. A more comprehensive understanding of each individual New Zealand species' chorusing behaviour can greatly assist our understanding of what factors are most important for structuring song timing in New Zealand songbird communities.

While North Island Kokako (*Callaeas wilsoni*) are present at Maungatautari, I did not detect any in my recordings, and was unable to establish their song onset timing and position in the chorus. While anecdotal accounts characterise Kokako as late singers that "finish" the dawn chorus (Gordon 1938), their exact position in the chorus and the influence their presence has on the song timing of other late singers is still unknown. Future studies of the dawn chorus that aim to establish the influence of Kokako presence in chorusing New Zealand songbird communities would aid in providing a more complete understanding of the chorus sequence, with all start times and positions within the sequence established. It should also be noted that most New Zealand forests are not

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predator free like Maungatautari, and that future studies need take into account the influence of mammalian predators, such as whether birds suppress or shorten their dawn song when predators are present. With the established importance of dawn singing for breeding behaviour and its correlation with breeding success (Murphy et al. 2008), the impact of predators on dawn singing could have implications for conservation.

The considerable shift in Tui start time as the breeding season progressed was a key finding of this study, and suggests that factors such as increased numbers of Tui and/or increased competition between males later in the season may be driving them to sing earlier (Sexton et al. 2007). Investigating whether these shifts occur in stable populations that do not receive an influx of migrant males in the spring would help establish if the arrival of transient males later in the season is responsible for the shift. Additionally, studies into breeding behaviours in populations that do see large numbers of migrant males arrive later in the season might help establish if these aggregations are "hidden leks" that facilitate extra-pair mating (Wagner 1998). The role of night singing in Tui and its relationship to dawn singing behaviour would also be an interesting avenue for future research. One function of nocturnal vocalisation is maintaining contact during migration (La 2012); thus, it is possible a link exists between increased night singing, and seasonal migration and aggregation which leads to lengthened dawn singing. Night singing is also a defining aspect of Tui in Māori oral tradition, where the bird is known as "child of the stars" (Gordon 1938), and so studies of night singing would be of significant cultural interest as well.

Studies investigating the role of individual heterospecific cues at dawn (Hodgson 2017) have yet to observe a change in start time. However, using an established sequence of the dawn chorus to test the influence of multiple successive cues by broadcasting multiple playback of different species in the natural order may help elucidate if songbirds use a combination of different cues to inform their start time. The shift in Tui song earlier than the playback stimuli highlights the value of understanding song timing and chorus sequence when it comes to designing experiments on the dawn chorus. For similar future playback experiments seeking to investigate the use of acoustic cues during the dawn chorus of New Zealand songbirds, I recommend selecting playback stimuli from species that are unlikely to start singing before the scheduled playback time.

Having now established the order and timing of song initiation among New Zealand songbirds, my study of the dawn chorus has provided a foundation for future research into dawn chorus singing in New Zealand communities. Aspects of the dawn chorus that my study was not able to address such as song rates and the function of dawn song in each individual species, will provide a fascinating avenue for future studies of the dawn chorus. I hope the findings of my studies have also been of cultural and conservational value, and that researchers planning future work on the dawn chorus in New Zealand and elsewhere will find them useful for informing their own work.

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Appendix

List of Māori names and English equivalents

Toutouwai – North Island Robin (*Petroica longipes*)

Korimako – Bellbird (*Anthornis melanura*)

Miromiro – Tomtit (*Petroica macrocephala*)

Riroriro – Grey Warbler (*Gerygone igata*)

Tauhou – Silvereye (*Zosterops lateralis*)

Pōpokatea – Whitehead (*Mohoua albicilla*)

Piwakawaka- New Zealand Fantail (*Rhipidura fuliginosa*)

Pīpīwharauroa – Shining Cuckoo (*Chrysococcyx lucidus*)

Koekoeā – Long-tailed Cuckoo (*Eudynamys taitensis*)