Sexual dimorphism of song and life history trade-offs in the New Zealand bellbird

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Frontispiece

A female (left) and male (right) New Zealand bellbird in flowering New Zealand flax (photos: Michelle Roper).

"Hutia te rito o te harakeke, kei whea to korimako e kō?"

"If the heart of the harakeke was removed, where will the bellbird sing?"

(A Maori proverb)

Abstract

Birdsong and its function is well studied in terms of male-male competition and female-mate choice. This has generated a male bias in the song literature and the dilemma that little is known about female song. However, recent research posits that female song is not only common but is also the ancestral state of songbirds. Therefore, it is timely that I investigate the ontogeny, structure and production of female song within the context of the life history of female songbirds in order to increase our current understanding of the function and evolution of birdsong. In this thesis, I use a wild population of New Zealand bellbirds (*Anthornis melanura*) as a model species. The New Zealand bellbird is ideal for this research as they produce complex but sexually dimorphic song. With a cross-sectional approach, I found the songs of each sex diverged and became more consistent as the song developed from juveniles to adults, and that their sexually dimorphic songs developed over similar timeframes, suggesting potentially related functions. I also compared how the adult song repertoire of each sex varied over time, and found that males had larger repertoires at both the population and individual levels. The syllable repertoire of each sex changed at a similar rate due to shifts in relative abundance over time, suggesting both sexes may have analogous song functions and are potentially under similar selection pressures. Sexual variation in song could theoretically be explained by differences in the syrinx structure but there is a lack of comparative research in this field. I found that bellbirds had greater sexual dimorphism in the size of their bronchial half rings compared to species both with and without female song. This suggests syrinx size alone cannot explain sexual dimorphism in repertoire size, but may have a stronger influence on sex- and species-specific song frequencies. Long-term studies provide insights to life history and my study population on Tiritiri Matangi Island has breeding data available as far back as 1977. The island's history of ecological restoration has resulted in exponential growth of the bellbird population, and I found correlated reproductive trade-offs with a reduction in clutch size over time, likely owing to increasing competition for resources. My research demonstrates how female songbirds develop and change their song over time and that they have flexible life-history traits that enable them to cope with changing breeding conditions. My research is significant in that it is one of the first to study female song in a wild population and provides important insights into male and female song development, structure and role.

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Permits and ethics

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Table of contents

List of Tables

List of Figures

List of Supplementary Materials

List of Abbreviations and Acronyms

Bellbird	New Zealand bellbird
NZ	New Zealand
Tiri	Tiritiri Matangi Island
FBS	First breeding season
N	Sample size
CI	Confidence interval
SE	Standard Error
HY	Hatch year
SY	Second year
ASY	After second year
DTW	Dynamic time warping
NMDS	Non-metric dimensional scaling
MRPP	Multivariate response permutation procedure
de	Empirical data
dp	Predicted data
a	Effect size
BIC	Bayesian information criterion
SPCC	Spectrographic cross-correlation
F_0	Fundamental frequency

MST	Male stutter syllable
DSH	Male down sweep harmonic syllable
FST	Female stutter syllable
F1	Female constant frequency flat harmonic syllable
SD	Female step down syllable
B1	First bronchial half ring
B2	Second bronchial half ring
B3	Third bronchial half ring
DSR	Daily Survival Rate
PCA	Principle components analysis

1 A song to be heard: Understated female song prevalence within the male biased world of birdsong

A female New Zealand bellbird in post-moult plumage, autumn 2015 (photo: Michelle Roper).

1.1 OVERVIEW

The underwhelming amount of research on female birdsong is a central theme to this thesis. To address this, my thesis aimed to explore 1) the development of female song in a wild songbird, 2) how a complex female song repertoire differs in size and stability compared to their male counterparts, and 3) how sexual dimorphism in the songbird vocal organ, the syrinx, could account for variation in song complexity. My final aim was to, 4) utilise long-term datasets on my study species to assess how their reproductive life history traits have responded to changing habitat on an ecologically restored island. A key and novel component of this study was that this research was field based. I studied a large population of New Zealand bellbirds on the relatively small island of Tiritiri Matangi Island. I was able to follow individual birds to obtain both longitudinal and cross-sectional data on aspects of the song repertoires and song development of bellbirds. Regular monitoring of this population for four field seasons allowed me to obtain naturally deceased specimens for studying sexual dimorphism of the bellbird syrinx structure and allowed for a large database of nesting data to be collected to study their breeding biology.

In this introductory chapter, I highlight the main theoretical concepts on song learning, development, and production that underpin the chapters of this thesis. I discuss the male-biased literature that has provided the foundation for what is known about why birds learn to sing and how songbirds develop their species-specific songs, the current literature on the prevalence of female song and what is known about female song development, and the morphology and function of the syrinx, highlighting current knowledge of syrinx sexual dimorphism. Additionally, I describe the life history of my study species and how the opportunity arose to explore their breeding biology, which may have adapted in response to living on an island in the process of ecological restoration. This is followed by a summary of my specific research questions and an outline of this thesis.

1.2 SONG ONTOGENY

1.2.1 LEARNING TO SING

The use of sound for communication in animals has many advantages over other communication modes (Thorpe, 1958). Many bird species, particularly those in the order Passeriformes, use song for communication; how they develop their songs has been a significant area of research in animal behaviour. Species belonging to the suborder Tyranni (also known as sub-oscines), such as the Eastern phoebe (*Sayornis phoebe*), can learn their species song and produce normal 'wild type' songs without auditory feedback (Kroodsma & Konishi, 1991). In contrast, true songbird species (suborder Passeres or oscines; Kroodsma & Konishi, 1991), must learn by hearing and memorising the song of their species from a tutor and then hear their own vocalisations to be able to produce their species song (Kroodsma, Meservey, & Pickert, 1983; Marler, 1970b; Marler, Mundinger, Waser, & Lutjen, 1972). Song learning also occurs in parrots and hummingbirds (Araya-Salas & Wright, 2013; Berg, Delgado, Cortopassi, Beissinger, & Bradbury, 2012). The timing of the learning process and relative importance of tutors varies between species and studies of many species are necessary to understand song development mechanisms and vocal strategies.

Why oscines evolved the ability to learn song rather than produce innate song is also of great interest. Many species have evolved local dialects (e.g. Marler & Tamura, 1962; Parker, Anderson, Jenkins, & Brunton, 2012). Dialects may occur for many different reasons, such as, 1) in response to habitat differences that affect song delivery (Derryberry et al., 2018; Nottebohm, 1975), 2) allow a male to gain extra-pair paternity (Beecher, Campbell, & Nordby, 2000), 3) female preference for specific song repertoires (O'Loghlen & Beecher, 1999), and 4) as a function of dispersal patterns (Xing, Alstrom, Yang, & Lei, 2013). Song repertoires are also affected by nutritional stress during development (Nowicki, Hasselquist, Bensch, & Peters, 2000; Nowicki, Peters, & Podos, 1998) and individual learning ability (Nowicki, Searcy, & Peters, 2002), hence song may be considered an honest signal of male quality. Larger song repertoires can be a signal of territory quality (Catchpole, 1986; McGregor, Krebs, & Perrins, 1981) and size (Buchanan & Catchpole, 1997; Yasukawa, Blank, & Patterson, 1980), stronger parasite immunity (Buchanan, Catchpole, Lewis, & Lodge, 1999) and higher reproductive success (Catchpole, 1986; Eens, Pinxten, & Rudolf Frans, 1991; Hasselquist, Bensch, & von Schantz, 1996; Lambrechts & Dhondt, 1986; McGregor et al., 1981). Females that choose males with larger song repertoires benefit by having offspring with increased post-fledging survival (Hasselquist, 1998). Males with larger song repertoires can also be better at learning new skills, such as locating food (Boogert, Giraldeau, & Lefebvre, 2008). Therefore, songbirds learn their species- and regional-specific song repertoires to potentially signal their quality and ultimately increase their reproductive fitness.

1.2.2 PHASES OF LEARNING

For a number of species, laboratory studies show that songbirds have distinct learning phases (Figure 1.1; Marler, 1970b; Marler et al., 1972). The first phase is memorisation: a sensitive period (critical period of learning; Nottebohm, 1969) where young birds memorise songs from tutors (Slater, 1989). If they are deafened or acoustically isolated during this phase, they develop abnormal songs (Marler, 1970b; Marler et al., 1972; Marler & Sherman, 1983; Nottebohm, 1968). These abnormal songs are less effective in communication (Searcy, Marler, & Peters, 1985) and may not contain species-specific identifying features (Searcy & Marler, 1987) such as syntax, i.e. structural organisation (Balaban, 1988). The duration and onset of the sensitive period varies between species; the duration is 10-50-days-old in white-crowned sparrows (Zonotrichia leucophrys nuttalli; Marler, 1970b) and onset is at 15-days-old in swamp sparrows (*Melospiza georgiana*) but as late as 250-300 days old (Marler & Peters, 1988). However, in some species, the sensitive period is not 'age-limited', e.g. song learning can be triggered after the 'normal' sensitive period in castrated Chaffinches (*Fringilla coelebs*) that are given testosterone (Nottebohm, 1969). The sensitive period can also be affected by the number of song learning opportunities, e.g. marsh wrens (*Cistothorus palustris*; Kroodsma & Pickert, 1980) and zebra finches (*Taeniopygia guttata*; Mann, Slater, Eales, & Richards, 1991) learn song after their 'normal' sensitive period if they have had limited exposure to their preferred song tutors. As well as learning from tutors, some species can also invent song syllables, e.g. swamp sparrows (Marler & Peters, 1981).

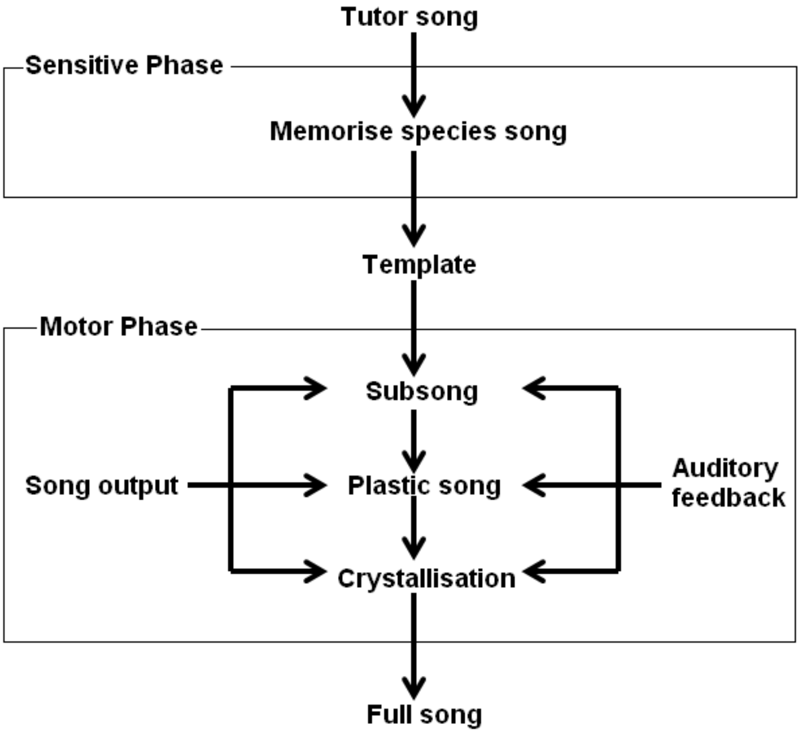

Figure 1.1. General pattern of song learning phases in oscines. Content from: Nottebohm (1968, 1969); Marler (1970b); Marler, Mundinger, Waser and Lutjen (1972); Slater (1989); Funabiki and Funabiki (2009).

The second phase of song development is the motor phase (Figure 1.1), where young birds begin to sing subsong; a highly variable and unstructured song form (Marler et al., 1972; Figure 1.1). Without auditory feedback during this phase, their song is simpler (Nottebohm, 1968), showing the importance of the ability to practice species-specific song and receive auditory feedback. Subsong progresses to plastic song that closely resembles the full song types of their species (Figure 1.1). Plastic song is variable until it develops into full song at the final crystallisation phase (Marler et al., 1972; Nottebohm, 1969; Figure 1.1). The timing of crystallisation does not appear to be dependent on how much an individual has practiced (Slater & Jones, 1998). For example, zebra finches that do not have a chance to crystallise a song before their usual time of crystallisation (90 days) are unable to correctly crystallise a song after this time (Funabiki & Funabiki, 2009). Zebra finches also seem to be able to learn their infrequently sung courtship song before their common song (Kojima & Doupe, 2011). Some species learn and sing more song syllables or types during early phases than are used after song crystallisation. This has been demonstrated in field sparrows (*Spizella pusilla*) that are able to match songs with territorial neighbours (Nelson, 1992).

1.2.3 MODE OF LEARNING

There are two modes of learning which can affect the duration and sequence of learning phases. For species that are closed-ended (or age-limited) learners, this sequence ends once birds have developed their full song repertoire; birds then continue to sing this repertoire throughout their lives (Marler & Peters, 1987; Wickler & Sonnenschein, 1989). Some factors can affect their song repertoire, such as, being deafened (songs become unstable and abnormal); although song can return to normal if hearing is restored (Leonardo & Konishi, 1999; Okanoya & Yamaguchi, 1997; Sober & Brainard, 2009; Watanabe & Aoki, 1998). In addition, some bird species can start to sing songs that they learnt during their sensitive phase (Geberzahn, Hultsch, & Todt, 2002) and even learnt to sing in their motor phase, but have not sung since their first year (Hough, Nelson, & Volman, 2000).

The other mode of learning is open-ended (or age-independent) learning. This is where songbirds continue to learn and change their song repertoire throughout their life (Beecher & Brenowitz, 2005; Eens, Pinxten, & Verheyen, 1992). Under laboratory conditions, the European starling (*Sturnus vulgaris*) increases its song repertoire over years but they can also delete songs; nevertheless, it appears that their ability to learn song may decrease with age (Eens et al., 1992). Pied flycatchers (*Ficedula hypoleuca*) are also able to learn from playback after the sensitive phase, although they do not increase their repertoire size, and appear to choose songs that may be more attractive to females (Eriksen, Slagsvold, & Lampe, 2011). Hence, open-ended learners can learn new songs and change their repertoire but not necessarily alter their repertoire size.

1.2.4 SONG TUTORS

The relationship between tutor song and learning is also primarily studied in a laboratory setting. There is a wide variety of tutor choices across songbird species. Species may learn their songs from their social father (Böhner, 1983; Greig, Taft, & Pruett-Jones, 2012), from tutors with songs similar to their father (Clayton, 1987), or from their neighbours after dispersing to their new territory (Beecher, Campbell, & Stoddard, 1994; Liu & Kroodsma, 2006; Nordby, Campbell, & Beecher, 2001; Payne, 1981). Some species can also learn songs early in life, then adjust their current repertoire and learn new songs to match the songs of their neighbours once a territory has been established (Nelson, 1992; Payne, 1981); known as 'delayed vocal ontogeny' (O'Loghlen & Rothstein, 2012). In contrast, other species learn their songs in a general area before territorial establishment and do not match with their territorial neighbours (Slater & Ince, 1982). Song sparrows (*Melospiza melodia*) use a combined strategy and alter some of their matched songs and retain individually distinctive songs (Nordby, Campbell, & Beecher, 2007).

Social factors can also affect songbirds' choice of tutor, for example the social interactions between tutor and tutee (Beecher, Burt, Ologhlen, Templeton, & Campbell, 2007; Payne, 1981). Some species will only learn from live tutors (Kroodsma & Pickert, 1984). Some species appear to choose tutors who are more aggressive (Jones & Slater, 1996), although others, such as song sparrows, learn more song from tutors they overhear than those they interact with vocally (Beecher et al., 2007). During song development, song sparrows are also more attracted to males' counter-singing (singing in response to each other) than males singing alone (Templeton, Akcay, Campbell, & Beecher, 2010). Hence, tutor choice can also be affected by social behaviours not just parental and geographic factors.

Cross-fostering experiments have played an important role in tutor choice studies. Such an experiment in the splendid fairy-wrens (*Malurus splendens*) showed that their song is learnt by cultural vertical transmission from their social father (Greig et al., 2012). The song these cross-fostered individuals learn resembles those of their social father and not their genetic father (Greig et al., 2012). In the Bengalese finch (*Lonchura striata var. domestica*), cross-fostered juveniles exposed to their social father and another unrelated tutor, tend to choose the social father (Soma, Hiraiwa-Hasegawa, & Okanoya, 2009). However, if their social father has a small repertoire size, they learn from the other tutor or they learn from both if each has a small repertoire size (Soma et al., 2009). Zebra finches also learn song amplitude from tutors (but not their genetic father), an important feature of song that can be variable between individuals (Ritschard & Brumm, 2011). Cross-fostering has also shown that the sound environment zebra finches are brought up in can affect their preferences for learning song of conspecifics. When zebra finches are cross-fostered with Bengalese finches, they lose the preference of the songs of either species (Campbell & Hauber, 2009). However, if cross-fostered birds are raised in an environment where they have exposure to multiple species song while developing their song, they prefer their species song (Campbell & Hauber, 2009).

1.2.5 LABORATORY FOCUS

Many of the studies within the field of song learning and production are laboratory based. Laboratory studies can provide various testing parameters and controls, but generally fail to replicate a songbirds' natural environment. Brown-headed cowbirds (*Molothrus ater*) in captivity learn their song in one year, whereas wild birds take up to 2 years (O'Loghlen & Rothstein, 2010). Hence, laboratory studies may not comprehensively reveal how and when birds learn their song in the wild.

Few field studies have been carried out on song learning and most focus on tutor choice. One significant field study is on Bewick's wren (*Thryomanes bewickii*), where individually identified male nestlings were observed to learn preferentially from territorial neighbours (Kroodsma, 1974). A similar field approach is taken in a study on the chipping sparrow (*Spizella passerina*), but these males learn their song after territory establishment and from only one territorial male neighbour (Liu & Kroodsma, 2006). Male Savannah sparrows (*Passerculus sandwichensis*) studied in the field have variable choices of tutors, but the most common are neighbours from either their natal territory or breeding year neighbours (Wheelwright et al., 2008).

Therefore, more research needs to be carried out song development in the wild, especially in species where both sexes sing.

1.3 FEMALE SONG RESEARCH

1.3.1 NORTHERN HEMISPHERE STUDIES OF FEMALE SONG

Female song has largely been neglected in studies on the ontogeny of birdsong (Riebel, 2003). There has also been less focus on female song due to birdsong function being most related to male territorial defence and female selection/attraction (Catchpole & Slater, 2008; Kroodsma & Byers, 1991). Females in the northern hemisphere who are known to sing, such as northern cardinals (*Cardinalis cardinalis*), only sing rarely (Lemon, 1968) but learn from tape recordings as well as males (Dittus & Lemon, 1969). However, this last study did not look at the females' phases of song learning. It was not until 1998 when a study found that the songs of the male and female cardinals are sexually dimorphic (Yamaguchi, 1998). Female cardinal song appears to more closely resemble that of juvenile plastic song, and is referred to as a crystallised neotenic version of male song (Yamaguchi, 1998). Female song sparrows sing rarely as well and they do not choose their fathers as their song tutor (Baptista & Morton, 1988). Their songs are also less complex than male song and, despite singing less frequent, female song sparrows sing more commonly during territorial establishment and conflict (Arcese, Stoddard, & Hiebert, 1988). Hence, perhaps it was less informative to study song learning in females who did not sing often, and their songs were not as developed or complex as males.

Most detail of female song ontogeny has come from studies where females are induced to sing. Konishi (1965) was the first to implant female white-crowned sparrows (*Zonotrichia leucophrys*) with testosterone implants and found that this induced females to sing; despite females not singing in the wild. Their induced songs resemble those of males and they learn the same local dialect (Konishi, 1965). Cunningham and Baker (1983) further examined song development in both males and testosterone implanted females exposed to tutors of local and distant dialects. Whilst males prefer to learn from tutors with the local dialect, females do not produce exact song replicas of any of their tutors. This means that Cunningham and Baker could not accurately determine their sensitive period and preferred tutor. However, as found for males, the female's songs become stable between their first and second years (Cunningham & Baker, 1983). Hence, whilst it was of significant interest that females that do not sing naturally could be induced to sing with testosterone, this does not advance our understanding of how female song develops.

Other studies on female song in the northern hemisphere have also revealed some aspects of female song. Female song is used for sexual communication between mates in the red-winged blackbird (*Agelaius phoeniceus*; Beletsky, 1985). In the montane white-crowned sparrows (*Zonotrichia l. oriantha*), 3 out of 15 females learn some parts of male song from live tutors (Baptista & Petrinovich, 1986). A study by Baptista et al. (1993) then compared female song between the montane white-crowned sparrow, which is a migratory subspecies, and the sedentary coastal white-crowned sparrow (*Zonotrichia l. nuttalli*). They found that the montane subspecies sing for a limited time of the year, primarily early summer, and their songs resemble those of males (Baptista et al., 1993). In contrast, the coastal subspecies sings more regularly, from autumn to spring, and their song is more distinctive from males (Baptista et al., 1993). A recent study on black-capped chickadees (*Poecile atricapillus*) has described female song as similar to that of males but with subtle sex-based features (Hahn, Krysler, & Sturdy, 2013). Outside of North America there has been attention on female song in the European starling where, on average, female song is thought to be less complex than male song but occasionally very similar (Pavlova, Pinxten, & Eens, 2005). However, studies that focussed on song learning in detail only used males (Chaiken, Böhner, & Marler, 1993, 1994). Female song also functions in mate attraction in alpine accentors, *Prunella collaris* (Langmore, Davies, Hatchwell, & Hartley, 1996), and dunnocks, *Prunella modularis* (Langmore & Davies, 1997), where female competition for mates is high. Female alpine accentors can increase their repertoire size from their first to second year (Langmore et al., 1996), but their learning mode is not known. Hence, there are various species where females sing, some with more regularity than others, but these northern hemisphere studies focus on when, why and from whom they learn to sing, and not on the learning process.

1.3.2 TROPICAL AND SOUTHERN HEMISPHERE STUDIES OF FEMALE SONG

While female song is known to be more common in the tropics and southern hemisphere (Brunton, Evans, & Ji, 2008b; Brunton & Li, 2006; Evans & Kleindorfer, 2016; Langmore, 1998; Mahr, Evans, Thonhauser, Griggio, & Hoi, 2016; Odom, Hall, Riebel, Omland, & Langmore, 2014; Slater & Mann, 2004), there has only been a small amount of research on song ontogeny with the main focus being on why females sing. Song development studied in the slate-coloured boubous (*Laniarius funebris*) showed the female sensitive phase is 6-8 months and that females learn from other females (Wickler & Sonnenschein, 1989). The learned calls of stripe-backed wrens (*Campylorhynchus nuchalis*) from South America are sexually dimorphic and they learn from same sex relatives (Price, 1998). Research on the Australian magpie (*Gymnorhina tibicen*) has only noted that juveniles of both sexes begin to sing shortly after leaving the nest and at 1 year old they still appear to be singing subsong (Brown, Farabaugh, & Veltman, 1988). In addition, magpie song syllables are not shared between males and females within local groups (Farabaugh, Brown, & Veltman, 1988). One type of syllable in the Australian magpie was found to be more complex in females and often specific to individuals (Brown & Farabaugh, 1991). Males and females both duet and hold permanent territories, hence territoriality is a likely function of song in both sexes of the Australian magpie (Brown & Farabaugh, 1991). In the Australian magpie-lark (*Grallina cyanoleuca*), it has been hypothesised that the sexes duet for mate guarding, in terms of protecting their pair bond to prevent divorce and polygamy (Hall & Magrath, 2000). Female song has also been described in the New Zealand bellbird (*Anthornis melanura*) which has distinct song types within each sex and different structural organisation (Brunton & Li, 2006). Possible functions for their song include polygyny prevention and sexual selection as females have been found to sing and respond most aggressively during courtship and chick-rearing (Brunton, Evans, Cope, & Ji, 2008a). Other studies on female song have found song functions in territorial and intrasexual aggression (Bradley & Mennill, 2009; Cooney & Cockburn, 1995; Hall & Peters, 2008; Levin, 1996). Hence, despite the recognition that female songbirds sing more prolifically in the tropics and southern hemisphere, few studies have examined female song ontogeny and function.

1.3.3 A CALL TO STUDY FEMALE SONG

Since the beginning of formulating this thesis, there has been a rise in attention to researching female song. Odom, Hall, Riebel, Omland and Langmore (2014) demonstrated that female song is more widespread in songbirds than once thought and is the ancestral state of oscine passerines. This has had a profound effect on how we think about female song and raises many questions. For example, if female song evolved concurrently with male song, does the development and function of female song also follow similar patterns to males? To find out, there are an increasing number of published studies describing female song (e.g. common yellowthroat, *Geothlypis trichas*, Taff, Littrell, & Freeman-Gallant, 2012; black-capped chickadee, *Poecile atricapillus*, Hahn, Krysler, & Sturdy, 2013; banded wren, *Thryophilus pleurostictus*, Hall, Rittenbach, & Vehrencamp, 2015; New Zealand bellbird, Brunton, Roper & Harmer, 2016; Venezuelan troupial, *Icterus icterus*, Odom et al., 2016; and white-throated dipper, *Cinclus cinclus*, Villain, Mahamoud-Issa, Doligez, & Vignal, 2017) and its function and evolution (Cain & Langmore, 2015, 2016; Illes, 2015; Krieg & Getty, 2016; Mahr et al., 2016; Odom, Omland, & Price, 2015; Reichard, Brothers, George, Atwell, & Ketterson, 2017; Soma & Garamszegi, 2015; Webb et al., 2016), and so it is timely that I further investigate female song development to underpin our understanding of birdsong evolution.

More recently, female song development has been studied under laboratory conditions with still limited studies in the wild. In laboratory studies on blue-capped cordon-bleus (*Uraeginthus cyanocephalus*), Gerberzahn and Gahr (2013) found males developed closer representations of adult song than females. Both sexes, however, learn from peers more than tutors and females sing songs they hear earlier than males (Geberzahn & Gahr, 2013). Male and female blue-capped cordon-bleus begin subsong at a similar age, with early similarities in structure that gradually diverge in duration and repertoire size (Lobato et al., 2015). With Gerberzahn and Gahr (2013) only finding a small proportion of birds developing song in these laboratory conditions, the optimal learning conditions were not reached and hence these data may not reflect song learning in the wild. Studies in the wild on superb-fairy wrens (*Malurus cyaneus*) identified the vocal tutors, with females and males learning song elements from both their mothers and social fathers (Evans & Kleindorfer, 2016). The offspring of each sex learn shared elements and unique elements of each parent, and develop a similar sized element repertoire by seven to 10-weeks-old; although, males are known to have larger repertoires than females, suggesting males continue to learn or female song undergoes selective attrition (Evans & Kleindorfer, 2016; Kleindorfer et al., 2013). Studies such as these are beginning to fill the current knowledge gap on female song learning, but more research is needed to compare aspects of song development, particularly between species where males and females sing distinct sexually dimorphic song types.

1.4 SYRINX MORPHOLOGY, FUNCTION AND SEXUAL DIMORPHISM

1.4.1 MORPHOLOGY

The syrinx is the vocal organ of birds. It is located at the junction of the trachea and bronchi in the thorax. The morphology of the syrinx varies across avian taxa (Ames, 1971). In oscines, the syrinx is a tracheobronchial syrinx where each bronchi represents a side of the syrinx (King, 1979; Suthers & Zollinger, 2006). The syrinx structure consists of a modified cartilaginous body (King, 1979). This consists of the tympanum, a combination of fused tracheal and bronchial rings, unfused bronchial half rings and the pessulus (Düring et al., 2013; Figure 1.2). It has an external network of muscles and an internal network of soft labia (King, 1979).

1.4.2 FUNCTION

The syrinx is able to produce vocalisations when the abdominal muscles contract and air is exhaled from the lungs through each bronchus and hence through the syrinx (Suthers, Goller, & Pytte, 1999). The main organs thought to be responsible for sound production within the syrinx are the medial and lateral labia (Goller & Larsen, 2002). A pair of lateral and medial labia exist within each bronchus (King, 1979) by which the syrinx is capable of two sound sources that are independently controlled (Suthers, 1990). As air moves past these labia on exhalation, they vibrate and result in sound (Goller & Larsen, 2002).

Each side of the syrinx is controlled by the equivalent side of the tracheosyringeal portion of the hypoglossal nucleus of the medulla (Nottebohm, 1971).

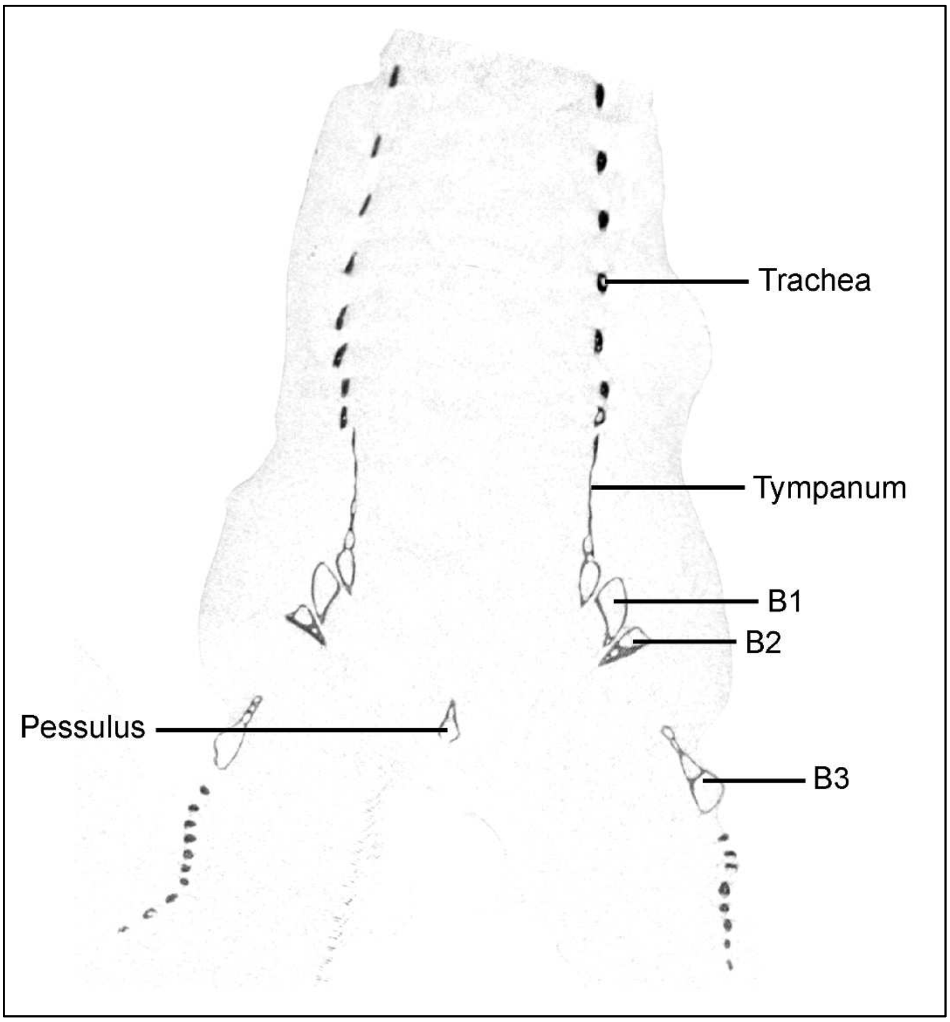

Figure 1.2. Modified cartilaginous structures of a songbird syrinx showing the examples of the trachea, tympanum, three enlarged bronchial half rings (B1, B2 and B3) and the pessulus.

Despite these two available sound sources, it has been found in several species that one side is more dominant than the other, as denervation of the dominant side can fully silence vocalisations (Nottebohm, 1971; Nottebohm & Nottebohm, 1976). Some species though, such as the brown thrasher (*Toxostoma rufum*), can use both sides independently and display no dominance (Suthers, 1990). However, regardless of whether a species has hypoglossal dominance or not, the left and right side of the syrinx seem to control the low and high frequencies of song, respectively (Nottebohm, 1971; Nottebohm & Nottebohm, 1976; Suthers et al., 1999). The external muscles contract fast enough to be responsible for the wide frequency range of a bird's song and play a part in temporal control (Elemans, Mead, Rome, & Goller, 2008). The modified cartilaginous structure of the syrinx (particularly bronchial half rings 1 and 2; Figure 1.2) may play a role in the ability of birds to sing high fundamental frequencies (Riede, Fisher, & Goller, 2010). Hence, the syrinx is a highly developed structure capable of producing song in the songbirds.

1.4.3 SEXUAL DIMORPHISM

Sexual dimorphism occurs in some structures of the syrinx. In zebra finches (where only males sing), the syrinx is 100% larger in males (Düring et al., 2013; Riede et al., 2010). The first bronchial half ring on both sides of the syrinx are significantly larger in males and the second right bronchial half ring is almost significantly larger (Riede et al., 2010). The male left medial labium is larger than in females, but the left lateral labium is smaller in males. The left tympaniform membrane is larger in females. The medial labium is connected to the first and second bronchial half rings and, with the help of external muscles, can control the tension of the medial labia (Riede & Goller, 2010a). The authors hypothesise that these larger bronchial half rings and medial labia allow for the higher fundamental frequencies sung by males (Riede & Goller, 2010a). There is more variation in the shape of the cartilaginous skeleton of the syrinx in females (Düring et al., 2013) and this may be due to the lack of song in females, hence no need for uniformity in the female (Düring et al., 2013). Other structures of the syrinx, such as, number of bronchial half rings, musculature and muscle attachment are the same for both sexes (Düring et al., 2013). However, the proportion of different muscle fibre types differs between male and female zebra finches, but this result was only found in the domesticated species and not the wild species examined in this study (Christensen, Allred, Goller, & Meyers, 2017). Therefore, certain structures of the syrinx are more highly developed in sexes that sing, showing the importance of syrinx structure for song production.

The amount of sexual dimorphism within a species is potentially dependent on their singing behaviour. In the European starling, both sexes sing and sexual dimorphism in the syrinx structure occurs (Prince, Riede, & Goller, 2011). The male syrinx is relatively larger than the females (35%) and the first (both sides) and second (right side) bronchial half rings are significantly larger in males. The left medial labium is also larger in males, but no difference exists between the left labium and for either labium on the right side (Prince et al., 2011). This may be explained by the smaller song repertoire of the female (Pavlova et al., 2005). Interestingly, compared to the sexual dimorphism that occurs in the zebra finch, it is to a lesser degree; perhaps as a result of no singing in female zebra finches (Prince et al., 2011). These results support the hypothesis that the sexual dimorphism in syrinx size coincides with the song repertoire or amount of singing between the sexes of a species. However, with only two studies on syrinx sexual dimorphism studied so far and female song being more widely spread than once thought (Odom et al., 2014), it is timely that more studies on syrinx sexual dimorphism be carried out to assess the link between syrinx structure and singing behaviour.

1.5 A MODEL SYSTEM FOR STUDYING FEMALE SONG: THE NEW ZEALAND BELLBIRD

The New Zealand bellbird (*Anthornis melanura*; hereafter bellbird) is a socially monogamous songbird in the family Meliphagidae. The bellbird is a New Zealand endemic species with a range of more than 1500 km from Three King Islands in the north (36.9029 ° S, 174.7547° E) to Auckland Islands in the south (50.6218° S, 166.1196° E) of New Zealand. Throughout their range though, bellbirds have undergone local extinctions, such as in the northern third of the North Island (north of Hamilton) by 1870 (Bartle & Sagar, 1987). The exact cause of these local extinctions is unknown but it is likely a combination of disease, presence of invasive predators, and loss of habitat (Bartle & Sagar, 1987; Lack, 1954). However, bellbirds are long distance dispersers and have high levels of genetic connectivity between populations, particularly within the Auckland, Hauraki Gulf, Coromandel and Tongariro regions (Baillie, 2011). The restoration of offshore islands has allowed bellbirds to self-reintroduce and flourish on conservation-managed islands such as Tiritiri Matangi Island (Tiri). The Tiri bellbird population declined to less than 24 birds by the time farming ended in 1972 (Baillie, 2011; Cameron & Davies, 2013), with only 6% native vegetation cover remaining in 1984 (Graham, Veitch, Aguilar, & Galbraith, 2013). The bellbird population has since significantly risen after intense habitat restoration, mammalian predator eradication and supplementary feeding (Baillie, 2011; Graham & Veitch, 2002; Roper, 2012).

Bellbirds breed in the austral spring and summer but there is regional variation in breeding parameters. Prior to Tiri's restoration in 1977/78, the few bellbirds on the island (ca. 150), bred from October to January with an average clutch size of 3.6 eggs (Anderson & Craig, 2003). In contrast, at a similar time (1978–1982) on Aorangi Island (north of Tiri, part of the Poor Knights island group), this high-density bellbird population had an earlier breeding season from September to December with a clutch size of 2.9 eggs (Sagar, 1985). Although the Aorangi bellbird population is recognised as a subspecies, *Anthornis m. obscura*, recent studies suggest there is insufficient evidence to support this (Baillie, 2011). Both biotic (Both, 1998; Ferrer & Donazar, 1996; Martin, 1987) and abiotic (Camfield, Pearson, & Martin, 2010; Martin, 1995; Sandercock, Martin, & Hannon, 2005) factors can cause these differences in reproductive biology that allow animals to adjust their life-history traits to suit their environment. With the increasing size of the bellbird population on Tiri, they may now be facing life-history trade-offs to compensate for increased levels of competition, not only within their species, but also with the growing number of other bird species introduced to the island (Galbraith & Cooper, 2013). Density-dependent reproductive output occurs as birds are either forced into lower quality habitat, or are faced with an increase in competition that causes a uniform decrease in habitat quality (Both, 1998; Ferrer & Donazar, 1996). Competition due to higher densities can lead to an increase in nest failure (Arcese, James, Hochachka, Rogers, & Ludwig, 1992; Both, 1998), reduce territory size and increase parental foraging time (Sillett, Rodenhouse, & Holmes, 2004). To compensate for high levels of competition, trade-offs are made to ensure an individual's reproductive output is maximised. For example, birds can first reduce egg volume to conserve energy but produce the same number of offspring, then reduce clutch size when smaller egg size compromises chick survival (Martin, 1987). Research on bellbird breeding biology on Tiri has accumulated from 1977/78 (Anderson & Craig, 2003) to 2010

(Brunton, D.H., unpublished). This data provides an excellent opportunity to examine how the life-history traits of bellbirds have changed over time and how this has influenced their breeding biology in response to a changing environment on a restoration island that is a strong hold for the conservation of New Zealand's endemic species.

The bellbird is my chosen species to further our knowledge on female song. As mentioned earlier, both sexes sing year-round but have differing singing patterns between the seasons (Brunton & Li, 2006). Female syllables (an acoustic unit) and song types are also different from males (Brunton & Li, 2006). Females sing song types that share syllables, unlike the males who have song types consisting of unique syllables. Brunton and Li (2006) further found that on average, females have a smaller repertoire size of 1.9 song types versus 5.4 for males, but this could be an underestimate due to recording methods. From 24 males and 12 females, the authors detected 36 syllable types: 17 'male' syllables, 12 'female' syllables and seven syllables shared by the sexes. Females tend to sing shorter and more variable song bouts than males, but despite both sexes having high year-round singing rates, females sing more than males in the breeding season (Brunton & Li, 2006). Possible functions of female song include territory defence, polygyny prevention and sexual selection (Brunton et al., 2008a; Brunton et al., 2016).

The complex nature of the singing behaviour of both sexes provides a basis to understand whether song development is equivalent between the sexes. My research involved recording the development of song in individuals from juveniles singing subsong, to adults singing crystallised song. This enabled me to look at whether song developed similarly for each sex. These results give pioneering descriptive data on female song learning. By following birds in the wild, these results give a realistic timeframe for song development. I followed individual adults over the period of this thesis to observe their song repertoire size (at the individual and population level), and whether their song changed over time (a potential indicator of whether bellbirds are open- or closed-ended learners). I then compared the morphological structure of the bellbird syrinx with previous studies on syrinx sexual dimorphism to reveal what aspects of the syrinx structure may be influencing the differences in singing behaviour between the sexes and species. The additional data I collected on bellbird breeding biology during the course of this study also allowed me to examine how their breeding biology has responded to the changing habitat that Tiri has undergone. A comprehensive understanding of the bellbirds' life history allows for exploration of the association of song with life-history traits (for example, reproduction; Appendix A). With most studies on why oscines sing biased towards males, learning how females develop their song, how it differs from male song, learning more about the vocal organ and the life history of female songbirds will provide a foundation to further research on the function and evolution of female song.

1.6 THESIS AIMS AND OUTLINE

The central theme of this thesis is to fill the knowledge gap on aspects of female song by studying a species where both sexes have complex singing behaviour. Concepts in birdsong development, song repertoires, song production and reproductive life-history traits are presented in four data chapters, all of which were studied in the field. Using the bellbird as a model species for comparing male and female song, I examined the singing behaviour, syrinx structure and breeding biology of this species to answer the four following research questions:

1) Is song development in male and female New Zealand bellbirds equivalent?
2) What is the degree of sexual variation in the syllable repertoire of the New Zealand bellbird and how does their song repertoire compare over time?
3) How does the structure of the syrinx compare between the sexes of the New Zealand bellbird and how does the structure influence aspects of song complexity?
4) Has the New Zealand bellbird faced trade-offs in reproductive life-history traits on an ecologically restored island?

In **Chapter 2**, I addressed question 1 by taking a cross-sectional approach to observe whether both sexes developed their sex-specific song and syllable types in a similar timeframe. I also examined whether their syllables' spectral parameters (e.g. duration and fundamental frequency) developed in a similar pattern, and if both sexes produced their syllables more consistently with age. **Chapter 3** reviews the sexual variation in song syllables present in the bellbird population on Tiritiri Matangi Island to answer question 2. I took both longitudinal and cross-sectional approaches to describe individual and population variation in syllable repertoire size, as well as how the syllable repertoires of each sex changed over time. **Chapter 4** addresses question 3 by comparing a potentially understudied structure of the syrinx, the first three bronchial half rings, which may play a role in the repertoire size and fundamental frequency of birdsong. I compared the bellbird sexes and reviewed how these results fit within the results of two previous studies on the sexual dimorphism of the syrinx. Through the collection of breeding biology data in this study, it allowed me to answer question 4 in **Chapter 5**. By adding my results to the long-term collection of bellbird breeding biology data on Tiritiri Matangi Island through published and unpublished studies, I was able to assess how changes in their breeding biology over time may be indicative of reproductive life-history trade-offs. To conclude, **Chapter 6** provides a synthesis of my findings in previous chapters. Here, I tie together the previous chapters' novel findings to provide a new outlook on female song research. I discuss the knowledge gaps that are still present and the further directions on what research is needed to fill these knowledge gaps on female birdsong.

Chapter 2 is published in the peer-reviewed journal *Animal Behaviour* and has been adapted for presentation in this thesis. Chapters 3 to 5 are as concise as possible for preparation to be submitted for publication in peer-reviewed journals. Author contributions are indicated in each chapter.

2 Developmental changes in song production in free-living male and female New Zealand bellbirds

A juvenile female bellbird singing (photo: Michelle Roper).

This chapter is modified from the manuscript:

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2.1 ABSTRACT

Song development research has been dominated by studies of northern hemisphere species where typically only males sing. However, female song is present in many species and recent research shows that female song is in fact the ancestral trait for songbirds. Here I present results from a field-based cross-sectional study comparing song development in both sexes of New Zealand bellbirds, *Anthornis melanura*. I asked whether both sexes develop song at a similar rate, and how the components of a song differ with age. The motor phases of each sex began at similar ages, with subsong starting at 3 weeks post-hatching and song types crystallising by 24 weeks. Song components were compared between three age groups; learning phase, first breeding season and adults. Song structure and acoustic properties were similar between sexes within the learning phase (except for mean fundamental frequency) but differed in adults. The variety of syllable types produced was more widespread in the learning phase and differed significantly between age groups and sexes. Individual syllable production varied in consistency between age groups for both sexes and I suggest that more complex syllables may require more practice to develop to maturity. The findings support the consensus that female and male bellbirds learn song at similar rates; however, differences between the sexes in the learned song components result in sexually dimorphic songs. This study is novel in that I used a field-based approach in which the complex song of male and female wild birds was compared between age groups ranging from fledging to adulthood. My study contributes to current knowledge of female song development, a topic important for further understanding the selection pressures driving song evolution in songbirds.

2.2 INTRODUCTION

Female song has been largely neglected in studies of bird song ontogeny (Riebel, 2003, 2016); primarily as the function of bird song is usually considered in the context of male territorial defence and sexual selection (Catchpole, 1982; Kroodsma & Byers, 1991; Searcy & Andersson, 1986). However, female songbirds sing in a range of different contexts and demonstrate varying capacity for song learning across species (e.g. northern cardinals, *Cardinalis cardinalis*, Dittus & Lemon, 1969, Lemon, 1968; montane white-crowned sparrows, *Zonotrichia leucophrys oriantha*, Baptista & Morton, 1988; song sparrows, *Melospiza melodia*, Arcese et al., 1988). Odom, Hall, Riebel, Omland and Langmore (2014) demonstrated that female song is more widespread in songbirds than once thought and is the ancestral trait of oscine passerines. There is an increasing number of published studies describing female song (e.g. alpine accentor, *Prunella collaris*, Langmore, Davies, Hatchwell, & Hartley, 1996; rufous-and-white wren, *Thryothorus rufalbus*, Mennill & Vehrencamp, 2005; European starling, *Sturnus vulgaris*, Pavlova, Pinxten, & Eens, 2005; New Zealand bellbird, *Anthornis melanura*, Brunton & Li, 2006; Brunton, Roper & Harmer, 2016 [Appendix A]; common yellowthroat, *Geothlypis trichas*, Taff, Littrell, & Freeman-Gallant, 2012; black-capped chickadee, *Poecile atricapillus*, Hahn, Krysler, & Sturdy, 2013; banded wren, *Thryophilus pleurostictus*, Hall, Rittenbach, & Vehrencamp, 2015; Venezuelan troupial, *Icterus icterus*, Odom et al., 2016; and white-throated dipper, *Cinclus cinclus*, Villain, Mahamoud-Issa, Doligez, & Vignal, 2017) and its function and evolution (Cain & Langmore, 2015; Garamszegi, Pavlova, Eens, & Møller, 2007a; Illes, 2015; Odom et al., 2015; Vondrasek, 2006; Webb et al., 2016), and so it is timely that I further investigated female song ontogeny to underpin our understanding of birdsong evolution.

Current understanding of female song ontogeny has come primarily from laboratory studies. Such studies have used species where females do not naturally sing but are induced to sing via testosterone implants (e.g. female white-crowned sparrows, *Zonotrichia leucophrys*; Konishi, 1965). These females were found to produce songs that resemble those of males, but it has proven difficult to identify song tutors (Cunningham & Baker, 1983; Konishi, 1965). More recently, song development has been studied under laboratory conditions in blue-capped cordon-bleus, *Uraeginthus cyanocephalus* (Geberzahn & Gahr, 2013; Lobato et al., 2015) Male and female blue-capped cordon-bleus begin subsong at a similar age, with early similarities in structure that gradually diverge in duration and repertoire size (Lobato et al., 2015). Although laboratory-based studies enable specific parameters to be tested, their results can be difficult to replicate in the field (Kroodsma, 1977; Marler, Kreith, & Tamura, 1962; O'Loghlen & Rothstein, 2010). Relatively few studies have been carried out on song ontogeny in free-living animals, and are almost exclusively focused on male song and tutor choice (Kroodsma, 1974; Liu & Kroodsma, 2006; Wheelwright et al., 2008). Studies on female song learning in the wild have also been limited to the social contexts of learning (Evans & Kleindorfer, 2016; Farabaugh et al., 1988; Price, 1998).

Understanding how the individual units of a song (syllables) develop is similarly biased towards studies of male song. These studies have found that syllables can vary in a number of ways during song development. For example, in some species, juvenile males overproduce syllables and go through the process of selective attrition as they age (e.g. North Island saddleback, *Philesturnus rufusator*, Jenkins, 1978; swamp sparrow, *Melospiza georgiana*, Marler & Peters, 1981; Marler & Peters, 1982; white-crowned sparrow, DeWolfe, Baptista, & Petrinovich, 1989; field sparrow, *Spizella pusilla*, Nelson, 1992). Juveniles can also differ from adults in a number of syntax and acoustic properties, including song duration, trill duration, number of trill syllables per song, inter-syllable gap between terminal trills, low and high frequency of terminal trill (Nuttall's white-crowned sparrows, *Z. l. nuttalli*; DeWolfe et al., 1989), amplitude (nightingales, *Luscinia megarhynchos*; Brumm & Hultsch, 2001), inter-syllable gaps and syllable transitions (zebra finches, *Taeniopygia guttata*; Glaze & Troyer, 2013). This range of potential differences between juvenile and adult song suggests there are diverse song ontogeny pathways across species. Further, the variability in song ontogeny between species raises the question of ontogenetic differences between the sexes within species.

Female song has been described in the New Zealand bellbird (hereafter bellbird), a species that has distinct sexually dimorphic song types and different syntax (Brunton & Li, 2006). This is a New Zealand endemic species (family Meliphagidae) where both sexes sing year round but have differing song types, with males singing a number of song types with unique syllables whereas females tend to sing song types that share syllable types (Brunton & Li, 2006). Their singing behaviour differs, with males often having longer song bouts whereas females have longer and more variable intervals between singing each song type. Brunton and Li (2006) found the average individual repertoire size to be 5.4 song types for males while only 1.9 for females (although this is possibly an underestimate due to methods of recording, as the range was one to six song types; Brunton & Li, 2006). From 24 males and 12 females, they detected a total of 36 syllable types: 17 'male' syllables, 12 'female' syllables and seven syllables shared by the sexes. Although year-round singing rates by both sexes are high, seasonal differences have been found, with females singing more than males during the breeding season and males singing more in the non-breeding season (Brunton & Li, 2006). Possible functions for female song in bellbirds include polygyny inhibition and sexual selection, as females have been found to sing and respond most aggressively during courtship and chick rearing (Brunton et al., 2008a). Females use song to defend their territory against neighbouring females during the breeding season (Brunton et al., 2008a); hence I predicted that both females and males must learn their adult songs by their first breeding season.

I aimed to identify when bellbirds begin each motor phase of song learning (subsong, plastic song and crystallisation; Marler, 1970; Nottebohm, 1969) and examine how syllable production develops across age groups. I used a cross-sectional approach to answer the question: do female and male songs develop along similar pathways? In addition, I examined how individual syllables develop and become more consistent to form their crystallised versions. Given that adult male and female bellbirds sing territorial song at similar rates and in similar contexts, I predicted females should develop their song in a similar timeframe to males. I also predicted that juvenile songs would be more variable than adult songs, but be more consistent in older age groups. Based on observed spectral and syntax differences between the songs of each sex, I predicted that these differences would become more pronounced in older birds. To my knowledge, this is one of only a few studies to examine female song development in a natural population.

2.3 METHODS

2.3.1 STUDY AREA AND SPECIES BACKGROUND

This study was conducted on Tiritiri Matangi Island (Tiri). Tiri is a low-lying 220 ha island in the Hauraki Gulf, 28 km north of Auckland, New Zealand (36.60°S, 174.89°E). The small island size and large bellbird population of approximately 10 birds per ha (Roper, 2012) made this an ideal study population for obtaining a large sample size of nests and individuals. Male and female bellbirds are easily distinguished in the field as they are sexually dimorphic in plumage (males are darker olive green and females have a white cheek stripe), size (females are approximately 20% smaller) and song (Brunton & Li, 2006; Heather & Robertson, 2005). Young juvenile bellbirds also differ from adults in plumage colour; juveniles of both sexes have a pale yellow cheek stripe, brown iris (red in adults) and plumage colour more closely resembling the female (Heather & Robertson, 2005).

2.3.2 DATA COLLECTION

The bellbird breeding season occurs during the austral spring and summer, from September to late January. I visited the island 4 days per week from September to

May 2012 to 2015, and September 2015 to January 2016. Bellbird territory establishment in early spring was monitored and once territories were identified, each territorial pair was observed for signs of breeding activities (e.g. copulation and nest building).

Throughout each breeding season, regular nest searches were conducted. Once a nest was found, it was monitored regularly (two to three times per week) to identify nesting stages (egg laying, incubation, chick rearing, and post-fledging periods). If a nest was located after eggs had been laid, then it was monitored more regularly to determine the hatching date. If a nest was found with chicks, their age was estimated based on their size and feather growth following Cope (2007). When the chicks were at least 8–9 days old, they were banded with a unique combination of three colour bands and a metal band. At this stage, sexes can be identified based on tarsus length (the male's tarsus is approximately 25% longer than the female's tarsus; Anderson & Craig, 2003; Bartle & Sagar, 1987). I observed a total of 255 nests and banded a total of 282 chicks and 109 hatch-year juveniles.

2.3.3 AUDIO RECORDINGS

Recordings were made using a directional shotgun microphone (Sennheiser ME66, Sennheiser, Germany) and a portable solid state recorder (Marantz Professional PMD 661, Marantz Professional, Cumberland, RI, U.S.A.) with 24-bit sampling precision and 48 kHz sampling rate. Recordings were made of colour-banded individuals that were banded as chicks at the nest and older birds caught with mist nets or at supplementary feeder stations. Recordings of juveniles were initially made on their natal territories. After they had fledged and left the natal territory, I intensively searched for these banded birds and recorded their song year round (except winter months) over the course of the study. I was equally likely to detect males and females of different ages as there is no evidence of sex-specific mortality and only low levels of sex-biased dispersal off the island (Baillie, 2011). Over the study period, I collected a total of 100 recordings from 22 females and 260 recordings from 50 males that were banded at the nest.

2.3.4 ACOUSTIC PROCESSING

Spectrograms and waveforms were produced to visualise the songs using Raven Pro 1.4 and 1.5 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) with standardised settings (a bandpass filter of 500 Hz to 22 000 Hz, size 256 samples, time grid overlap 50%, and normalised by amplifying to fill the waveform window). Syllables were selected and measured from spectrograms (FFT algorithm) of song samples using the open-source software Luscinia (Lachlan, 2007). For Luscinia settings, see Suppl. 2.1.

2.3.5 MOTOR PHASES

For several songbird species, laboratory studies show that males have distinct learning phases (Marler, 1997). The first phase is memorisation, a sensitive period (critical period of learning; Nottebohm, 1969) where young birds memorise songs from tutors (Slater, 1989). The second phase is the motor phase where young birds begin to sing subsong, followed by plastic song and finally song crystallisation (Nottebohm, 1969, 1970). My audio recordings were converted to spectrograms and visually inspected to detect the earliest age that each motor phase was produced. I followed definitions of Marler, Mundinger, Waser, and Lutjen (1972) for subsong as highly unstructured song, and plastic song as when I could first identify a resemblance to adult song in syllable types, song types and syntax type. Song crystallisation is defined as the first stage that full adult song types are produced (Marler et al., 1972). However, the variation in singing pattern (single songs versus multiple song sequences) and syntax between the sexes (Brunton & Li, 2006) made it difficult to precisely determine when a song had crystallised for each sex. (See Figure 2.1 for examples of song types.) Hence I also used spectral characters to determine crystallisation, where the song spectrograms are pure, clean and lacking noisy outlines (i.e. that have a high stability of frequency; Marler et al., 1972). Here I present my estimates of crystallisation in terms of the first full song type that I repeatedly detected with a minimum of four song type repeats.

2.3.6 SONG COMPONENT COMPARISONS

Song is defined as a group of syllables that are sung in consistent order, and song types may share a differing number of syllables (Podos, Peters, Rudnicky, Marler, & Nowicki, 1992). A syllable is a single song unit made up of one or more continuous traces of sound on a spectrogram, with each trace being referred to as an element (i.e. a note; Konishi, 1964; Marler & Isaac, 1961; Ritschard & Brumm, 2011). Syllables were categorised according to the shape of the element trace, based on features such as frequency modulation, fundamental frequency and harmonics. Additionally, syllables with more than one element were defined by having elements that were repeatedly found together (Kershenbaum et al., 2016). I set a maximum

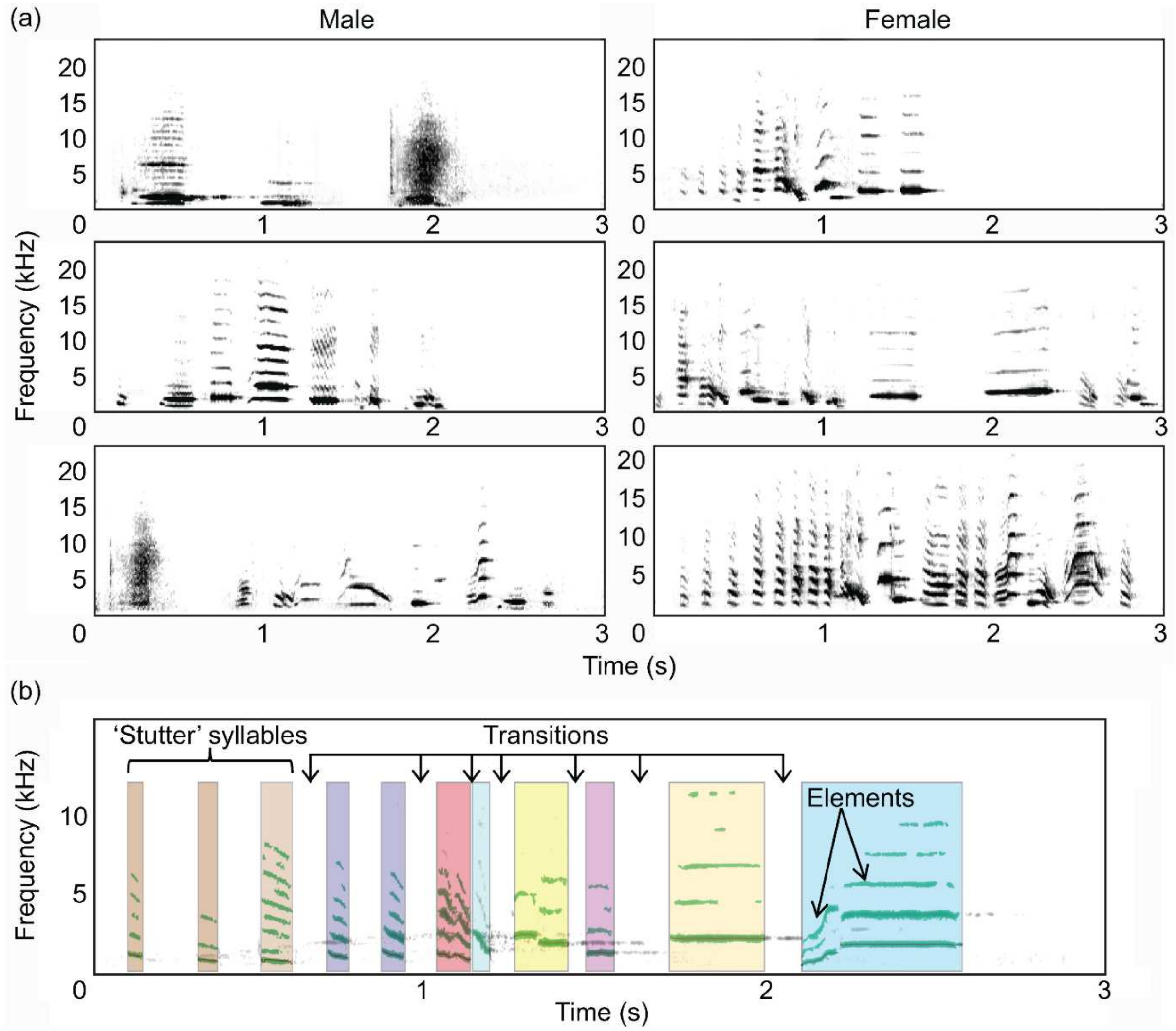


Figure 2.1. (a) Examples of song types showing the variation between different song types for male and female bellbirds. (b) Song parameters defined and analysed in the study are shown in an example of female song: total number of syllables (each coloured box is one syllable), number of unique syllables (different colours represent different syllable types), transitions between unique syllables, inter-syllable gap (end time of selection box to start time of next selection box), syllable duration (start to end time of selection box) and fundamental frequency (lowest frequency selection for each element). Examples of introductory 'stutter'-like syllables are also labelled.

gap length of 10 ms between elements to define a syllable based on my observations of large numbers of recordings. Adult bellbirds have multiple song types that are approximately 2–3 seconds long, sung in singing bouts of varying duration (Brunton & Li, 2006). See Figure 2.1 for examples of adult bellbird songs, syllables and elements. Juveniles often sing songs of longer durations (>10 s) with fewer clear demarcations of when a song type starts and ends (personal observation; example in Suppl. 2.2). Hence, for age-based comparisons I used song selections that were 3 s long.

Owing to constraints in following wild juveniles throughout their first year of life, I took a cross-sectional approach by sampling different individuals of known age across three age groups: learning phase (6–29 weeks), first breeding season (39–74 weeks) and adults (>104 weeks; sample sizes in Table 2.1). All birds recorded as part of this study were of known age and were banded either pre- or post-fledging. The learning phase group combined juveniles singing various stages of the motor phases, primarily subsong and plastic song. I separated first breeding season (FBS) birds from older adults as previous studies found the songs of older adults differ from those of first year breeders (Cucco & Malacarne, 2000; de Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009; Garamszegi et al., 2007b; Motes-Rodrigo, Labra, & Lampe, 2017). For the learning-phase and FBS age groups, a number of individuals were recorded on two to four occasions (over 4–71 days); these recordings were treated as independent song selections.

Table 2.1. Summary of sample sizes for the syllable components, syllable similarity and syllable consistency analyses.

Analyses	Variables for *N*	Syllable	Male			Syllable	Female		
			Learning phase	FBS	Adult		Learning phase	FBS	Adult
Syllable components[1]	Song selections		69	42	72		15	33	36
Syllable similarity[1]	Song selections per individual mean ± SE		6.9 ± 0.5	3.3 ± 0.27	3.0		3.8 ± 0.6	3.3 ± 0.31	3.0
	No. of individuals		11	12	24		4	10	12
	(no. of individuals recorded repeatedly)		(8)	(1)			(1)	(1)	
	Syllables		645	266	385		145	486	522
	Clusters		4	8	7		5	9	10
Syllable consistency[2]	Syllables per individual mean ± SE[3] (no. of individuals)	MST	7.7 ± 2.1 (7)	2.8 ± 0.7 (6)	3.5 ± 2.5 (2)	FST	13.8 ± 5.8 (4)	21.0 ± 4.0 (10)	17.4 ± 5.6 (10)

	DSH	2.0 ± 1.0 (2)	4.7 ± 1.6 (6)	3.7 ± 1.8 (3)	F1	3.3 ± 1.2 (3)	9.7 ± 3.9 (6)	5.3 ± 1.4 (8)
	Cough	6.2 ± 2.0 (5)	5.0 ± 1.3 (7)	7.0 ± 2.4 (4)	SD	9.0 ± 3.1 (3)	2.1 ± 0.4 (8)	2.5 ± 1.0 (8)

[1] Syllable component comparisons and syllable similarity used three × 3 s samples from individuals of known age (banded either pre- or post-fledging). Individual recordings were divided into three broad age groups: learning phase (6–29 weeks), first breeding season (FBS: 39–74 weeks) and adults (>104 weeks). A number of individuals were recorded on two to four occasions (over 4–71 days) within the learning-phase and FBS age groups; these recordings were treated as independent song selections.

[2] For syllable consistency, syllables were selected from all available recordings for each individual within an age group; sample sizes and mean ± SE number of syllables selected per individual are shown. Male syllables: male stutter (MST), down sweep harmonic (DSH) and cough; female syllables: female stutter (FST), constant frequency (F1) and step down frequency (SD).

[3] Not all syllables occurred in all songs recorded.

To reduce any potential effect of phenotypic-dependent survival, only individuals known to survive to their first breeding season were selected for this study. The majority of song exemplars for a given individual were collected on the same day. The samples were taken from up to three of the best quality recordings available. If samples were from one long recording, they were chosen by taking song from within the first 10 s, the middle of the recording and the last 10 s of the song sequence. If no song was at the sampling point in the recording, then I chose the nearest song sequence to the sampling point.

I identified syllables in all song selections. I measured the total number of syllables, number of unique syllables and number of transitions between unique syllables, as these measures have been used in previous studies on bellbird song (Brunton et al., 2016; Appendix A) and are frequently used measures of song complexity (e.g. Hill, Amiot, Anderson, & Ji, 2017). The bioacoustics analysis software, Luscinia (Lachlan, 2007), was used to export measurements of syllable duration, inter-syllable gap and mean fundamental frequency of syllables, as these measures have been reported to change with song development in other species (e.g. male zebra finches; Glaze & Troyer, 2013). See Figure 2.1 for examples of these measurements. To verify my definition and method of identifying a syllable, a second observer repeated the same measurements for 14 randomly selected song samples. Any syllables categorised differently (<10% in total) were then examined and a consensus agreed upon and all selections were re-measured to ensure all syllables were identified consistently. I investigated broad-scale differences in song structure using generalised linear mixed models in *R* (lme4 package; Douglas, Maechler, Bolker, & Walker, 2015; R Core Team, 2015). Total syllables per song, number of unique syllables per song, transitions between unique syllables, syllable duration, inter-syllable gap and mean fundamental frequency (see Figure 2.1 for examples of each term) were modelled with age group (learning phase, FBS and adult) and sex as fixed effects (Poisson distribution for count data, Gaussian for continuous data). As I had multiple song samples for each bird, individual ID was included as a random effect. A significance threshold of $P = 0.05$ was used for all analyses in this study. The mean ± 95% confidence interval (CI) for each of the above song components was calculated and plotted in *R* (plyr and ggplot2 packages; R Core Team, 2015; Wickham, 2011, 2016).

2.3.7 Syllable similarity

Using the same song selections from the song component comparisons, syllables were compared using the dynamic time warping (DTW) algorithm within Luscinia (Lachlan, 2007; see Suppl. 2.1 for settings). The DTW for syllables was weighted for duration (10), fundamental frequency (1), fundamental frequency normalised (1) and harmonicity (0.5). The DTW produced pairwise dissimilarity scores for all syllables that were then used for non-metric dimensional scaling ordination (NMDS) to plot syllable similarity and to perform a multivariate response permutation procedure (MRPP; de = empirical delta, dp = predicted delta, a = effect size). The effect size for MRPP tests is also known as the agreement statistic and is calculated as 1 – de/dp (McCune & Grace, 2002). Both tests take the average for each individual. The NMDS plot produced using *R* (plyr and ggplot2 packages; R Core Team, 2015; Wickham, 2011, 2016) shows how the syllables are separated within the acoustic space (mean ± SE for syllable similarity scores) by age group and sex. The MRPP tested for differences in the means between each age group and sex.

Cluster models to categorise syllables for each age group were used to assess the similarity of different syllables and place each syllable within a group of similar syllables. The models were created from the NMDS output created in Luscinia (Lachlan, 2007). Using *R* (mclust package; R Core Team, 2015; Scrucca, Fop, Murphy, & E, 2017), Bayesian information criterion (BIC) models were created to find the optimal number of clusters (Table1). To assess how many clusters best represented the number of syllable groupings, I considered: 1) the optimal number of clusters generated by my model; 2) visual inspection of syllables using the NMDS output in Luscinia; and 3) examination of the BIC scores and levels of uncertainty. Uncertainty levels were assessed by dividing the proportion of uncertainty into quartiles. A higher proportion in the 100% quartile indicates that the majority of syllables are well classified.

2.3.8 SYLLABLE CONSISTENCY

Recent research has found that stereotypic repetition of the same song, phrase or element may indicate age in some bird species (e.g. tropical mockingbird, *Mimus gilvus*, Botero et al. 2009; great tit, *Parus major*, Rivera-Gutierrez, Pinxten & Eens, 2010). To determine how syllables differed in consistency with age, I used spectrographic cross-correlation (SPCC; Clark, Marler & Beeman, 1987) in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). SPCC calculates pairwise similarity between spectrograms and the comparisons are made by sliding the spectrograms across each other in time until the best fit occurs (see Suppl. 2.3 for additional methods). The final consistency value came from the matrix of pairwise comparisons of syllables averaged for each syllable within individuals and for each age group. I then plotted the age groups versus mean ± SE peak correlation value for each syllable measured from all individuals.

I chose the six most common syllable types found within my recordings for individuals in each age group (three male and three female; see Table 2.1 for sample sizes) for the SPCC analysis. Syllables were selected from all available recordings for each individual within an age group. Not all syllables analysed occurred in every song selection; hence the sample sizes analysed varied across age groups and with the variable analysed (Table 2.1 provides a summary of sample sizes). Syllables were ranked for complexity based on spectral characteristics such as duration, harmonics and use of both sides of the syrinx, following Cardoso and Mota (2007) and Cardoso, Hu, and Mota (2012). The male syllables chosen in order of increasing complexity were a short duration harmonic stutter (MST), a down sweep harmonic of moderate duration (DSH) and a cough (a rapid introductory click element immediately followed by high entropy and broad frequency buzz element of longer duration). For female syllables in order of increasing complexity, I compared a short duration harmonic stutter (FST), a constant frequency flat harmonic with a frequency range of approximately 2300-2700 Hz and moderate duration (F1), and a syllable composed of two constant frequency elements that slightly overlap (indicating double syrinx involved) with the second constant stepping down to a lower frequency (SD). See Suppl. 2.4 for examples of these syllables. For this aspect of the study I used only high-quality recordings of individuals recorded for each age group.

2.3.9 ETHICAL NOTE

Capture, banding and recording of New Zealand bellbirds throughout the study was permitted by the New Zealand Department of Conservation (20666-FAU, 34833-FAU, 2008/33) and the Massey University Animal Ethics Committee (12/32, 15/21). All bird capture, handling and banding procedures were carried out in accordance with guidelines provided by the New Zealand Department of Conservation. Care was taken to minimise disturbance to habitat and surrounding wildlife, such as following existing paths and diverting off track only when necessary. Care was taken around nests to minimise my impact on the parents and I did not capture birds for banding with mist nests during the incubation stage. Females with brood patches caught at supplementary food cages were released after being banded but without measurements and blood sampling.

2.4 RESULTS

2.4.1 MOTOR PHASES

The age of onset of the three motor phases was similar for both sexes (subsong: male = 3 weeks, female = 3 weeks; plastic song: male = 13 weeks, female = 15 weeks; crystallised song: male = 24 weeks, female = 24 weeks; Figure 2.2). The 3-week-old

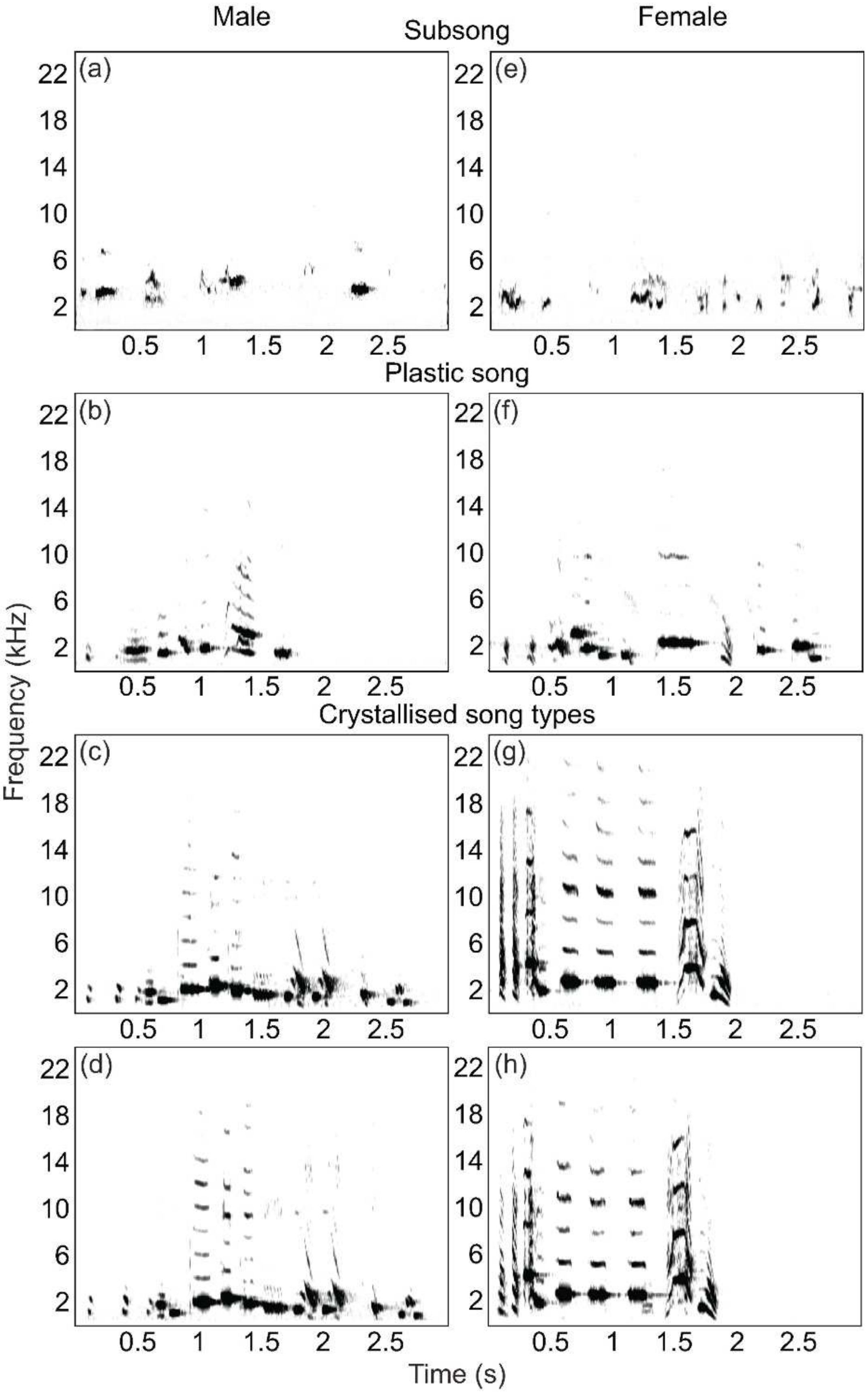

Male
Subsong
Female
(a)
(e)
Plastic song
(b)
(f)
Crystallised song types
(c)
(g)
(d)
(h)
Frequency (kHz)
22
18
14
10
6
2
0.5
1
1.5
2
2.5
Time (s)

Figure 2.2. Spectrograms of the motor phases for (a–d) male and (e–h) female bellbirds. (a, e) Subsong, (b, f) plastic song and (c, d, g, h) crystallized song types. Subsong is represented at 6 weeks old for the female as we did not have sufficient recordings for the 3-week-old female. Subsong for the male is at 3 weeks old. Plastic song is at 15 weeks old for the female and 13 weeks old for the male. Crystallized song types are at 24 weeks for each sex and two examples of a repeated song type are shown.

male and female were observed singing subsong on their respective natal territories with siblings nearby. A 6-week-old female was found singing subsong (Figure 2.2) approximately one to two territories away from her natal territory (ca. 150 m). All other recordings of juveniles were made away from their natal territories. For the 24-week-old female, I had six repeats of a song type over 4 days of recording (6 days between first and last recording) and for the male I had four repeats over 1 day of recording.

2.4.2 SONG COMPONENT COMPARISONS

All song components measured and tested had significant age-sex interaction effects; sex alone did not have a significant effect for any measure except mean fundamental frequency (F_0) of syllables (Table 2.2). The total number of syllables produced per 3 s sample was similar between learning-phase males and females, but this changed, with older females singing more syllables and older males singing fewer syllables (Figure 2.3; Table 2.2). The number of unique syllables produced and syllable transitions were also similar between the sexes in the learning phase, but

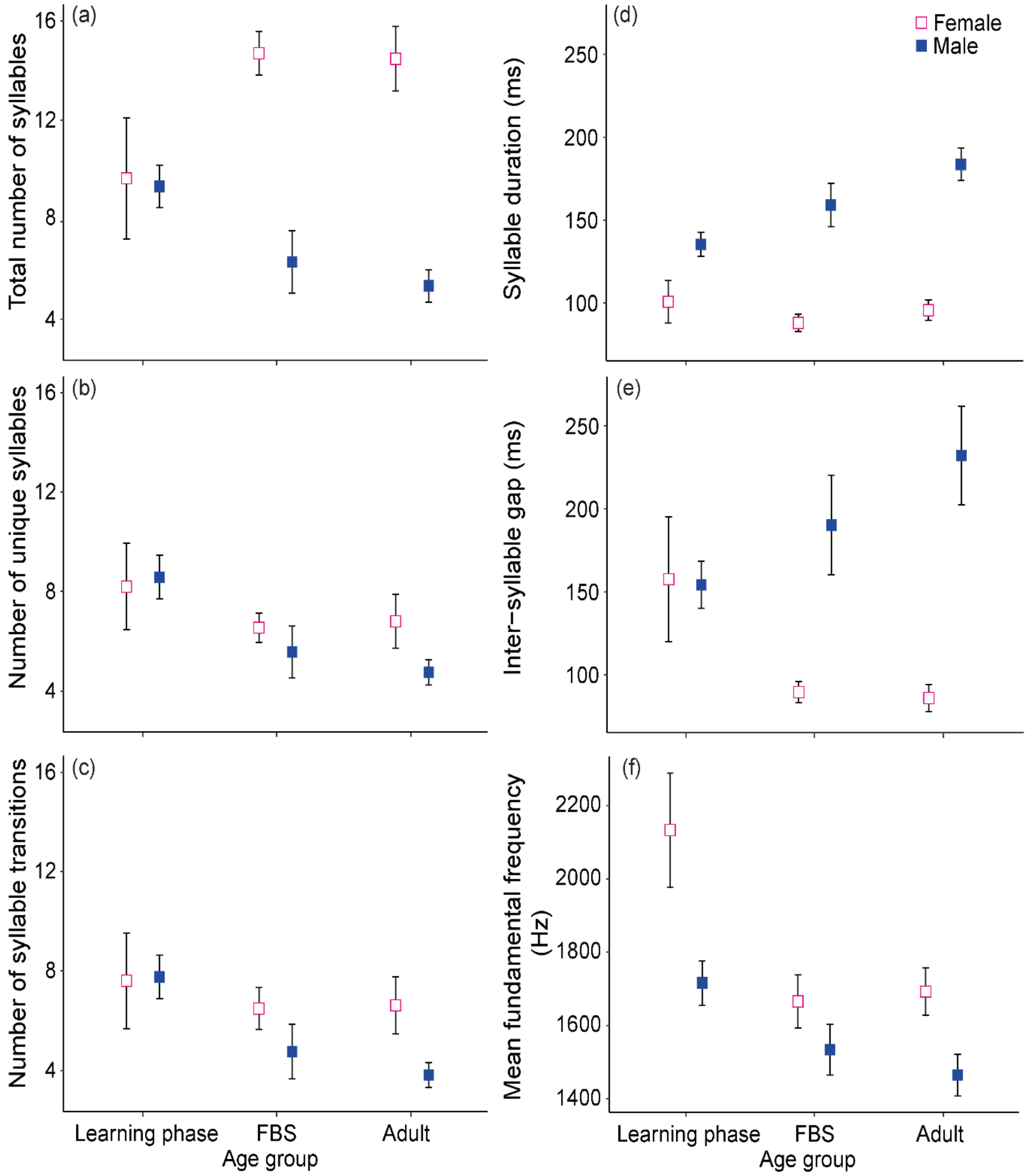


Figure 2.3. The mean ± 95% confidence interval (CI) for (a) total number of syllables, (b) number of unique syllables, (c) number of syllable transitions, (d) syllable duration, (e) inter-syllable gap and (f) mean fundamental frequency (F_0) per 3 s song sample for males and females of three age groups: learning phase (6–29 weeks); first breeding season (FBS; 39–74 weeks), and adult (>104 weeks). See Table 2.1 for *N*.

diverged with age. Adults showed the greatest sex difference with males producing significantly fewer unique syllables and transitions than adult females (Figure 2.3). Syllable duration differed significantly with age, while there was a strong trend for sex differences ($P = 0.072$) with male syllable duration being on average longer than for females across all age groups (Figure 2.3; Table 2.2). Sex differences in duration of syllables were also greater for adult birds than other age groups, with older males singing syllables of longer duration than older females (Figure 2.3). The inter-syllable gap was similar between the sexes in the learning phase but was longer for older males and shorter for older females (Figure 2.3; Table 2.2). The mean F_0 of syllables produced was the only measure that differed with sex independent of age, but it also differed between the age groups (Table 2.2). Mean F_0 of syllables produced by females was higher overall than males (Figure 2.3). FBS and adults of both sexes produced syllables with a significantly lower mean F_0 than learning-phase birds (Table 2.2).

2.4.3 SYLLABLE SIMILARITY

Syllables varied significantly between age groups (MRPP, de = 0.268, dp = 0.271, $P < 0.001$, a = 0.01) and sex (MRPP, de = 0.262, dp = 0.271, $P < 0.001$, a = 0.03; Figure 2.4). However, owing to the small effect sizes, it remains difficult to draw any conclusions about the biological importance of these broad-scale differences in syllable parameters between ages and sexes. Syllables were on average more similar within each sex than between sexes (Figure 2.4; sample sizes in Table 2.1). However,

Table 2.2. Results of generalised linear mixed models relating age and sex to the total number of syllables, number of unique syllables, number of syllable transitions, mean syllable duration, mean inter-syllable gap and mean fundamental frequency per 3 s song sample.

	Effects	Comparison	Estimate	z/t value	*P*
Total syllables	Age	Learning-FBS	-0.37 ± 0.08	-4.51	<0.001
		Learning-Adult	-0.57 ± 0.08	-6.84	<0.001
	Sex	Male-Female	0.02 ± 0.13	0.18	0.858
	Age*Sex	Learning-FBS	0.80 ± 0.15	5.36	<0.001
		Learning-Adult	0.97 ± 0.15	6.43	<0.001
Unique syllables	Age	Learning-FBS	-0.41 ± 0.09	-4.73	<0.001
		Learning-Adult	-0.61 ± 0.09	-6.92	<0.001
	Sex	Male-Female	-0.08 ± 0.13	-0.58	0.564
	Age*Sex	Learning-FBS	0.21 ± 0.17	1.26	0.208
		Learning-Adult	0.43 ± 0.17	2.58	0.010
Syllable transitions	Age	Learning-FBS	-0.46 ± 0.10	-4.74	<0.001
		Learning-Adult	-0.73 ± 0.10	-6.97	<0.001
	Sex	Male-Female	-0.06 ± 0.16	-0.36	0.721
	Age*Sex	Learning-FBS	0.33 ± 0.19	1.72	0.086
		Learning-Adult	0.60 ± 0.19	3.08	0.002
Syllable duration	Age	Learning-FBS	-34.82 ± 15.50	-2.25	0.025
		Learning-Adult	-19.72 ± 19.02	-1.04	0.304
	Sex	Male-Female	33.68 ± 18.43	1.83	0.072
	Age*Sex	Learning-FBS	46.17 ± 16.93	2.73	0.006
		Learning-Adult	62.00 ± 22.94	2.70	0.009
Inter-syllable gap	Age	Learning-FBS	-86.41 ± 36.31	-2.38	0.017

		Learning - Adult	-84.86 ± 57.77	-1.47	0.147
	Sex	Male - Female	24.91 ± 54.81	0.45	0.651
	Age*Sex	Learning - FBS	100.12 ± 39.14	2.56	0.011
		Learning - Adult	176.83 ± 71.27	2.48	0.016
Mean fundamental frequency	Age	Learning - FBS	-313.87 ± 116.60	-2.69	0.007
		Learning - Adult	-316.99 ± 127.85	-2.48	0.016
	Sex	Male - Female	-374.42 ± 125.79	-2.98	0.004
	Age*Sex	Learning - FBS	278.38 ± 130.20	2.14	0.033
		Learning - Adult	113.18 ± 152.80	0.74	0.462

Note: Individual was included as a random effect. Learning = learning phase; FBS = first breeding season.

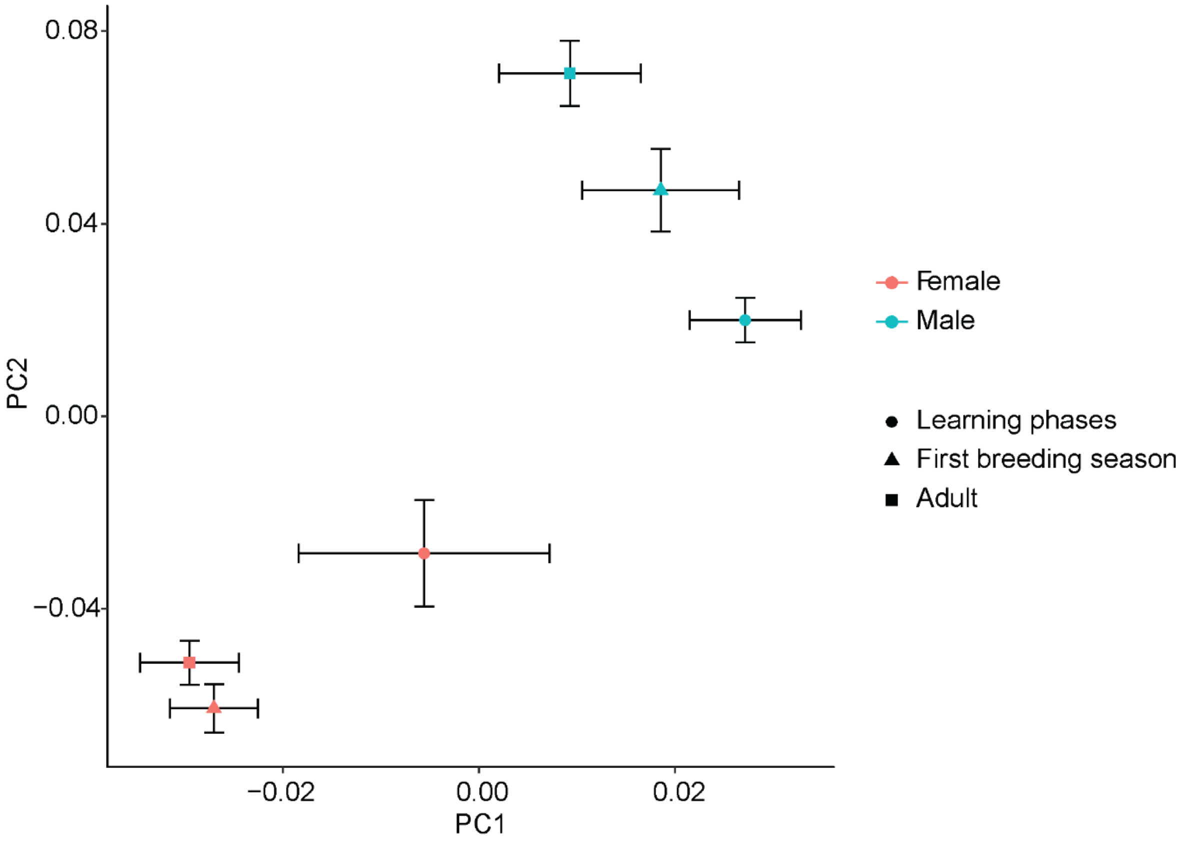


Figure 2.4. Nonmetric dimensional scaling (NMDS) plot summarized as mean ± SE for male and female syllables for the learning phase, first breeding season (FBS) and adult age groups (stress value = 0.066).

syllables also varied between age groups within sex, particularly for males (Figure 2.4).

The optimal cluster number predicted by BIC models matched my predictions in all age groups and sexes except for FBS male birds, where another model was chosen with eight clusters (optimal five). This model produced eight clusters of similar syllables with little overlap. See Suppl. 2.5 for uncertainty values. The distribution of syllables in the acoustic space varied between the learning phases and older age groups (Figure 2.5). Syllables in the learning phases were widely dispersed with only four and five clusters being detected for males and females, respectively (Figure 2.5). Male learning-phase syllables were more tightly clustered than those of females, most probably due to the inclusion of birds from 15 to 29 weeks old, which the female group did not have. Overall, I could visually see that syllables were distributed into more discrete clusters for FBS (eight male, nine female) and adult (seven male, ten female) birds.

2.4.4 SYLLABLE CONSISTENCY

Average SPCC values for males showed that adults produced more consistent syllables than the learning-phase age group (Figure 2.6). MST was the male syllable produced most consistently, while FBS males had values that were closer to those of the learning phase. The DSH was the next most consistent male syllable. Interestingly, FBS birds were more consistent than adults at producing the DSH syllable. The cough was the least consistent syllable over all age groups, although FBS and adults were both more consistent than the learning-phase group.

Average SPCC values for females also showed that adults produced more consistent syllables (Figure 2.6). F1 was the most consistent female syllable, varying the least across age groups. SD was the second most consistent female syllable with similar average values in both FBS and adult birds, but with very low consistency in the learning-phase group. FST was produced the least consistently by females across

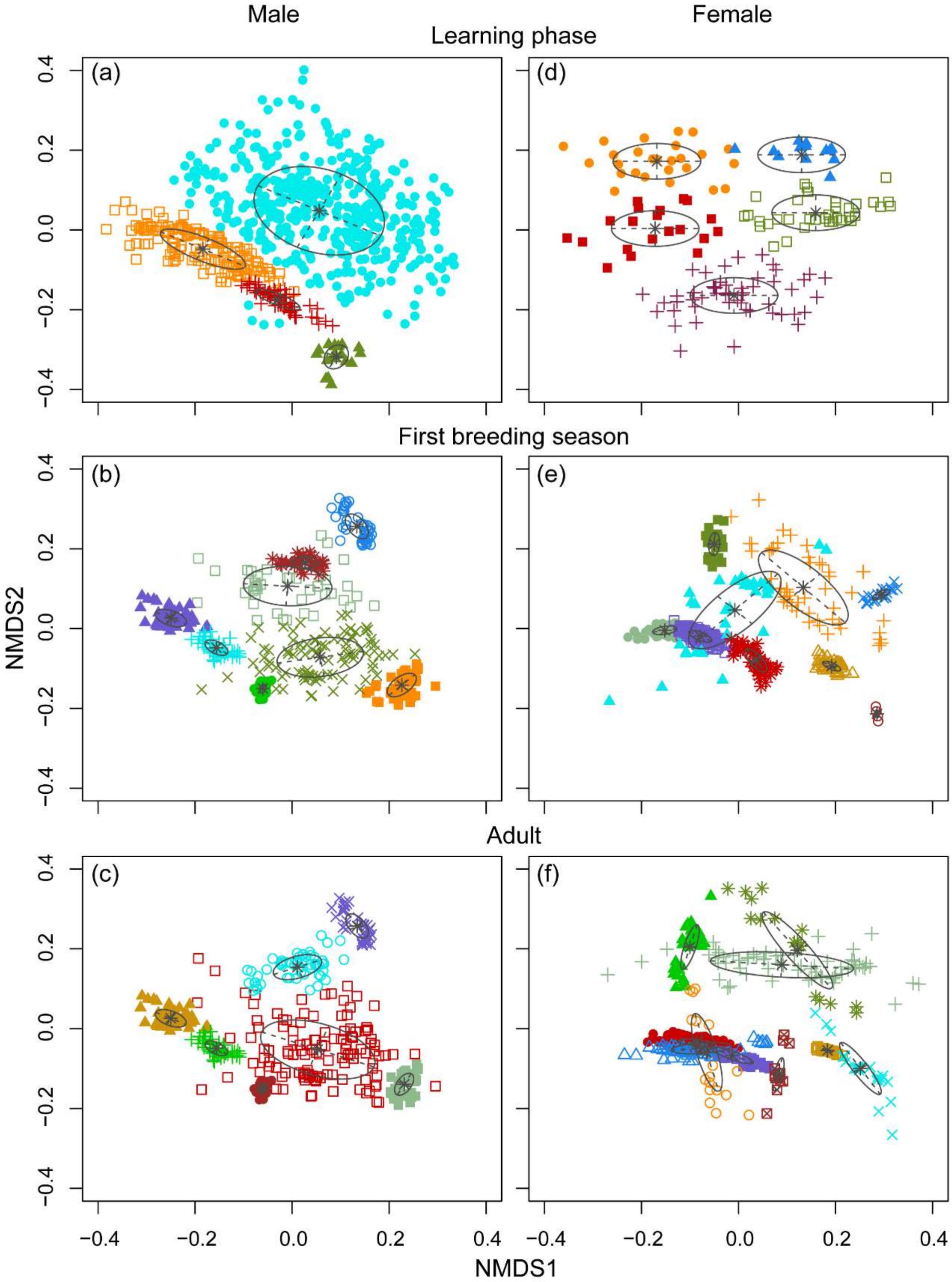


Figure 2.5. Syllable clusters based on Bayesian information criterion models for the learning phase, first breeding season (FBS) and adult age groups for each sex: (a–c) males and (d–f) females. Colours and symbols do not reflect the same syllable clusters between each age group and sex.

age groups (unlike the male stutter) with only a slight increase in SPCC values from learning phase to adult.

2.5 DISCUSSION

For New Zealand bellbirds, I found that male and female juvenile song development began at similar ages. Subsong began as early as 3 weeks post-hatching for both sexes and song types crystallised from 24 weeks old. Male and female song components were most similar during the learning motor phases but by the adult stage, male and female songs were distinct. The number of unique syllables and transitions decreased with age but in females the total number of syllables produced during 3 s increased. Males of all age groups produced syllables of longer duration than females, with the greatest difference being between adults. Inter-syllable gap correspondingly decreased with age in females but increased in males. Mean F_0 of syllables differed most between the sexes during the learning phase but then the difference decreased with age. However, across all age groups females had a higher mean F_0. Across all spectral measurements, syllables differed with sex and age, but the effect of this difference was small which makes it difficult to interpret the biological significance of the effect of age and sex on the spectral parameters. However, the NMDS plot shows the spectral measurements were most similar between the learning phases of each sex and this is supported by the similarities in most of the separate syllable components that were tested. For both sexes, syllables developed into distinct types and were sung more consistently as adults. However, I found differences between syllable types in how quickly they were sung consistently across age groups.

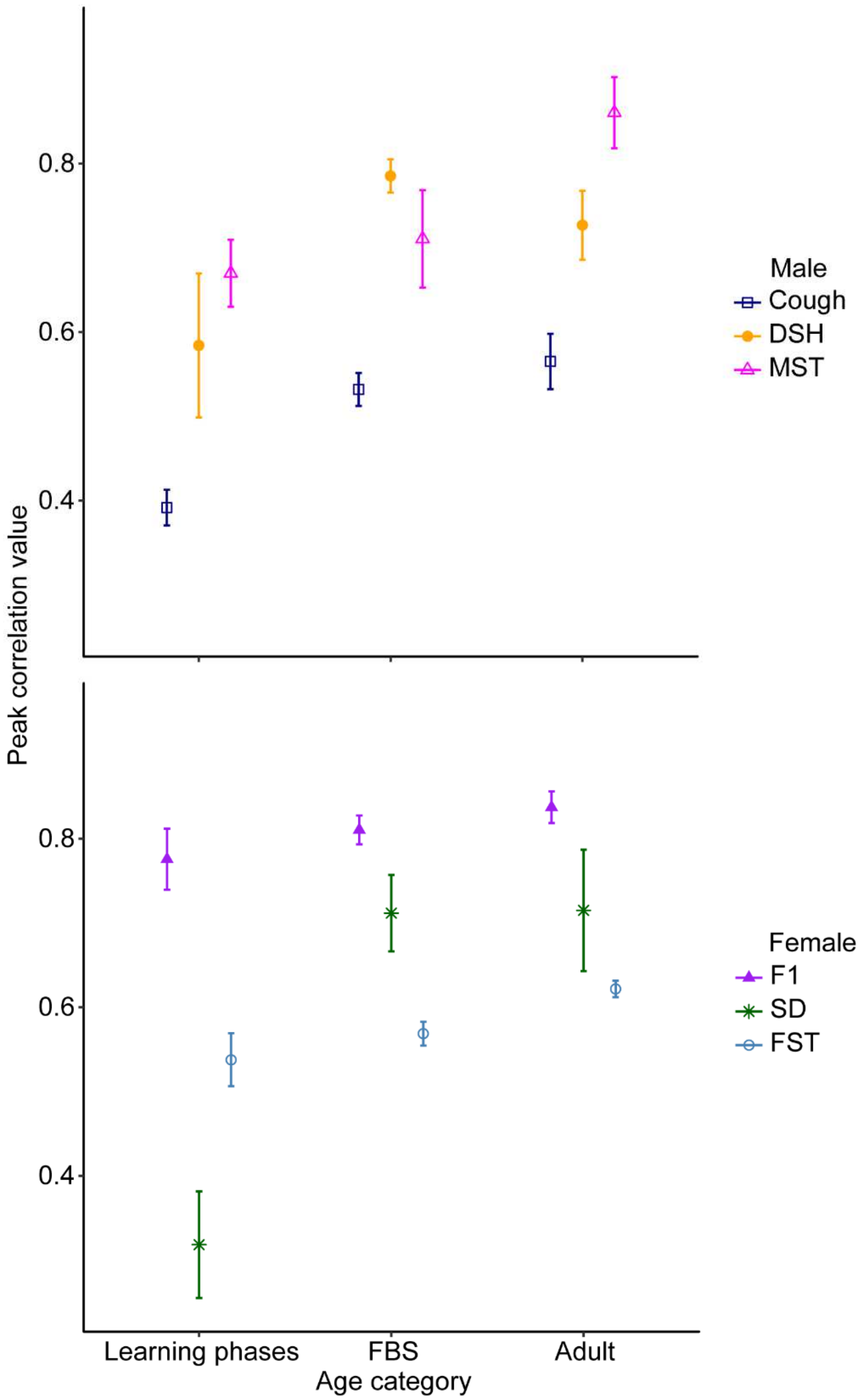


Figure 2.6. Comparison of mean ± SE peak correlation values between six syllable types for each sex across the learning phase, first breeding season (FBS) and adult age groups. Male syllables: cough, down sweep harmonic (DSH), and male stutter (MST); female syllables: constant frequency (F1), step down frequency (SD), and female stutter (FST). See Table 2.1 for *N*.

My results show that male and female bellbirds are learning to sing within similar timeframes and that they crystallise their songs before their first breeding season. This is particularly significant in this species as both male and female bellbirds use sex-specific song in intra-sexual competition to defend breeding territories (Brunton et al., 2008a; Brunton & Li, 2006). Similarity in song development timelines of sexes within a species have been found in the few studies that have been published; for example, blue-capped cordon-bleu (Lobato et al., 2015), grey catbird (*Dumetella carolinensis*; Kroodsma, Houlihan, Fallon, & Wells, 1997), and Nuttall's white-crowned sparrow (Baptista et al., 1993). Despite the different onset and duration of motor phases between species (Beecher & Brenowitz, 2005), for the few species where male and female song learning have been studied, the timelines in song development are much more comparable. I could only present the minimum age that each bellbird sex began subsong, but the similar age at which I found each motor phase and results from previous studies suggest the sexes learn in a similar timeframe.

Few studies have documented song structure differences between the sexes with age, but in studies on species where both sexes sing, the components of song in juveniles are more similar between sexes than in adult birds. During early male song development, syllables are often over-produced (Marler & Peters, 1982a; Nelson, 1992). As the male song develops they undergo selective attrition such that they only retain a select number of syllables and song types. Male and female blue-capped cordon-bleus have similar sized syllable repertoires early in development but, with age, females reduce their repertoire significantly more than males (Lobato et al., 2015). Lobato et al. (2015) suggested that these repertoire differences combined with sexual dimorphism in the song regions of the brain in blue-capped cordon-bleus may indicate different developmental pathways. While female bellbirds produced more syllables per 3 s as adults, both male and female adults developed syllable types that formed distinct groups compared to the large spread within the acoustic space seen in juveniles. Such grouping has been referred to as statistical learning, where syllables are categorised as the bird practices and learns to sing its songs (Fehér, Ljubičić, Suzuki, Okanoya, & Tchernichovski, 2017). While I cannot yet infer selective attrition in bellbirds from this study, my results, along with the study on blue-capped cordon-bleus, suggest that each sex undergoes refinement in the song components they produce from the learning phases to adulthood.

While in general the syllables that make up the song repertoires of a species develop according to the nature and function of their song, syllable development can also differ between the sexes. The song of northern cardinal females has been referred to as a neotenic version of male song due to its similarity to juvenile male song (Yamaguchi, 1998), but in bellbirds I saw male and female song diverging during the learning phases and developing distinct adult spectral characteristics. One significant difference that I found between the bellbird sexes during early song development was a higher mean F_0 for female song. This is probably due to sexual size dimorphism (Ryan & Brenowitz, 1985) with bellbird females being on average 20% smaller than males (Heather & Robertson, 2005). However, the songbird syrinx allows a wide production of frequencies in both sexes (Prince et al., 2011; Ryan & Brenowitz, 1985), so in combination with morphological limitations and environmental factors affecting the transmission of certain frequencies (Ryan & Brenowitz, 1985), multiple factors could explain why female bellbirds sing syllables with higher fundamental frequency. The duration of the syllables also differed between the sexes in bellbirds, with adult females more often singing shorter syllables, and adult males singing longer syllables, than younger birds. Male white-crowned sparrows also show increasing syllable duration with age (DeWolfe et al., 1989) but zebra finches do not (Glaze & Troyer, 2013). The average shorter syllable duration in adult females is primarily due to repetition of the short stutter syllable (for examples see Figure 2.1), a syllable used as an introductory syllable for most female song types (Brunton & Li, 2006). Hence, not only is there a diversity of potential developmental pathways between species, differences in syllable development are occurring between the sexes of a species and further research is needed to answer why this is the case (for example, could social and reproductive costs be involved).

Syllable consistency has been reported to change with age in several species (Botero et al., 2009; Brumm & Hultsch, 2001; de Kort et al., 2009; DeWolfe et al., 1989). Here I have presented the first results for wild birds, to my knowledge, on how different syllables become more consistent from the motor phases to adulthood. While I cannot separate individual effects from age (see Suppl. 2.6 for the mean ± SE SPCC score for each individual), the pattern of increasing consistency is clear between the different syllables for each sex. I found that the more complex, long duration, two-element syllables sung by bellbirds had the lowest average consistency score in the learning-phase group, which suggests that complex syllables may require additional practice before being produced consistently. Complex syllables probably require use of both sides of the syrinx (Zollinger, Riede, & Suthers, 2008) and need a higher level of coordination within the vocal tract, including muscular control of the syrinx (Pytte & Suthers, 2000; Suthers et al., 1999), respiration (Veit, Aronov, & Fee, 2011) and beak movements (Nelson, Beckers, & Suthers, 2005). Hence this coordination may need to be learned before juveniles can start performing complex syllables with higher consistency. Syllable development can also be affected by the amount of interaction with potential tutors (Margoliash, Staicer, & Inoue, 1994; Ritschard & Brumm, 2011), an aspect beyond the scope of my study. Improvements in male song stability with age have also been linked to higher reproductive success and arguably play a role in sexual selection (Botero et al., 2009). For bellbirds, now that I have shown that male and female song becomes more stable and consistent over time, future work is needed to assess the function of this stability and why individual syllables vary in consistency.

Field-based studies have a number of challenges: large population size, local movement and mortality, weather and often poor recording conditions, and low probability of relocating free-living individuals throughout their first year. Ideally this study would have taken an entirely longitudinal approach by following a large number of individuals across all motor phases through to adulthood. This approach would reduce potential bias from factors such as phenotypic-dependent survival, individual variation and asynchronous hatching. Previous studies of this bellbird population, however, indicate no significant sex bias in mortality (Baillie, 2011); thus, I was equally likely to record both sexes at different ages. Despite this, I obtained more recordings of males than females as males tended to more regularly visit supplementary feeding stations which are dominated by males (Roper, 2012). Juveniles were often predated during this study by native predators (such as morepork, *Ninox novaeseelandiae*, a small owl), which became apparent as I found the remains of banded nestlings. Owing to these limitations, I used a cross-sectional approach. To minimise (song) phenotypic-dependent survival I only included data from juveniles that were known to survive to their first breeding season. Studies comparing longitudinal and cross-sectional age-related changes in song have revealed some differences when comparing first-, second-, and third-year birds (Forstmeier, Hasselquist, Bensch, & Leisler, 2006; Gil, Cobb, & Slater, 2001). However, the relationships are not consistent, with some studies showing links between song traits and survival (Lambrechts & Dhondt, 1986; Rivera-Gutierrez et al., 2010) and others linking song traits with age (Garamszegi et al., 2007b) and breeding experience (Motes-Rodrigo et al., 2017).

2.5.1 CONCLUSIONS

This study of wild songbirds provides some of the first evidence of song development in a system where both males and females are prolific, year-round singers. Song structure and acoustic properties were similar between sexes during the learning phase, but the sexes diverged as adults. Individual syllables varied in their rate of development, with more complex longer syllables potentially requiring more practice to develop. Although females and males were observed to produce songs at similar rates, differences between the sexes in the song components learned resulted in sexually dimorphic songs as adults, suggesting different developmental pathways. I found that although both sexes had considerable reduction in the number of syllables with age, they also had increasing syllable consistency and distinctiveness. In the case of New Zealand bellbirds, I speculate that strong selection to sing competitive adult songs will occur for both males and females. My study provides a better understanding of how female songbirds develop song in the wild and a foundation for further examining the evolution and function of female song.

2.6 AUTHOR CONTRIBUTIONS

Michelle M. Roper contributed to the design of the study, developed the methodology, conducted the fieldwork, managed field assistants, performed statistical analyses and wrote the manuscript. Aaron M. T. Harmer performed aspects of the statistical analyses and wrote sections of the manuscript. Dianne H. Brunton designed the study, developed methodology, assisted with fieldwork and contributed to the writing of the manuscript.

2.7 SUPPLEMENTARY MATERIAL

SUPPL. 2.1. LUSCINIA SETTINGS

The following setting changes from the default for the spectrogram were recommended by R. Lachlan (personal communication): max. frequency 12 000 Hz; frame length 10.667 ms; spectrograph points 470; spect. overlap 90.63%; deverberation was set to 100% to reduce echo; dynamic range was altered between 30 and 60 to obtain the best estimation of fundamental frequency when selecting elements; high pass threshold 300 Hz.

TIME-WARPING OPTIONS

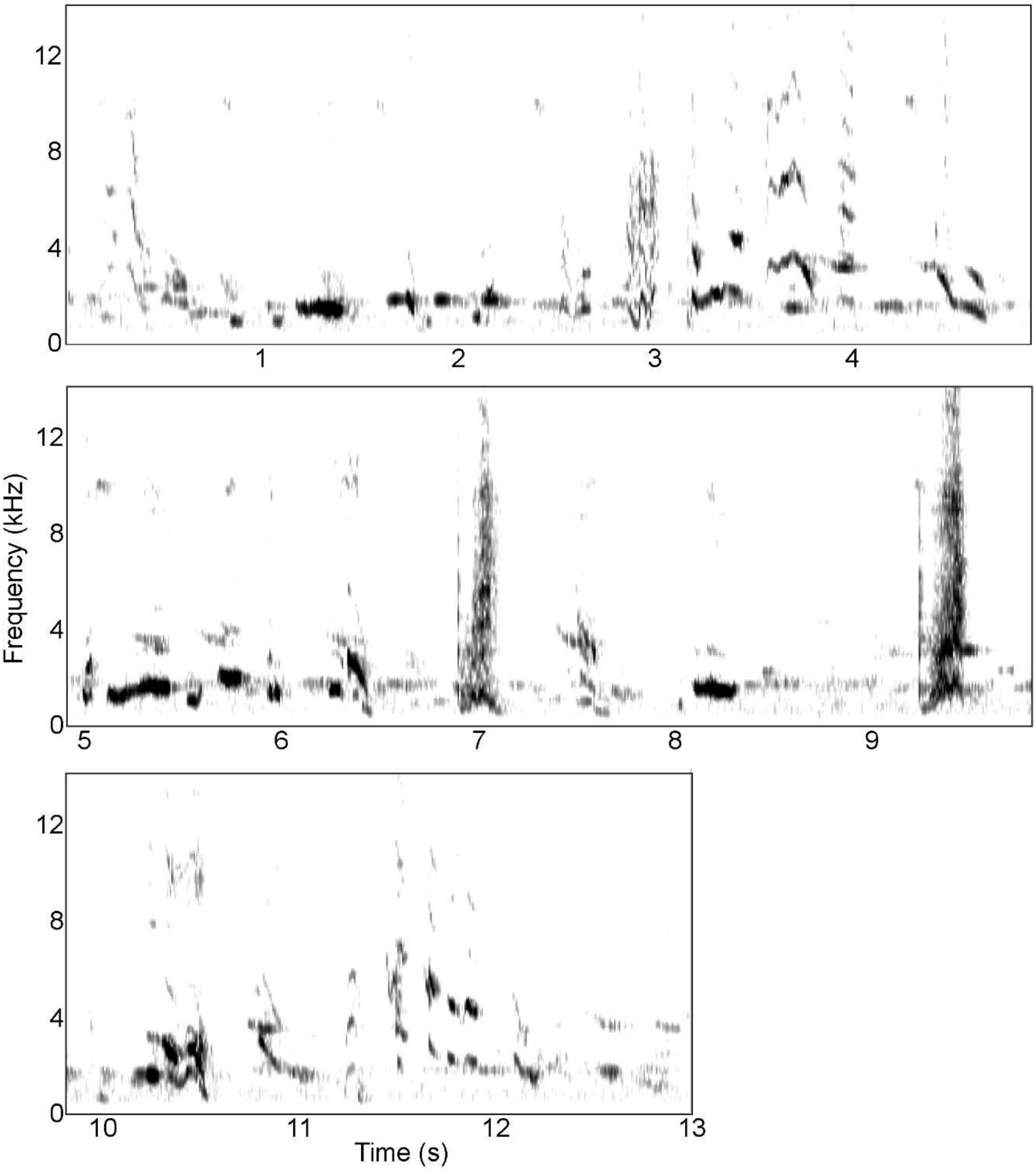
For the dynamic time warp (DTW) algorithm, the following settings were used as recommended by R. Lachlan (personal communication): compression factor 0.1; minimum element length 10; time SD weighting 1; non-time SD weighting 0; ArcTan transform weight for freq slope 0; syllable repetition weighting 0; maximum warp 100; cost for stitching syllables 0; cost for alignment error 0.2. The following options were selected: weight by relative amplitude; log transform frequencies; weight features with SDs, interpolate in TW; dynamic warping; syllable comparison method: both; alignment points: five points.

NONMETRIC MULITDIMENSIONAL SCALING (NMDS)

The number of dimensions chosen for NMDS was 2.

MULTIVARIATE RESPONSE PERMUTATION PROCEDURE (MRPP)

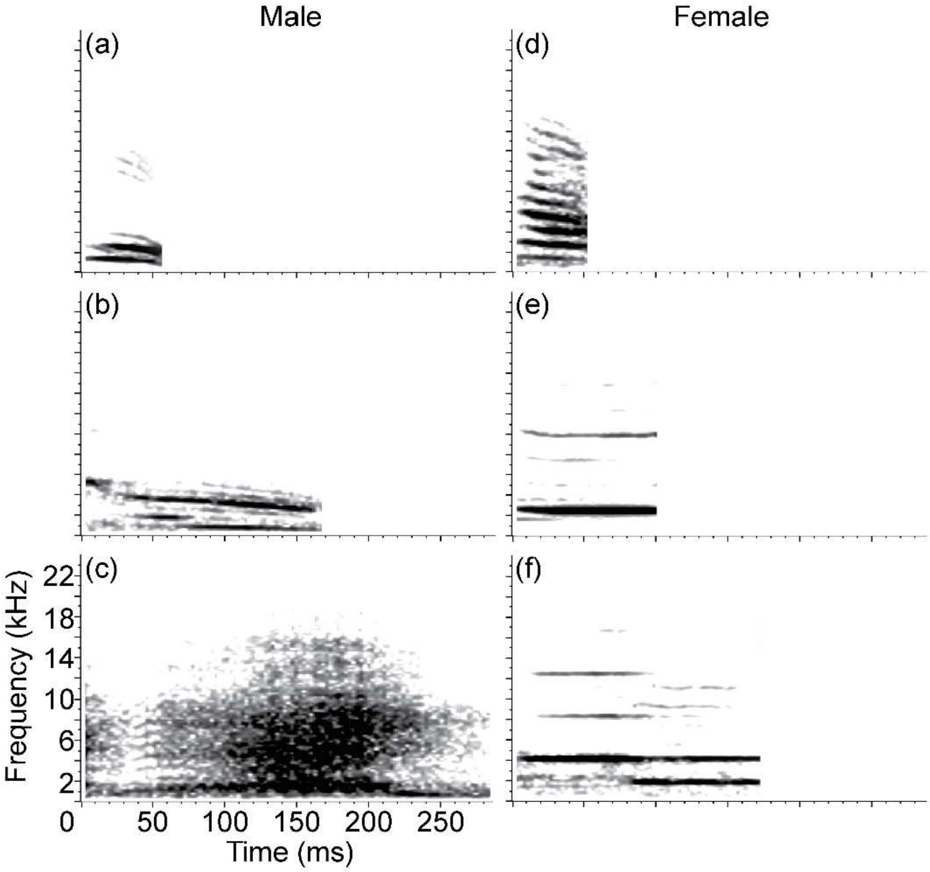
The number of resamples was 10 000. Levels compared were age group and sex. Weighting method: n. Option to calculate pairwise differences was selected. Methods used to calculate MRPP in Luscinia (Lachlan, 2007) were based on methods by Anderson (2006).



Suppl. 2.2. Example of a long sequence of juvenile male bellbird song (age 9 weeks post-hatching).

SUPPL. 2.3. SYLLABLE CONSISTENCY: SPECTROGRAPHIC CROSS-CORRELATION EXTENDED METHODS AND RESULTS

SPCC values were computed with Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.; band-pass filtered from 500 Hz to 22 000 Hz, DFT = 256, normalised and linear power). The outcome of a spectrographic cross-correlation (SPCC) is a matrix with the peak cross-correlation value of the pairwise comparison, which reflects the structural similarity (particularly frequency and duration) of the analysed syllables (Clark, Marler, & Beeman, 1987). These values reflect the similarity between two sounds, and range from 0, when there is no similarity, to 1, when the sounds are identical. With bellbird syllables having high variation in frequency and duration, particularly in juveniles, this made it an ideal analysis to compare age groups. Examples of the three most common syllables chosen from each sex for this analysis are presented in Suppl. 2.4. The table in Suppl. 2.6 is provided to show the mean ± SE for each individual's average consistency score within each age group and for each sex.



Suppl. 2.4. Examples of the three most common adult syllables chosen for the spectrographic cross-correlation analysis: male stutter (MST; a), male down sweep harmonic (DSH: b), male cough (c), female stutter (FST; d), female flat harmonic (F1; e) and female step down (SD; f).

Suppl. 2.5. Uncertainty values of optimal and non-optimal Bayesian cluster models used to help determine the number of groups of categorised syllables.

Sex	Age Group	Clusters (*N*)	0%	25%	50%	75%	100%	Selected
Male	Learning phase	4*	0.0000	0.0000	0.0000	0.0585	0.6547	Yes
		2	0.0000	0.0000	0.0000	0.0722	0.4930	No
		5	0.0004	0.0440	0.1178	0.2504	0.5659	No
	FBS	5*	0.0000	0.0066	0.0220	0.0814	0.4977	No
		8	0.0000	0.0024	0.0112	0.0454	0.5069	Yes
	Adult	7*	0.0000	0.0002	0.0087	0.0514	0.4807	Yes
		11	0.0000	0.0029	0.0226	0.0975	0.5880	No
		13	0.0000	0.0012	0.0132	0.0634	0.5254	No
Female	Learning phase	5*	0.0000	0.0005	0.0057	0.0528	0.5385	Yes
		11	0.0001	0.0095	0.0512	0.1605	0.5609	No
		3	0.0000	0.0015	0.0046	0.0395	0.4827	No
	FBS	9*	0.0000	0.0074	0.0195	0.0843	0.5235	Yes
		10	0.0000	0.0112	0.0460	0.1743	0.4927	No
		11	0.0000	0.0114	0.0382	0.1290	0.5053	No
	Adult	10*	0.0000	0.0046	0.1088	0.2844	0.6512	Yes
		8	0.0000	0.0025	0.0309	0.1334	0.5468	No

Note: An asterisk (*) indicates optimal cluster size. FBS = first breeding season.

Suppl. 2.6. Mean ± SE spectral peak cross-correlation values for each individual under the corresponding age group and syllable type.

Male				Female			
Syllable	Learning phase	FBS	Adult	Syllable	Learning phase	FBS	Adult
MST	0.46 ± 0.10	0.67 ± 0.02	0.83 ± NA	FST	0.40 ± 0.02	0.45 ± 0.04	0.41 ± 0.03
	0.37 ± 0.03	0.86 ± 0.02	0.87 ± 0.01		0.50 ± 0.03	0.78 ± 0.02	0.38 ± 0.02
	0.44 ± 0.04	0.74 ± 0.02			0.66 ± 0.01	0.44 ± 0.02	0.64 ± 0.02
	0.87 ± NA	0.72 ± 0.02			0.52 ± 0.11	0.53 ± 0.02	0.29 ± 0.06
	0.59 ± 0.09	0.68 ± 0.05				0.51 ± 0.01	0.65 ± 0.00
	0.74 ± 0.05	0.80 ± NA				0.35 ± 0.01	0.62 ± 0.01
	0.81 ± 0.02					0.61 ± 0.01	0.43 ± 0.02
	0.89 ± NA					0.59 ± 0.01	0.61 ± 0.03
	0.94 ± NA					0.71 ± 0.00	0.64 ± 0.02
	0.68 ± 0.02					0.81 ± 0.02	0.75 ± 0.01
	0.93 ± NA					0.73 ± 0.01	
	0.96 ± NA						
	0.90 ± NA						
	0.87 ± 0.03						
	0.52 ± 0.06						
	0.92 ± NA						
	0.72 ± 0.04						
	0.87 ± NA						
	0.96 ± NA						
	0.69 ± 0.04						
	0.80 ± 0.02						
DSH	0.16 ± NA	0.47 ± 0.10	0.77 ± NA	F1	0.61 ± 0.04	0.94 ± 0.02	0.76 ± 0.02
	0.23 ± 0.13	0.65 ± 0.03	0.80 ± 0.02		0.78 ± 0.01	0.85 ± 0.01	0.80 ± 0.01
	0.61 ± 0.02	0.81 ± 0.01	0.72 ± 0.01		0.82 ± NA	0.81 ± 0.00	0.85 ± 0.01
	0.78 ± NA	0.81 ± 0.00	0.73 ± 0.07		0.81 ± 0.01	0.78 ± 0.01	0.83 ± 0.01
		0.74 ± 0.02				0.88 ± 0.02	0.87 ± 0.03
		0.75 ± 0.01				0.82 ± 0.03	0.88 ± 0.01
							0.72 ± 0.05
							0.76 ± 0.10
Cough	0.33 ± 0.01	0.48 ± NA	0.69 ± 0.00	SD	0.24 ± 0.02	0.70 ± 0.05	0.19 ± 0.18
	0.23 ± 0.05	0.50 ± 0.02	0.56 ± 0.01		0.39 ± 0.06	0.81 ± 0.03	0.23 ± 0.23
	0.31 ± 0.04	0.54 ± 0.01	0.43 ± 0.01		0.65 ± 0.02	0.75 ± 0.05	0.70 ± 0.03
	0.44 ± NA	0.57 ± 0.01	0.58 ± 0.01		0.56 ± NA	0.69 ± 0.02	0.69 ± 0.05
	0.38 ± 0.01	0.51 ± 0.01				0.69 ± 0.03	0.28 ± 0.20

0.36 ± 0.01	0.56 ± 0.00	0.71 ± 0.03	0.75 ± 0.06
0.45 ± 0.01	0.59 ± NA	0.84 ± 0.04	0.71 ± 0.08
0.48 ± 0.02	0.50 ± 0.01	0.63 ± 0.06	0.76 ± 0.02
0.66 ± NA		0.74 ± NA	

FBS = first breeding season.

3 Sexual variation and changes in song repertoire over time

A male New Zealand bellbird singing (photo: Michelle Roper).

3.1 ABSTRACT

How song repertoires vary between species and change over time is well studied in male songbirds. However, with it now recognised that female song is more common and widespread than once assumed, it is timely that more research is carried out on how female song repertoires compare to male counterparts, especially in species where females have complex song. I determined the syllable repertoire size for each sex at the population and individual level in the New Zealand bellbird (*Anthornis melanura*) to give a detailed description of their syllable repertoire. I used both cross-sectional and longitudinal approaches to assess how the syllable repertoire changed over time from 2012 to 2015. For each sex at the population level, I calculated similarity coefficients for syllable types present between years and compared the relative abundance of syllable types present for each recording year. The same analyses were carried out for individuals who had more than two song selections per year. Overall, 96 syllable types were detected in the population over four recording years, of which 58% were unique to males, 32.3% unique to females and 9% were shared between the sexes. I identified 20 syllable family groups, with 13 shared by males and females, six unique to males, and one unique to females. The individual syllable repertoire size was 20.6 ± 2.7 ($N = 7$) for males and 11.0 ± 1.7 ($N = 6$) for females. However, there was individual variation, ranging from 15 to 32 syllables for males and six to 15 syllables for females. Two individual females sang syllable family types that were more commonly sang by males. At the population level, the number of syllable types added, deleted and shared between years was similar for both sexes. The similarity score for syllable repertoires between recordings years was within a similar range for both sexes (53.1–73.7%) but did not reduce with increasing time between years. The longitudinal comparisons between

individuals were less consistent, as their full repertoire may not have been captured each year, but the individuals from each sex with the most song recordings had comparable similarity indices to that of the population. Overall, the syllable repertoire size for females was smaller than males, but individual variation suggests there may be differences in individual learning abilities or social influences on what syllable types they sung. With the syllable repertoire changing over time at a similar rate for both sexes and a change in the relative abundance of syllable types over time, this suggests selection pressures may be acting on both sexes for an analogous function of their song, such as resource defence.

3.2 INTRODUCTION

Female birdsong is widely thought to be difficult to study (Catchpole, 1980). Particularly in the northern hemisphere, females are less conspicuous and those that sing tend to sing less often (Arcese et al., 1988; Baptista et al., 1993). This has given rise to research focused on male song and the idea that song repertoires are under direct selection by female choice and male-male competition (Catchpole, 1980). However, with more research showing that female song is in fact common (Garamszegi et al., 2007a; Odom et al., 2014; Riebel, 2003), there is a call for more research on female song (Odom & Benedict, 2018; Riebel, Hall, & Langmore, 2005). The prevalence of female song in species varies from no song, such as the zebra finch (Taeniopygia guttata; Zann, 1996), to species where females have comparable song repertoires to males, such as streak-backed orioles (*Icterus pustulatus*; Hall, MacDougall-Shackleton, Osorio-Beristain, & Murphy, 2010). Hence, additional research describing female song repertoires is needed to explore what selection pressures are acting on the evolution of female song.

Song repertoires are under selection pressure from both inter- and intra-sexual interactions within species (Catchpole, 1980). Female choice can select for male song repertoires that are larger, which can be a signal of territory quality (Catchpole, 1986; McGregor et al., 1981) and size (Buchanan & Catchpole, 1997; Yasukawa et al., 1980), stronger parasite immunity (Buchanan et al., 1999) and higher reproductive success (Catchpole, 1986; Eens et al., 1991; Hasselquist et al., 1996; Lambrechts & Dhondt, 1986; McGregor et al., 1981). Alternatively, females may base mate choice on specific repertoire elements rather than size alone, hence males will change their repertoire to produce songs that are more attractive to females (Eriksen et al., 2011). Males tend to display their full repertoire when in the presence of females, singing song types with immediate (e.g. AGDBCE) or eventual variety (e.g. AAAGGGCCC; Weary, Lemon, & Stephane, 1994). During male-male interactions, males tend to sing repetitions of the same song type, e.g. AAAAA (Weary et al., 1994), which tends to be a different song than used in the presence of a female (Byers, 1995, 1996a, 1996b) and may reflect a male's consistency in song production (Byers, 2007; Rivera-Gutierrez, Pinxten, & Eens, 2011). Repertoire size may also be under selection in intra-sexual interactions, as unoccupied territory where larger male song repertoires are experimentally played back will tend to be avoided the longest by neighbouring males (Krebs, Ashcroft, & Webber, 1978). Within songs, particular syllables (an acoustic unit) and their spectral features have been referred to as 'sexy syllables', as in male canaries (*Serinus canaria*), and the production of these syllables increases the number of copulation displays by females (Vallet, Beme, & Kreutzer, 1998; Vallet & Kreutzer, 1995). There is contrasting evidence for which phrase types (a repeated sequence of syllables) are used by male European starlings (*Sturnus vulgaris*) in interactions with females, but their song functions in both inter- and intra-sexual interactions (Eens, Pinxten, & Rudolf Frans, 1993). Hence, there has been a focus on determining what selection pressures are acting on male song repertoires. However, the question remains, what are the selection pressures acting on female song repertoires?

Less is known about the selection pressures acting on female song, but researchers suggest their song may have a role in both inter- and intra-sexual interactions (Riebel, 2003). Females sing different song types depending on the interaction. For example, female red-winged blackbirds (*Agelaius phoeniceus*) have two song types; one produced in the presence of males, particularly their mate, and the other in the presence of females (Beletsky, 1983; Beletsky, 1985). Female song is used differently in different social systems, for example, cooperative breeders such as superb fairy wrens (*Malurus cyaneus*) sing more towards stranger females (Cooney & Cockburn, 1995). On the other hand, non-cooperative breeders, such as New Zealand bellbirds (*Anthornis melanura)*, sing more towards neighbouring females (Brunton et al., 2008a). In species with more complex mating systems where females must compete for males, female song is used for mate attraction (Langmore & Davies, 1997; Langmore et al., 1996). Female song is also linked to reproductive success, for example, higher singing rates towards territorial intruders (Cain, Cockburn, & Langmore, 2015), spontaneous female song and song complexity

(Brunton et al., 2016; Appendix A) are positively correlated with the number of fledglings. These studies suggest that female song is under intra-sexual selection but whether their song is under direct or indirect inter-sexual selection is less clear.

How songbirds learn and change their song repertoire over time is similarly biased towards research on males. Song is learnt from tutors and this sensory phase of learning can either end after their full repertoire has developed (closed-ended learners; Marler & Peters, 1987; Wickler & Sonnenschein, 1989), or it can continue throughout their life (open-ended learners; Beecher & Brenowitz, 2005; Eens et al., 1992). Under laboratory conditions, male European starlings can increase their song repertoire size over years but they can also lose songs; although it appears that their ability to learn song may decrease with age (Eens et al., 1992). Male pied flycatchers (*Ficedula hypoleuca*) are also able to learn from playback, although they do not increase their repertoire size and are thought to choose songs that may be more attractive to females (Eriksen et al., 2011). Changes to an individual's song repertoire can, however, change in other ways for species with either of these two types of learning modes. For closed-ended learners, some bird species can start to sing songs that they learnt during their sensitive phase (Geberzahn et al., 2002) and even learnt to sing in their motor phase but haven't sung since their first year (Hough et al., 2000). Learning is also not the only way open- and closed-learners can add to their song repertoire. Juveniles can invent songs during song development, with male swamp sparrows (*Melospiza georgiana*) retaining up to half of these invented syllables into their adult repertoire (Marler & Peters, 1981) and male nightingales (*Luscinia megarhynchos*) can potentially continue to invent syllables up until at least three years old (Hughes, Hultsch, & Todt, 2002). Another method is to improvise syllables, which is a mixture of learning and invention where the bird creates a new syllable based on a tutor's syllable (Beecher & Brenowitz, 2005); although this is less common in swamp sparrow repertoires (Marler & Peters, 1981). Some syllables can also arise through incorrect copying of a tutors' song (Marler & Peters, 1981).

Fewer studies are available for us to understand how female song repertoire sizes are learnt and change over time. During development, the song repertoire of female blue-capped cordon-blues (*Uraeginthus cyanocephalus*) has higher levels of selective attrition (i.e. discarding syllables from their repertoire that were learnt prior to song crystallisation) than males; as while both sexes have a similar song repertoire size during development, females have a significantly smaller adult repertoire size than males (Lobato et al., 2015). During development, female slate-coloured boubous (*Laniarius funebris*) invent syllables, but this is not common and does not occur in males (Wickler & Sonnenschein, 1989). European starling females can change their song repertoire by adding new and deleting old phrase types as in males, but their repertoire size decreases with age (Pavlova, Pinxten, & Eens, 2010). However, some female European starlings increase their repertoire size with age, as in males (Eens et al., 1992; Pavlova et al., 2010). Female alpine accentors (*Prunella collaris*) increase their syllable repertoire size, particularly between their first and second year of age (Langmore et al., 1996). This research indicates that females can change their song repertoire over time, but little research has examined species with a much higher degree of sexual dimorphism in their song repertoires. This needs exploring to understand the selection pressures driving the evolution of female song in an array of species.

The song repertoire of the New Zealand bellbird (*Anthornis melanura*; hereafter bellbird) is unique compared to previously studied female song, as their song is highly sexually dimorphic (Brunton & Li, 2006). Females sing song types that share syllables, unlike the males who have song types consisting of unshared syllables. Brunton and Li (2006) further found that on average, females have a smaller repertoire size of 1.9 song types versus 5.4 for males, but this could be an underestimate due to the recording methods used (the range is from one to six song types for individual females). From 24 males and 12 females, the authors detected 36 syllable types: 17 'male' syllables, 12 'female' syllables and seven syllables shared by the sexes. Females tend to sing shorter and more variable song bouts than males, but despite both sexes having high year-round singing rates, females sing more than males in the breeding season (Brunton & Li, 2006). Both sexes develop their songs in a comparable timeframe (Roper, Harmer, & Brunton, 2018; Chapter 2; Appendix B) and possible functions of female song include territory defence, polygyny prevention and sexual selection (Brunton et al., 2008a; Brunton et al., 2016; Appendix A). In this study, I aimed to obtain the full syllable repertoire of bellbirds on Tiritiri Matangi Island at both the population and individual level to compare the syllable repertoire of each sex and determine whether they shared more syllable types at the family level (i.e. syllables with similar spectral characteristics) compared to the syllable type level. I predicted that I would find more syllables types than Brunton and Li (2006) due to the longer duration of my study, but that the relative abundance of female to male syllable types and proportion of shared syllables types should be the same. I recorded bellbird song across four years and took both cross-sectional (population level) and longitudinal (individual level) approaches to assess how the syllable repertoire of each sex changed over time and whether this occurred at a similar rate for both sexes.

3.3 METHODS

3.3.1 STUDY SITE AND DATA COLLECTION

I recorded the song of bellbirds for this study on Tiritiri Matangi Island (Tiri). Tiri is a low-lying 220 ha island in the Hauraki Gulf, 4 km off the coast of the Whangaparaoa Peninsula and 25 km north of Auckland, New Zealand. The small island size, high bellbird density (Roper, 2012) and pre-existing banded population made this an ideal site for targeting individual birds. I visited the island four days per week during the breeding season (August to January) and post-breeding season during autumn months, between September 2012 and January 2016. I recorded bellbirds while searching for individually banded birds and un-banded birds on known territories. I also sporadically recorded individuals during searching for breeding season territories. Post-breeding season, bellbirds formed loose flocks near food resources (e.g. kanuka trees, *Kunzea ericoides*, for honeydew, or the supplementary sugar water feeders; personal observation), where I targeted individuals for recording.

On a regular basis, I banded individual bellbirds as part of this study and a wider project on bellbird ecology. I captured the adults using mist nets on bellbird territories or at specially modified cages containing sugar-water feeders. The birds were banded with colour and metal bands. A full description of the banding protocols (measuring and blood taking) can be found in chapter 5. All capture, handling and banding protocols were conducted under permits from the New Zealand Department of Conservation (20666-FAU, 34833-FAU, 2008/33) and the Massey University Animal Ethics Committee (12/32, 15/21). I avoided capturing near nests when I knew a female was incubating. For females caught with an engorged brood patch, I banded and weighed the bird but bypassed other measurements to reduce handling time.

3.3.2 AUDIO RECORDING AND ACOUSTIC PROCESSING

I recorded bellbird song using a directional shotgun microphone (Sennheiser ME66, Sennheiser, Germany) and a portable solid state recorder (Marantz Professional PMD 661, Marantz Professional, Cumberland, RI, U.S.A.) with 24-bit sampling precision and 48 kHz sampling rate. Recordings were made of colour-banded individuals that were banded prior to and during the study and un-banded individuals. Recordings were made year-round (except winter months) over the course of the study. The male-female ratio in the population was approximately equal based on previous surveys (Roper, 2012) and no evidence of sex-specific mortality (Baillie, 2011). However, there was a male bias in detecting individuals because males were more conspicuous than females, as males tended to dominate the supplementary sugar-water feeders (Roper, 2012). Recording time was approximately 110 hrs and 2557 recordings (note that this is not an indicator of total field recording effort as it does not include time spent following individuals waiting for singing to occur).

Recordings were processed in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY) with standardised settings (a bandpass filter of 500 Hz to 22 000 Hz, size 256 samples, time grid overlap 50%, and normalised by amplifying to fill the waveform window). Songs or bouts of singing (hereafter 'song selection') were selected from each raw recording. I created Excel (Microsoft Corporation) databases to enter metadata for each raw recording and song selection. The metadata included filename, date, time of recording, track time, call quality (categories: excellent, very good, good, ok, bad), call type (e.g. song, alarm call), primary subject, background species, band ID, age, sex, nest, stimulus for sound, behaviours, specific locality, distance, and notes. The song selections with call quality of excellent, very good, good and some ok were then imported into the open-source software Luscinia (Lachlan, 2007).

I chose syllables as the acoustic unit for measuring repertoire size to compare between the sexes, as individuals do not sing stereotypical song types and have different styles of singing a range of highly variable song types (Brunton & Li, 2006). I defined syllables as consisting of one or more elements (i.e. note; a single sound trace on spectrogram) with less than a 15 ms interval between elements or the elements were consistently repeated together within a song type (Kershenbaum et al., 2016; Marler & Isaac, 1961). See Figure 3.1 for examples of male and female bellbird syllable types. Elements and syllables were selected from spectrograms

(FFT algorithm) of song samples using Luscinia (Lachlan, 2007). I used the following settings for viewing spectrograms in Luscinia, as recommended by R. Lachlan (personal communication): max. frequency 12 000 Hz; frame length 10.667 ms; spectrograph points 470; spect. overlap 90.63%; deverberation was set to 100% to reduce echo; dynamic range was altered between 30 and 60 to obtain the best estimation of fundamental frequency when selecting elements; high pass threshold 300 Hz. The syllables selected in Luscinia were then imported into the new open-source database program Koe (Fukuzawa et al. *In prep*; www.koe.io.ac.nz) where syllables were systematically labelled into categories. Syllables were categorised based on a range of features including shape of components (elements), fundamental frequency, frequency modulation, harmonics and duration. I then used additional ordering information within the song types (i.e. syntax) to ensure consistent labelling of the syllables and agreement was made with an additional experienced observer. To verify that my labelling was consistent, machine learning algorithms (supervised and unsupervised) were used to assess how well the syllable labels clustered using the algorithm t-SNE (t-distributed Stochastic Neighbour Embedding; van der Maaten & Hinton, 2008) and I determined the accuracy rate using various machine algorithms (see Suppl. 3.1 for additional methods). The syllable labels showed a high degree of clustering (Suppl. 3.2) and syllables were labelled with 96.6 ± 1.0% accuracy (Suppl. 3.3). Syllables were then grouped into broader 'syllable family' groups where syllables with similar spectral characteristics were given a family label (e.g. pure tone syllables were in the family 'pipe'; see Figure 3.1 for examples of syllable family types).

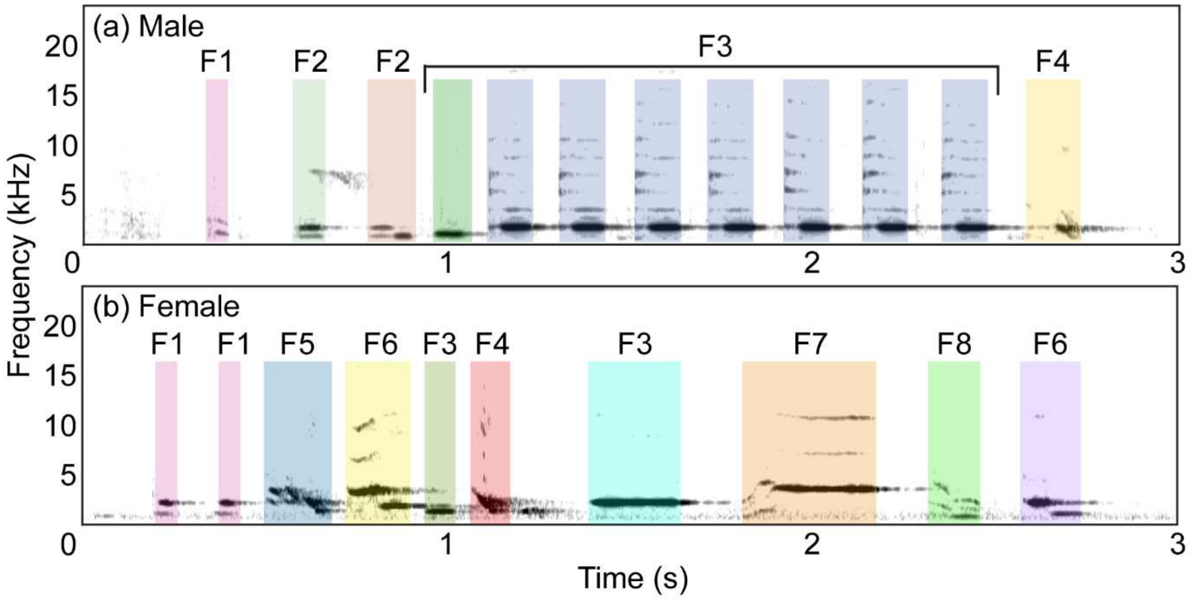


Figure 3.1. Examples of bellbird syllable types (different syllable types are represented by a different coloured box) for (a) male and (b) female bellbirds with syllable family types labelled with the following codes: F1 = stutter, F2 = waah, F3 = pipe, F4 = chump, F5 = down transition, F6 = step-down, F7 = flat-squeak, F8 = down-squeak.

3.3.3 POPULATION SYLLABLE REPERTOIRE

With the Koe database, I summarised the number of syllable and syllable family types for the entire study period and between years. A year of recording consisted of both the breeding season months and post-breeding season months, and the four years of recording were numbered consecutively (Year 1 = October 2012 to May 2013, Year 2 = September 2013 to April 2014, Year 3 = September 2014 to March 2015, and Year 4 = September 2015 to January 2016). I plotted cumulative curves of syllable repertoire size for each sex over all years and each year with package ggplot2 (Wickham, 2016) in the open source statistical software R Studio (R Core

Team, 2015). This was to determine whether the entire population syllable repertoire was captured, determined by whether the cumulative curve reached an asymptote. For syllables, I calculated the total number of types in the population, number of types sung by each sex and how many types were shared by the sexes, across all years of recording and separately for each year.

3.3.4 VARIATION IN POPULATION SYLLABLE REPERTOIRE OVER TIME

To determine how the population repertoire changed over time, I compared the syllable types present each year using Jaccard's similarity coefficient (MacDougall-Shackleton, Stewart, Potvin, & Tennenhouse, 2009; Podos et al., 1992; Tracy & Baker, 1999), their presence and absence between years, and relative abundance in the population. To measure the similarity of syllable types across years separately for males and female, I calculated Jaccard's coefficient (S_j) following Tracy and Baker (1999) as:

$$Sj = s / (x + y + s)$$

where s = how many syllables are shared by year X and year Y, x = the number of syllables present in year X but not in year Y, and y = the number of syllables present in year Y but not in year X. The yearly totals of syllable additions, syllable deletions and shared syllables was calculated to assess whether any differences in similarity were due to additions or deletions or a combination. Since some syllable types may have been undetected in the repertoire due to rarity (and hence were counted as deletions), I calculated the relative abundance of each syllable type. For each syllable type, the total number of individuals singing that type was tallied and I calculated the proportion of individuals singing each type for each year. I used four categories of abundance based on the percentage of individuals singing each syllable type: rare <15%, uncommon 15–45%, common 46–75%, and abundant >76%. To determine if any syllable changes were occurring at small scale (i.e. within syllable family type) or large/novel scale (i.e. new syllable family additions or old family deletions), I totalled the number of syllable types within each syllable family across each year.

3.3.5 INDIVIDUAL SYLLABLE REPERTOIRE AND VARIATION OVER TIME

A cumulative curve of syllable repertoire size for individuals of each sex was plotted with package ggplot2 (Wickham, 2016) in the open source statistical software R Studio (R Core Team, 2015). Individuals having at least five song selections for their repertoire curve to reach an asymptote were selected for calculating syllable repertoire size. I calculated the syllable repertoire size range and mean ± standard error (SE) for these individuals of each sex. I tallied the number of syllable types within each syllable family for individuals to compare the level of syllable diversity between individuals of each sex. I calculated the relative abundance of syllables for the individuals with complete repertoire size, using the same method as for the population level, to confirm the results found for syllable abundance when using all birds recorded in the population. To compare individual repertoire sizes between years, I selected individuals that had more than two song selections per year. As for the population, I calculated Jaccard’s similarity coefficient for the syllable types present between years and tallied the number of syllable additions and deletions.

3.4 RESULTS

3.4.1 POPULATION REPERTOIRE

A cumulative plot of the number of new syllables versus number of song selections approached asymptote, showing the majority of the population repertoire was captured (Suppl. 3.4). In total across the four years of the study, I identified 96 syllable types (Table 3.1). From this, 58.3% of syllables were unique to males, 32.3% were unique to females and the sexes shared 9.4% of syllable types (Table 3.1). The male population syllable repertoire was hence almost twice as large in size (80.5% larger) than the female population syllable repertoire. The syllable types were categorised into 20 syllable family types (Table 3.2). There were six families unique to males, one family unique to females, and 13 shared between the sexes.

Table 3.1. Number of syllable types across sexes and recording years (Year 1 = 2012–2013, Year 2 = 2013–2014, Year 3 = 2014–2015, Year 4 = 2015–2016).

	All years	Year 1*	Year 2	Year 3	Year 4
Total	96	58	71	74	71
Male	65	42	48	50	49
(number of individuals)	(110)	(32)	(26)	(31)	(21)
Female	40	19	30	28	28
(number of individuals)	(62)	(9)	(17)	(19)	(17)
Shared	9	3	7	4	6

*Note that for females, the population repertoire did not asymptote in this year.

Table 3.2. Syllable families present in the repertoire of each sex for each recording year.

Family	Male				Female			
	Year 1	Year 2	Year 3	Year 4	Year 1*	Year 2	Year 3	Year 4
Alarmy	2	1	1	1				1
Chortle	2	2	2	2	▨	▨	▨	▨
Chump	1	1	1	1	1	1	1	1
Click	1	1	1	1		1	1	1
Cough	1	1	1	1	▨	▨	▨	▨
Down-squeak	1	1	1	1	1	2	1	1
Down-squeak pipe	1	2	2	2	▨	▨	▨	▨
Down transition	▨	▨	▨	▨	4	4	4	4
Flat-squeak	1	1	3	1	1	1	1	1
Peak-squeak	1	2	2	2	1	1	1	2
Pipe	11	12	9	11	4	8	9	6
Pipe down-squeak	2	2	3	4	1	1	1	1
Step-down	2	2	2	2	3	3	4	4
Step-up	1	1	2	1	▨	▨	▨	▨
Stutter	2	2	2	2	3	4	4	6
Stutter up-squeak	1	1	1	0		2		
Trill	2	4	4	3	▨	▨	▨	▨
Up-squeak	1	2	1	1		1		
Waah	8	9	11	12		1	1	
Warble	1	1	1	1	▨	▨	▨	▨

*Note that the female population did not reach an asymptote in this year.

3.4.2 VARIATION IN POPULATION SYLLABLE REPERTOIRE OVER TIME

For each year, the cumulative plot showed the syllable repertoire reached an asymptote for each year except for females in year 1 (Suppl. 3.5). The similarity coefficient (S_j) for syllable types present between years fell within a narrow range from 52.6 to 73.7% (Table 3.3). If the syllable repertoire changed due to deletions and additions over time, I expected that the further the years were apart, the less similar the syllable repertoire would be. However, I did not find a consistent trend. The average similarity between years with 1-year difference was 69.4% and 61.2%, 2 years difference 62.9% and 60.3%, and 3 years difference 62.5% and 62.1%, for males and females, respectively. This suggests that syllable types may change in their relative abundance (i.e. become rare) between years rather than being permanently deleted from the repertoire. Between most years (except for Year 1), the number of syllable types added and deleted were very similar (Table 3.4). The changes in syllable types between years were always within the existing family types (Table 2), except for females; although these new family types for females were existing male syllable family types rather than novel family types. For both males and females, the proportion of syllable types that were commonly or abundantly sang by individuals in the population was 10% or lower (Figure 3.2). Between 60% and 80% of syllable types were rare and sung by a few individuals (Figure 3.2). This suggests there could be significant variation between the repertoire of individuals or the presence of microgeographic song variation across the island.

Table 3.3. Syllable similarity (Jaccard's similarity coefficient; proportion) between years.

		Female			
		Year 1*	Year 2	Year 3	Year 4
Male	Year 1*		53.1	67.9	62.1
	Year 2	62.5		65.7	52.6
	Year 3	58.6	71.9		64.7
	Year 4	62.5	67.2	73.7	

*Note that in year 1 (2012–2013), fewer recordings were collected and although for males the repertoire did asymptote, for females the repertoire did not.

Table 3.4. Syllable additions and deletions, and number of syllables shared between years.

Sex	Years	Added	Deleted	Shared
Male	Years 1–2*	13	7	35
	Years 2–3	9	7	41
	Years 3–4	7	8	42
	Years 1–3*	16	8	34
	Years 2–4	10	9	39
	Years 1–4*	14	7	35
Female	Years 1–2*	13	2	17
	Years 2–3	5	7	23
	Years 3–4	6	6	22
	Years 1–3*	9	0	19
	Years 2–4	8	10	20
	Years 1–4*	9	1	18

*Note that in year 1 (2012–2013), fewer recordings were collected and although for males the repertoire did asymptote, for females the repertoire did not.

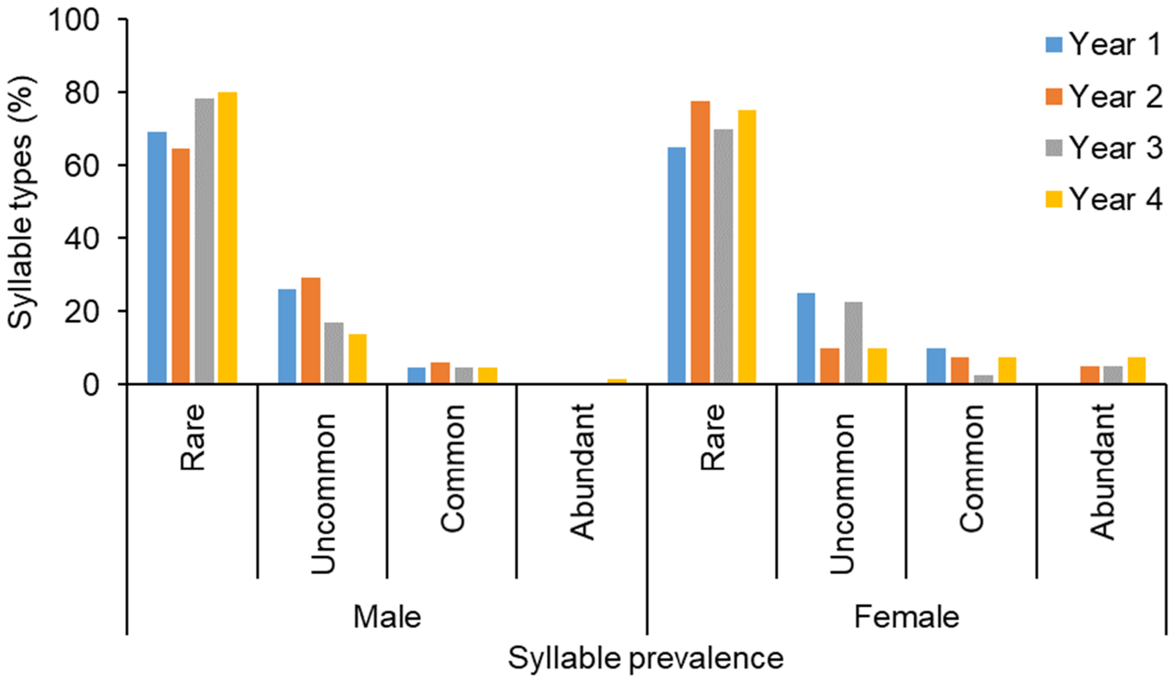


Figure 3.2. Syllable prevalence based on number of individuals singing each syllable type (rare <15%, uncommon 15–45%, common 46–75%, abundant >76%) for all individuals recorded and each recording year (Year 1 = 2012–2013, Year 2 = 2013–2014, Year 3 = 2014–2015, Year 4 = 2015–2016). See Table 3.1 for the number of individuals within each year.

3.4.3 INDIVIDUAL SYLLABLE REPERTOIRE AND VARIATION OVER TIME

Seven male and six female syllable repertoires reached an asymptote (Figure 3.3). The average male syllable repertoire was 20.6 ± 2.7 and ranged from 15 to 32 syllable types (Suppl. 3.6). The female syllable repertoire size was almost half the size of males at 11.0 ± 1.7 and ranged from six to 15 syllable types (Suppl. 3.6). Hence, there was variation in the syllable repertoire size of individuals and slight overlap in the size of male and female syllable repertoires. There was variation in the number of syllable family types that individuals sang (Suppl. 3.6). Some syllable

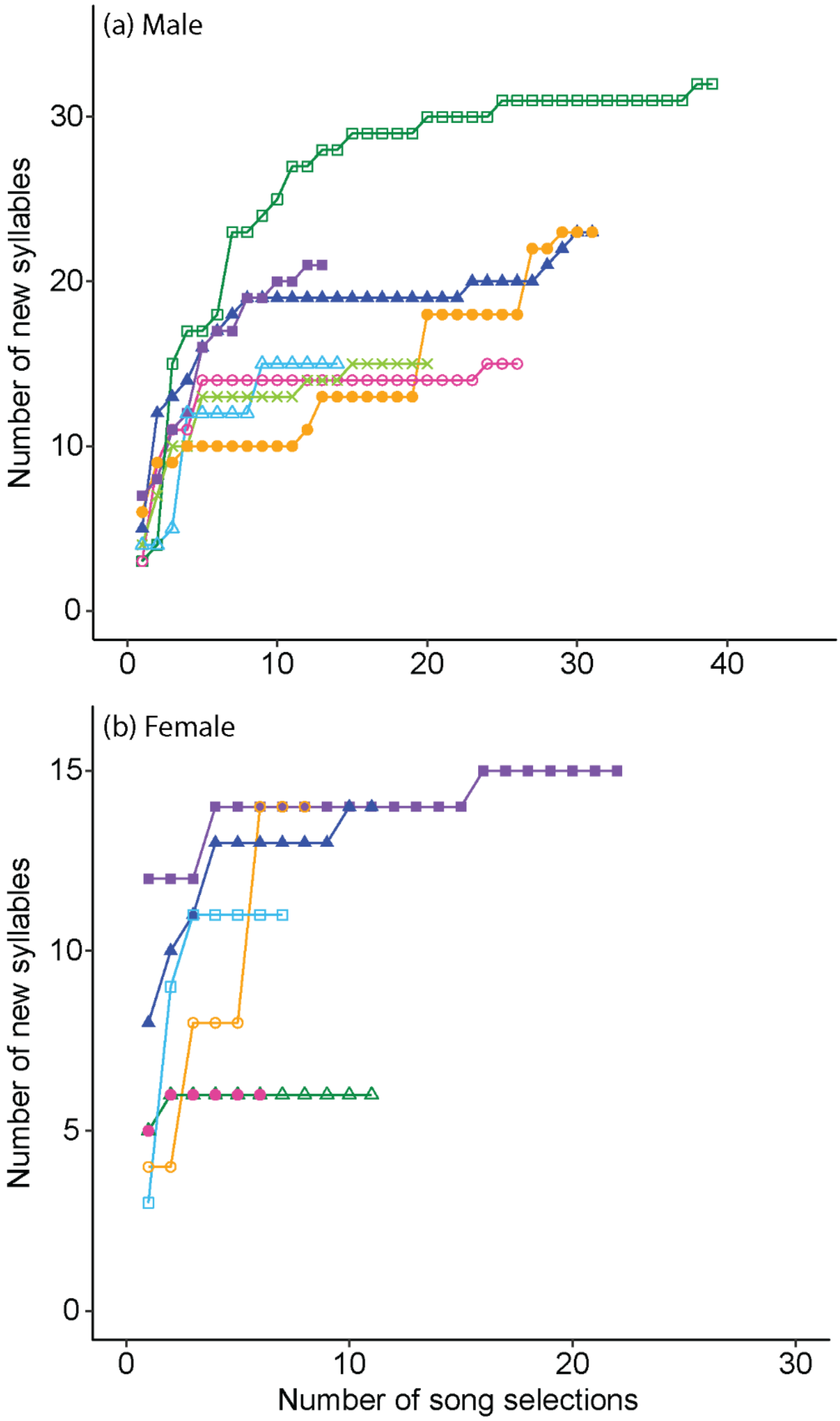


Figure 3.3. Cumulative plot of number of new syllables versus number of song selections for individual (a) male and (b) female bellbirds (corresponding to the individuals in Suppl. 3.6) to estimate their total syllable repertoire size.

family types, however, were only sung by one individual, for example, only one male sang a syllable type in the family 'stutter up-squeak' and one female that sang a syllable type in the family 'waah' (which is more commonly sang by males). As for all individuals at the population level, syllable type prevalence among individuals with complete repertoires showed similar trends with most syllables types being sung by few individuals (rare and uncommon), and only a few syllable types were sung by many individuals (common and abundant; Figure 3.4).

I was able to compare three males and one female across years to examine changes in syllable repertoire over time (Table 3.5; see Suppl. 3.7 for the number of song selections). The female had the highest syllable repertoire similarity between years, with only two syllables not present in the second year of recording her song (Table 3.5). Male syllable repertoire similarity between years varied from 23.1 to 68.8% and there tended to be more syllable deletions than additions (Table 3.5). The variation in similarity and higher number of syllable deletions than additions is possibly due to rare syllable types going undetected in years with fewer recordings (Suppl. 3.7), hence some years I may not have detected the full syllable repertoire. For the male (1) and female (1) with the most song selections, and hence I more likely had captured most of their syllable repertoires, their syllable similarity between two years was moderately high (68.8% and 86.6%, respectively). This is similar to the population data, suggesting that the change in population syllable repertoire over time is in part due to small changes in individual repertoires between years (versus juvenile recruitment of novel syllables or immigrating individuals introducing new syllables not present in this population).

Table 3.5. Syllable types added, deleted, shared and similarity (Jaccard's similarity coefficient) between years for three individual males and one individual female.

Sex	Individual	Years*	Added	Deleted	Shared	Total	Similarity (%)
Male	1	Years 3–4	2	8	22	32	68.8
	3	Years 3–4	5	5	3	13	23.1
		Years 1–3	0	11	8	19	42.1
		Years 1–4	3	14	5	22	22.7
	8	Years 1–2	7	7	10	24	41.7
Female	1	Years 3–4	0	2	13	15	86.7

*See Suppl. 3.6 for the number of song selections for each individual per year.

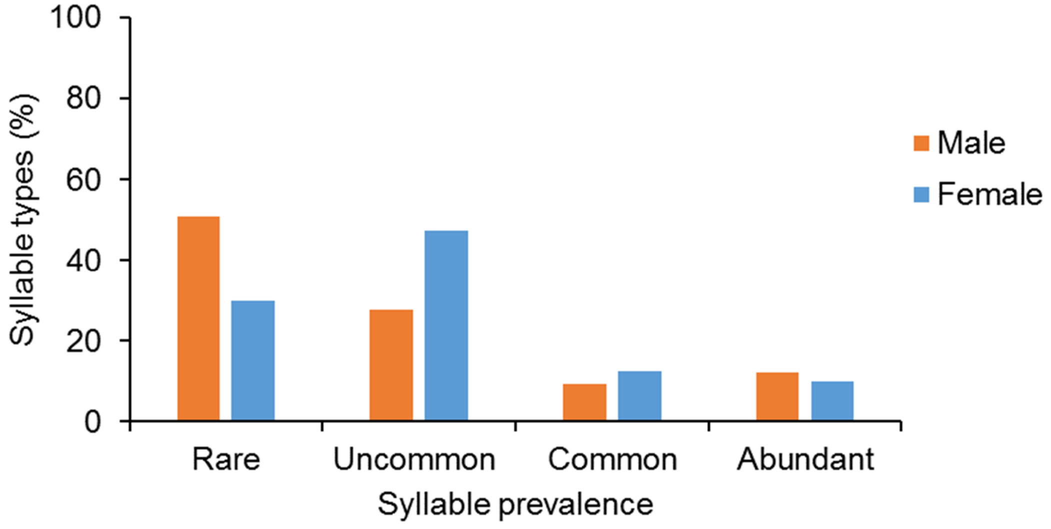


Figure 3.4. Syllable prevalence based on number of individuals singing each syllable type (rare <15%, uncommon 15–45%, common 46–75%, abundant >76%) for the individuals where the full repertoire was obtained (corresponding to the individuals in Suppl. 3.6).

3.5 DISCUSSION

Male bellbirds had a larger syllable repertoire than females at both the population and individual level. The population and individual syllable repertoire was on average almost twice the size in males than in females. However, there was considerable individual variation with syllable repertoire size ranging from 15 to 32 in males and ranging from six to 15 in females. However, individual differences in repertoire size arise due to, for example, differences in nutritional stress during early development (Nowicki et al., 1998), learning abilities (Nowicki et al., 2002), density of the local population (Doutrelant, Blondel, Perret, & Lambrechts, 2000), and health (Buchanan et al., 1999) and dominance of the individual (Voigt, Leitner, & Gahr, 2007). I found the sexes shared 9.4% of syllable types, approximately half the amount of shared syllables found by Brunton and Li (2006). Over half of the syllable family types were shared between the sexes, but there were more syllable families unique to males than females with only one unique syllable family. The number of syllables added, deleted and shared between years was similar for both sexes (except for year 1, 2012–2013, where the female syllable repertoire was not fully captured). The similarity of repertoires between years did not reduce with increasing time, suggesting that syllables may vary in relative abundance between years rather than being completely lost; this was supported by my finding that syllable types vary in their prevalence within the population for both sexes. The longitudinal comparisons between individuals were less consistent (due to not being able to acquire individuals' full repertoire for each year), but the individuals from each sex with the most song selections had comparable similarity coefficients to that of the population.

Few studies so far have identified significant sexual dimorphism in song repertoires. The two song types that female red-winged blackbirds sing are different in structure compared to male song (Beletsky, 1983; Catchpole & Slater, 2008), but there is no detail on what syllables they may share. Some species have similar syllable structure between the sexes but have differences in the overall spectral parameters of their song (Hahn et al., 2013; Yamaguchi, 1998). For example, Northern cardinal (*Cardinalis cardinalis*) female song has been described as a neotenic version of male song, but it also differs from males in the amplitude of harmonics and syllable stereotypy (Yamaguchi, 1998). A novel finding of my study is that male and female bellbirds share very few syllable types. The sex-based syllables also differ in spectral parameters, such as fundamental frequency, as found in previous research on bellbird song (Roper et al., 2018; Chapter 2; Appendix B). The fact that the bellbird sexes share so few syllable types suggests that song functions mostly in intra-specific interactions in bellbirds. This is supported as both males and females respond significantly less to songs of the opposite sex in natural conditions (Brunton et al., 2008a). As the sexual dimorphism in song is so striking, it is unlikely to be solely for sex recognition. Only small changes in the frequency of the 'fee' syllable song of black-capped chickadees (*Poecile atricapillus*) appears to be both a signal of sex and individual identity (Hahn et al., 2013). Bellbirds are highly territorial (Craig & Douglas, 1986) and females tend to be excluded from food resources more often than males (Roper, 2012). Female bellbirds also sing more in response to neighbouring females (Brunton et al., 2008a). With no duetting between the sexes of this species (personal observation) and females being subordinate to males, at least in the non-breeding season (Roper, 2012), this could suggest that there may be costs or benefits to the amount of song sharing between the sexes and further research is needed to address this.

While the bellbird sexes share so few syllables types, they still share common spectral features at the syllable family level. Sharing such features could be due to the limits posed by their vocal organ, the syrinx (Suthers & Zollinger, 2006; Chapter 4), or for species recognition (Catchpole & Slater, 2008), as their close relative and competitor, the tui (*Prosthemadera novaeseelandiae*), also sings complex song (Hill, 2011; Hill et al., 2017). Deducing from trends in current literature (Catchpole & Slater, 2008), males are more likely under both inter- and intra-sexual selection, and perhaps male bellbirds have more unique syllable and family types than females due to their more diverse functions, such as the 'sexy syllables' found in male canaries (Vallet et al., 1998; Vallet & Kreutzer, 1995). Whereas, if female song is only under social selection (i.e. intra-sexual competition for male parental care and resources, such as food), there may be less pressure to develop a larger repertoire size and unique female syllable types. I also found that there was a greater difference in the syllable repertoire size at the individual level than the population level. This may be explained by the individual variation in syllable family types sung by females. For example, I only found one female singing a syllable type from the 'waah' family and one female singing a syllable from the 'pipe-down-squeak' family, suggesting that there are individual females that sing more 'male-like' syllable family types. European starling females also have considerable levels of individual variation in repertoire size, with some individuals also singing particular phrase type families that in general are sung by all males (Pavlova et al., 2005). Pavlova *et al.* (2005)

suggested these phrase types may be sung in different social conditions or at different population densities, as an earlier study did not find any females singing these phrase types (Hausberger, Henry, & Richard, 1995; Hausberger, Richard-Yris, Henry, Lepage, & Schmidt, 1995). Hence, the different selection pressures acting on song repertoires need further research to tease apart the functions of distinctive male and female repertoires.

Songbirds can change their song repertoires from year to year (Catchpole & Slater, 2008). At the individual level, I did not have the full repertoire per individual across multiple years, so I could not address the question of how individual syllable repertoires changed between years. However, for all individuals with sufficient recordings, there were small changes in the syllable types sung between years, regardless of sex. At the population level (cross-sectional analysis), I had the full syllable repertoire for each year (except for females in year 1, 2012–2013) and the difference found between each year was within a similar range. However, this did not depend on whether the comparisons were one year or three years apart. This suggests that bellbirds may be changing the relative abundance at which they sing certain syllables between years (e.g. a syllable type was rarely sung in one year but common in another). This was supported by my finding that less than 10% of syllables were either commonly or abundantly sung by individuals and most syllable types were only sung by a few individuals. This trend was also supported at the individual level with few syllables being commonly/abundantly sung by most individuals. This pattern is similar to one found in Darwin's medium ground finches (*Geospiza fortis*) where males appear to prefer singing rare syllables, hence syllables may change in abundance over the years and become rare rather than being completely deleted from the population syllable repertoire (Gibbs, 1990). Males singing rare syllable types may improve their reproductive success (Gibbs, 1990; Lemon, Weary, & Norris, 1992). Hence for the syllables that were considered as either added or deleted between years, some at least might not have been detected each year due to being sung by so few individuals. Why there were more syllable types sung by few individuals could also be explained by different syllable types being sung in different regions of the island. This microgeographic variation may arise through individuals tending to share more syllable or song types with territory neighbours than individuals on distant territories (Barišić, Ćiković, Tutiš, Kralj, & Hoi, 2018; Briefer, Aubin, Lehongre, & Rybak, 2008).

While cross-sectional studies are less informative than longitudinal studies for assessing changes in repertoire over time (Gil et al., 2001), a similar change in repertoire size was found for males and females. Both sexes also had fewer commonly sung syllables types and more rare types. Changes in syllable repertoire over time could hence be a signal in both sexes for shared functions, such as resource defence (Brunton et al., 2008a; Brunton et al., 2008b; Craig & Douglas, 1984). Therefore, the different selection pressures acting on male and female bellbird song may change the sexes syllable repertoire over time in a similar way but affect the size of their syllable repertoire differently, as males tend to acquire larger syllable repertoires than females.

3.5.1 CONCLUSIONS AND FUTURE DIRECTIONS

Overall, female bellbirds had a smaller repertoire size than males, however, they shared very few syllables with males and there was considerable individual variation in syllable repertoire size. This suggests female song repertoires may also be affected by individual differences in learning abilities or act as a signal of female quality. These individual differences may reflect competitive ability for female bellbirds, for example, during intra-specific interactions with neighbouring females (Brunton et al., 2008a). When I grouped syllables into families, I then observed more overlap between the sexes, but males still had more unique syllable families than females. Such differences between the sexes may suggest different selection pressures acting on male and female song repertoire size. With some females tending to sing more 'male-like' syllable family groups, perhaps there are costs or benefits for individuals to sing syllables more commonly sung by the other sex depending on, for example, their social rank in their dominance hierarchy. For the first time, to my knowledge, I have shown that the syllables sung by the bellbird sexes changed at a similar rate over time, suggesting that similar selection pressures are acting on the rate of repertoire change for a shared function, such as resource defence. Whereas, the changes in relative abundance of syllable types over the four years indicates that there may be different selection pressures acting on different syllables types, such as 'sexy syllables' used in mate attraction. However, with only a few syllables types common throughout the population for both sexes, this may also be a potential indicator of microgeographic variation; hence, further analyses are needed to explore such patterns. I also recommend future playback experiments that artificially alter the syllable types present in a song to test the function of syllable types by presenting them to each sex at different life history stages. This will help determine to what degree inter- and intra-sexual selection pressures are acting on the evolution of bellbird song.

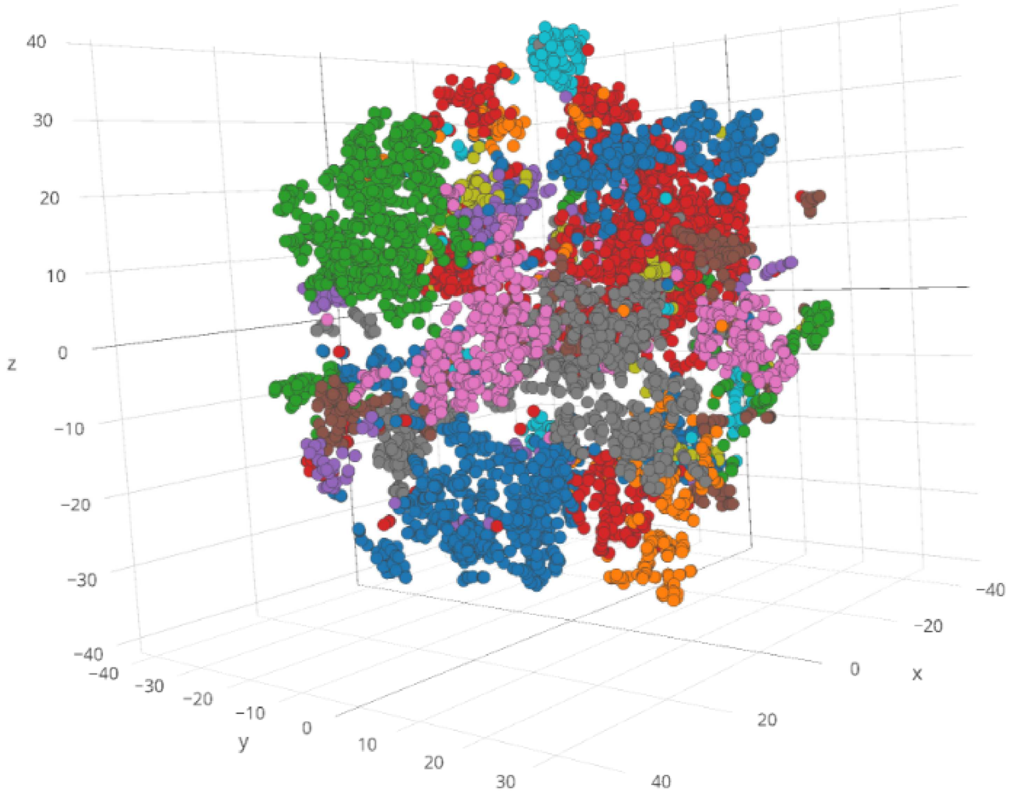
3.6 AUTHOR CONTRIBUTIONS

Michelle M. Roper contributed to the design of the study, developed the methodology, conducted the fieldwork, managed field assistants, contributed to syllable labelling, performed analyses and wrote the manuscript. Wesley H. Webb imported song selections into the software Luscinia and Koe, and labelled syllables. Christine Evans contributed to syllable labelling. Yukio Fukuzawa developed the new software Koe, imported syllable selections into Koe, performed machine learning algorithms for verifying syllable labels and contributed to analyses. Aaron M. T. Harmer contributed to methodology and assisted with writing the manuscript. Dianne H. Brunton designed the study, developed methodology, assisted with fieldwork, assisted with analyses and contributed to the writing of the manuscript.

3.7 SUPPLEMENTARY MATERIAL

SUPPL. 3.1. ADDITIONAL METHODS

To verify that my syllable labelling was consistent, two investigations were performed using machine learning. The database of syllables first had to be transformed into their feature representation using 25 different acoustic and spectral features. The results have different lengths, which correspond to the original durations of the syllables, e.g. the MFCC (Mel-frequency cepstral coefficient) representation of a syllable that is 500ms long is a vector twice as long as that of a 250ms long syllable. The results were aggregated by extracting their means, standard deviations, medians and their dynamic time warp (DTW) distances to several template syllables. Details of the feature extraction can be found in Fukuzawa et al. (*In prep*). After this step, each syllable was represented by a 735-dimensional vector and the t-distributed Stochastic Neighbour Embedding (t-SNE) algorithm was used to assess how well the syllable labels clustered. Then recognition accuracy was assessed using various machine learning algorithms. Supervised machine learning was used to make the computer “learn” how to associate feature values with the actual labels. The trained model could then be used to recognise new instances that the model had never seen before. The recognition accuracy therefore depends on having an appropriate feature representation of the syllables and the correctness of the given labels. High accuracy could only be achieved if both conditions were satisfied. Thus, several different machine learning algorithms (including Gaussian Naïve Bayes, Random Forest classifier, Support Vector Machine, LDA and PCA classifiers) were trained using k-fold validation and their accuracies recorded.

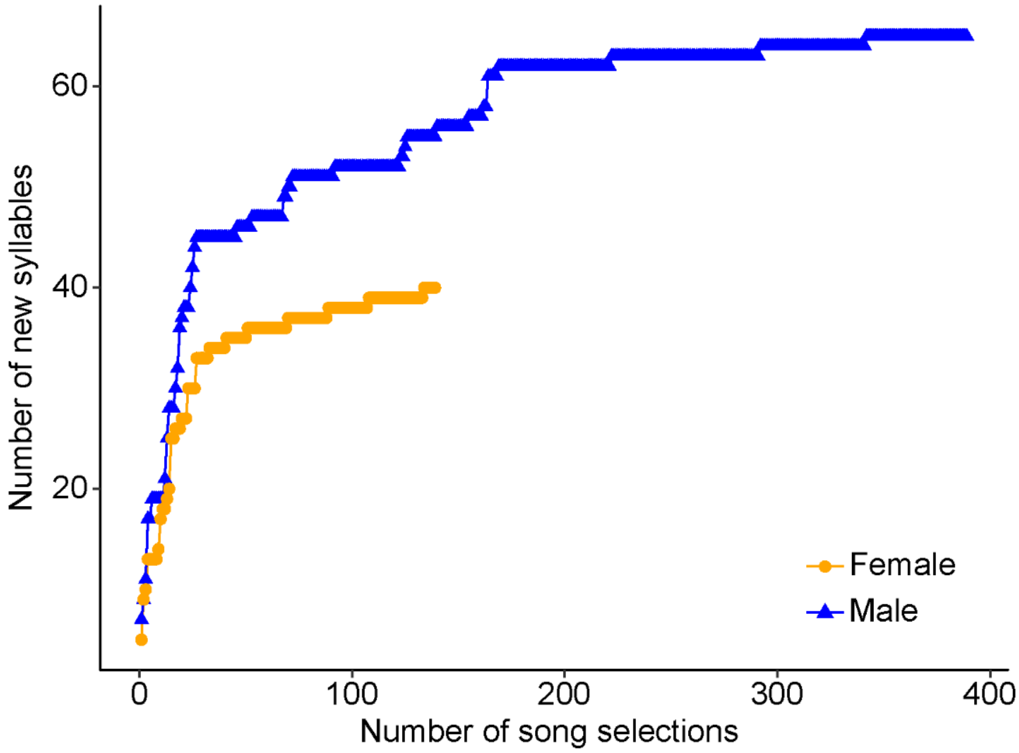


Suppl. 3.2. 3D plot of unsupervised clustering of 7003 syllables using t-SNE (t-distributed Stochastic Neighbour Embedding). Each colour represents the different given syllable labels (although due to there being many label names, the colours are repeated for different labels). Similar syllables cluster together and the tight clusters of similar colours confirms the labelling of these syllables types.

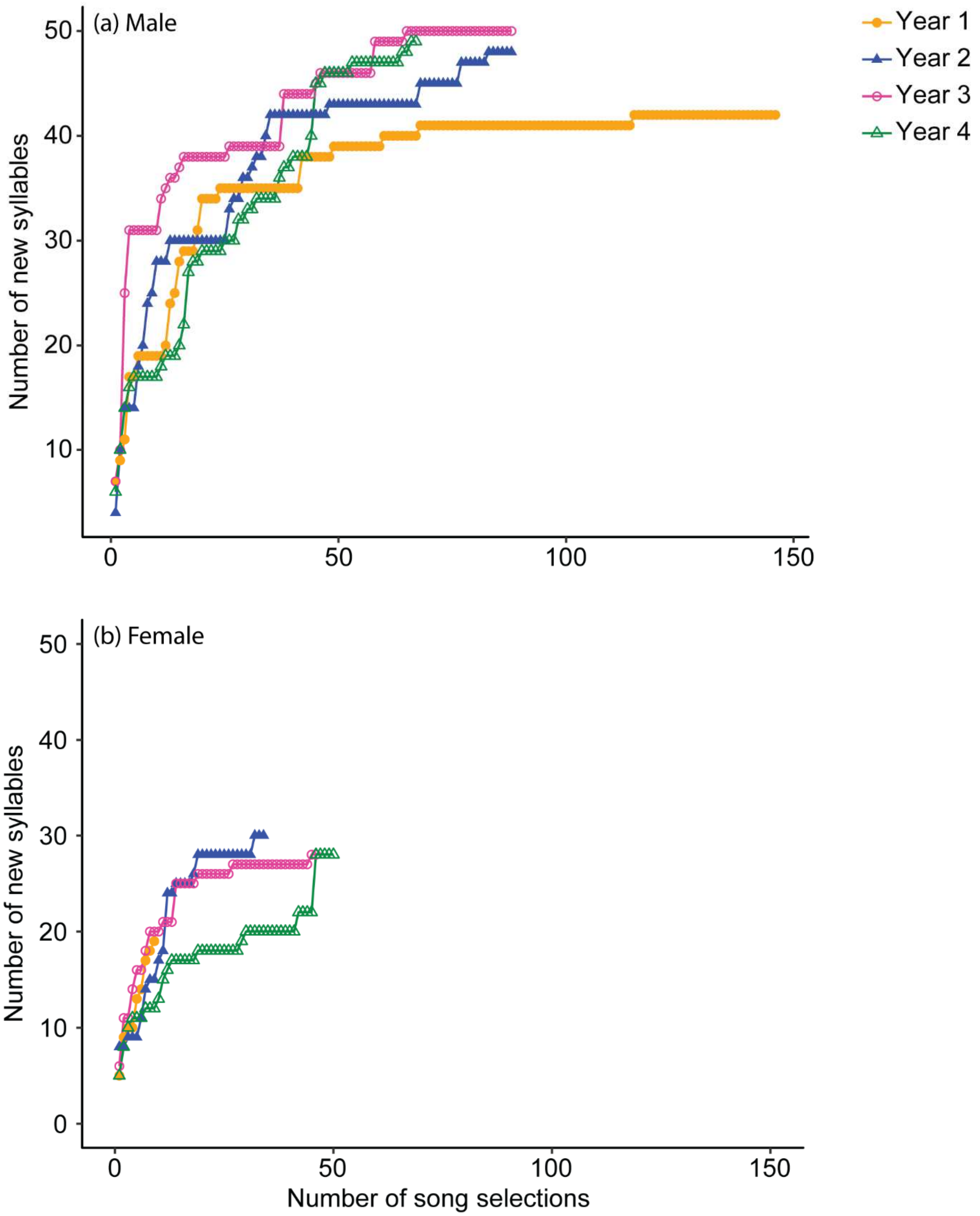
Suppl. 3.3. Recognition accuracies of different supervised machine learning methods using k-fold validation (k=25).

Classifier	Accuracy (%)
Gaussian Naïve Bayes	89.5 ± 1.7
Linear Discriminant Analysis	96.4 ±1
Random Forest Classifier	82.6 ± 2.26
Support Vector Machine	96.6 ± 1

Note: Each algorithm ran 100 iterations and randomisation was applied at each validation. The result is the mean ± standard deviation of the accuracies.



Suppl. 3.4. Cumulative plot of number of new syllables versus number of song selections for male and female bellbirds on Tiritiri Matangi Island from year 1 (2012–2013) to year 4 (2015–2016).



Suppl. 3.5. Cumulative plot of number of new syllables versus number of song selections for male and female bellbirds on Tiritiri Matangi Island for each year 1 (2012–2013), year 2 (2013–2014), year 3 (2014–2015) and year 4 (2015–2016).

Suppl. 3.6. Syllable repertoire size within each syllable family for male and female individuals with data on number of song selections, recording duration and the time period over which each individual was recorded.

Family	Male							Female					
	1	2	3	4	5	6	7	1	2	3	4	5	6
Alarmy	1					1							
Chortle	2	1	1	1		2							
Chump	1	1	1	1	1	1	1	1	1				1
Click	1	1		1		1		1	1				1
Cough	1	1	1	1	1	1	1						
Down-squeak	1	1	1	1	1	1	1	1				1	1
Down-squeak pipe	2	1	1	1	1	1	1						
Down transition								1	1	1	1	2	1
Flat-squeak	2	1	1	1		1	1	1				1	
Peak-squeak	2	1							1				1
Pipe	3	4	8	1	4	4	3	4	2	1	1	2	5
Pipe down-squeak	2	1			1	1			1				
Step-down		1		1		1	1	3	2	1	1	1	3

Step-up	2												
Stutter	2	1	2	1	1	1	1	3	5	3	3	3	1
Stutter up-squeak						1							
Trill	3	1	2	1		1	1						
Up-squeak	1	1				1							
Waah	6	4	6	3	5	3	3					1	
Warble				1		1	1						
Syllable repertoire size	32	21	24	15	15	23	15	15	14	6	6	11	14
Song selections	39	13	31	26	20	31	14	22	11	6	11	7	8
Recording duration (mm:ss)	37:40	18:21	34:07	24:54	08:59	29:20	10:37	18:12	21:48	06:13	08:23	14:31	05:19
Time period (months)	10	26	33	1	0	3	2	13	3	1	2	18	5

Suppl. 3.7. Number of song selections per year for each individual that was used to compare changes in repertoire size between years.

	Individual	Year 1	Year 2	Year 3	Year 4
Male	1			31	8
	3	17	2	5	7
	8	5	9	1	
Female	1			17	5

4 Sexual dimorphism of the New Zealand bellbird syrinx: the potential influence of syrinx size on song complexity

Reconstructed image of a female New Zealand bellbird syrinx

4.1 ABSTRACT

The vocal organ of songbirds, the syrinx, allows them to produce a wide diversity of songs of differing complexity. Current research on sexual dimorphism of the songbird syrinx structure hypothesises that syrinx size contributes to differences in vocal frequency range and singing behaviour. However, with only two species studied so far, it is not clear whether this hypothesis will hold for all species given the diversity of song systems and singing behaviour. I examined the syrinx of the New Zealand bellbird (*Anthornis melanura*) to explore the relationship between syrinx sexual dimorphism and song complexity of a species where both sexes sing complex songs. Given the similarity in song complexity of male and female bellbirds, I predicted the degree of sexual dimorphism for bellbirds to be more similar to the European starlings (*Sturnus vulgaris*), where females also sing, and less like the zebra finches (*Taeniopygia guttata*), where only males sing. I used micro-computed tomography to create three-dimensional images of the syrinx of an adult male and adult female bellbird. Using the size of the first three bronchial half rings as a measure of the degree of sexual dimorphism, I compared this with previous research on the zebra finch and European starling. The male and female bellbird syrinx was comparable in structure, but the male half rings ranged from 1.09 to 2.18 times larger than the female. The first two half rings tended to be larger in the male than the female on both sides of the syrinx. Males had a syllable repertoire size on average twice as large (20.6 ± 2.7, $N = 7$) as females (11.0 ± 1.7, $N = 6$). This high level of sexual dimorphism in half ring size did not fit my prediction, as this level of dimorphism was more comparable and often greater than found in the zebra finch, where females do not sing. Differences in body mass could not alone account for differences in half ring size between the sexes. This suggests half ring size may not

pose limits on a bird's repertoire size. I found a weak correlation between two morphometric measures, body mass and tarsus length, and the frequency bandwidth sung by each sex and species, suggesting body size may not be a reliable indicator of frequency range. The size of the syrinx half rings (and corresponding muscles) hence likely play an important role in certain aspects of the spectral features of a song, particularly fundamental frequency bandwidth. This could be an adaptation for increased song diversity; but it does not limit other aspects of song complexity such as song repertoire size. Future research on sexual dimorphism in both the syrinx and song complexity is needed to determine the link between the size of specific half rings and spectral variables that differ with song differences of sexes and species.

4.2 INTRODUCTION

Songbirds have an incredible range of song diversification and varying levels of song complexity. This diversity and complexity in singing behaviour is defined by differences in repertoire size, temporal features and spectral parameters such as fundamental frequency (e.g. Gaunt, 1983; Hill et al., 2017). Song diversity tends to be viewed as being under selection by female mate preferences and male-male competition (Catchpole & Slater, 2008). However, female song across species can also be highly diverse, ranging from no female song (e.g. zebra finches, *Taeniopygia guttata*; Zann, 1996), to species where the female song repertoire is comparable to males (e.g. European starlings, *Sturnus vulgaris*; Pavlova et al., 2005), and female singing rates are higher than males (e.g. stripe-headed sparrows, *Aimophila r.*

ruficauda; Illes, 2015; Illes & Yunes-Jimenez, 2009). To help us understand how this diversity in inter-sexual song complexity has evolved, learning the mechanisms of vocal production can help us to understand the constraints on performing complex song.

Production of complex song is regulated by neuro-muscular control of the vocal tract, including both sides of the syrinx (the sound producing organ; Zollinger et al., 2008), respiratory tract (Riede & Goller, 2010b), and beak movements (Nelson et al., 2005). Sexual dimorphism occurs within the central nervous system (Nottebohm, 2005; Nottebohm & Arnold, 1976), mass of syrinx musculature and skeletal (ossified cartilage) structure of the syrinx (Christensen et al., 2017; Prince et al., 2011; Riede et al., 2010). Sex differences in the song control regions of the brain are not consistently correlated with inter-sexual differences in repertoire size and singing rate, as these regions of the brain, such as the HVC (used as proper name), are always smaller in females regardless of repertoire differences (e.g. Brenowitz & Arnold, 1986; Hall et al., 2010; Lobato et al., 2015; Schwabl et al., 2015). The lack of correlation between HVC size and song complexity/repertoire size suggests that the smaller size does not constrain the learning and development of complex singing behaviour. On the other hand, syrinx musculature and skeletal structure do exhibit correlations between body size and song characters (Christensen et al., 2017; Prince et al., 2011; Riede et al., 2010). With few studies on sexual dimorphism of the syrinx, I aimed to assess the level of sexual dimorphism within the syrinx and its correlation with singing behaviour and complexity.

Two studies on sexual dimorphism of the syrinx structure have revealed contrasting results that warrant further investigation on their relationship with song behaviour and complexity. The mass of the syrinx is twice as large in the male zebra finch compared to the female, who does not sing (Riede et al., 2010). Whereas, male European starlings have only a 35% larger syrinx mass compared to the singing females that on average have a smaller song repertoire size and narrower frequency range (Pavlova et al., 2005; Prince et al., 2011). While this difference in syrinx mass is not fully explained by the difference in body mass (Prince et al., 2011), syrinx size and muscle mass in general does correlate with body mass (Christensen et al., 2017). The composition of the different muscle fibre types present in the syrinx musculature exhibit no difference between the sexes of several species (except for domesticated species like the zebra finch; Christensen et al., 2017). Muscle structure and mass is hence not likely to be a suitable measure for untangling the link between syrinx morphology and singing behaviour. The level of sexual dimorphism in the size of the ossified cartilaginous half rings of the syrinx, however, revealed that the larger half rings may support males singing song components of higher fundamental frequency (Riede et al., 2010). Compared to the zebra finch, the European starling has less sexual dimorphism in the size of the half rings, and the difference in frequency range of their songs between the sexes is considerably less (Table 4.1; Prince et al., 2011). Minimum song frequency is inversely correlated with body mass across all animals (Fletcher, 2004), including songbirds (Derryberry et al., 2018; Mason & Burns, 2015; Wallschläger, 1980). While maximum frequency may have an inverse relationship to body mass, for example in tanagers

Table 4.1. A comparison of the sex's vocal range, morphology and syringeal bronchial half rings (B1-B3) between the zebra finch, New Zealand bellbird and European starling.

	Zebra finch	Bellbird	European starling
Frequency range (Hz)			
Male	480-7000 [a]	150-10,270	300-10,000 [d-f]
Female	534-652 [a]	400-6140	500-8000 [d-f]
Syllable repertoire			
Male	3 to 8 [b]	20.6 (15-32)	47.6 (29-67) [d-g]
Female	0 [b]	11.0 (6-15)	21.1 (11-36) [g,h]
Male-female ratio			
Body mass	1.16 [a]	1.32	1.09 [f]
Tarsus length	0.96 [c]	1.08	1.02 [f]
Half ring			
B1 - left	1.75 [a]	1.69	1.16 [f]
B2 - left	0.99 [a]	1.74	1.06 [f]
B3 - left	1.01 [a]	1.09	1.19 [f]
B1 - right	1.36 [a]	1.72	1.11 [f]
B2 - right	1.21 [a]	2.18	1.24 [f]
B3 - right	1.13 [a]	1.76	1.05 [f]

[a] Riede et al. (2010a); [b] Zann (1996); [c] Honarmand et al. (2010); [d] Eens (1997); [e] Jensen et al. (2007); [f] Prince et al. (2011); [g] number of phrase types but each phrase contains a repetition of a different syllable type; [h] Pavlova et al. (2005).

(Thraupidae; Mason & Burns, 2015) and ovenbirds (Furnariidae; Derryberry et al., 2018), in species such as zebra finches and European starlings, this relationship does not occur and males are able to sing higher maximum frequencies than the smaller females (Prince et al., 2011; Riede et al., 2010). Hence body mass may not be the only predictor of maximum fundamental frequency and other aspects such as tarsus size (Liu et al., 2017) and syrinx half ring size (Riede et al., 2010) may have a stronger association with the maximum frequency of birdsong. These two studies suggest the half ring structure of the syrinx could be an important constraint on song frequency and complexity, but more species with female song must be studied to further corroborate these trends.

With so few studies carried out on sexual dimorphism in syrinx morphology, more research is required to progress current understanding of the relationship between song complexity and sexual dimorphism. The New Zealand bellbird (*Anthornis melanura*; hereafter bellbird) is a model subject as both sexes are year-round singers but exhibit sexual dimorphism in their singing behaviour (Brunton & Li, 2006). However, unlike the European starling, female bellbirds have different singing behaviour compared to males. Brunton and Li (2006) found females sing song types that share syllables in a range of combinations in contrast to males that have song types comprised of more song-specific syllables. On average, Brunton and Li observed that females have a smaller repertoire size of 1.9 song types versus 5.4 for males, but this could be an underestimate, as the range is one to six song types for individual females. Females tend to sing shorter and more variable song bouts than males but despite both sexes having high year-round singing rates, females sing more than males in the breeding season (Brunton & Li, 2006). Both sexes develop their songs in a comparable timeframe (Roper et al., 2018; Chapter 2; Appendix B) and possible functions of female song include territory defence, polygyny prevention and sexual selection (Brunton et al., 2008a; Brunton et al., 2016; Appendix A).

This study of the bellbird syrinx aims to describe the degree of sexual dimorphism in syrinx structure for a species where both sexes produce complex song and singing behaviour. To do this, I measured the size of the three enlarged half rings within the syrinx that have shown sexual dimorphism within the zebra finch and European starling. I compared these results with the zebra finch and European starling; any differences found in the syrinx morphology between the sexes may reflect differences in their syllable (acoustic unit) repertoire size. After accounting for the sexual dimorphism in body size, I predicted that the level of sexual dimorphism in the bellbird half rings would be less than the zebra finch and more comparable to the European starling where both sexes sing, as in bellbirds. European starlings produce a wider range of fundamental frequencies than zebra finches (Prince et al., 2011; Riede et al., 2010). Hence, I predicted that body mass and tarsus length, as a proxy for syrinx size, would have a positive relationship with the frequency bandwidth that each species and sex could sing.

4.3 METHODS

4.3.1 SPECIMEN COLLECTION AND STUDY SITE

Specimens used in this study were collected from the wild, after they were found already naturally deceased. I was limited to collecting naturally deceased specimens as bellbirds are a protected species and I did not have permission to euthanise live birds. I collected the specimens for this study from Tiritiri Matangi Island (Tiri). Tiri is a low-lying 220 ha island in the Hauraki Gulf, 4 km off the coast of the Whangaparaoa Peninsula and 25 km north of Auckland, New Zealand. The small island size and large bellbird population (Roper, 2012) made this an ideal site for finding naturally deceased specimens. Visits to the island occurred 4 days a week from September/October to April/May from 2012 to 2016 as part of larger study on the ecology of bellbirds. I only collected one adult male and one adult female for use in this study. The male was collected on 27 May 2014 and the female on 6 January 2016. The three male and one female hatch year bellbirds I collected will be utilised for further studies. During this time, I collected recordings of adult bellbird song for estimating their syllable repertoire size. I contacted local regional parks and animal rehabilitation centres for additional specimens, but none were available at the time.

4.3.2 MICRO-COMPUTED TOMOGRAPHY

I prepared the two specimens following methods of Düring et al. (2013) for micro-computed tomography (μCT) scans to obtain images of the isolated syrinx. Prior to dissection, I took two measurements each of the specimen's wing and tail length with a wing rule, and tarsus length (short and long) with Vernier calipers. I could not record measurements of the head and bill (and mass), as they had been removed prior for another study. I dissected the syrinxes with the surrounding organs still intact (lungs, trachea and part of the oesophagus) to keep the syrinx in a natural position for imaging. To preserve this position during fixing in 4% paraformaldehyde (PFA) in phosphate buffered solution (PBS) for seven days (stored at approximately 3-4°C), the specimens were mounted onto silicone sheets (3mm thick) with stainless steel insect pins (0.1 mm). After fixing, the specimens were stored in PBS and kept refrigerated (3-4°C). I took photos of the specimens pre and post-fixing to measure the length (cranial to caudal) and determine the amount of shrinkage due to fixing as in Düring et al. (2013). Düring et al. (2013) measured from the interbronchial ligament to tracheal ring 2, however, my photos were not clear enough and I measured from top of the trachea of the specimen to the most caudal point of the lung. There was no shrinkage but an increase in length of 8.3% and 10.5% for the male and female, respectively.

I delivered the syrinx samples for scanning at the Auckland Bioengineering Institute, University of Auckland (Auckland, New Zealand). The samples were scanned in a Bruker SkyScan 1272 instrument (Bruker microCT, Kontich, Belgium) using the following settings: 1800 ms exposure time at 4 µm pixel resolution, 75 kV source voltage, 120 µA source current, no filter, rotation steps of 0.2° over 180° and a frame averaging of 2 and random movement of 4. The scanning time took approximately 1 h 30 min. Data reconstruction was performed using InstaRecon (Bruker microCT). I used the Bruker software Data Viewer v.1.5.1.9 (Bruker microCT) to reduce the size of the image stack by a factor of 6, where 1 voxel = 24 µm^3, for easier processing, and transformed the view to coronal.

4.3.3 3D ANALYSIS SOFTWARE

I used Drishti v.2.6.4 software package (Limaye, 2012) for 3D volume rendering, visualisation and measuring volume. In Drishti Paint (Limaye, 2012), the first three bronchial half rings (hereafter I will refer to each bronchial half ring, from cranial to caudal, as B1, B2, B3, etc.) on each side of the syrinx were each segmented independently. I used the volume tool within Drishti paint to measure the entire volume of each bronchial half ring. In Drishti Render (Limaye, 2012), I then visualised the 3D volume of the whole syrinx for the male and female. I set the bounding box so that only the first seven tracheal rings appeared for comparing each sex and I set a scale bar of 2.4 mm. Images were saved of the dorsal, ventral and lateral (left and right) views for each sex.

4.3.4 SYLLABLE REPERTOIRE

Recordings of bellbird song were made to estimate the syllable repertoire size and frequency bandwidth of each sex's song. Bellbird songs were recorded using a directional shotgun microphone (Sennheiser ME66, Sennheiser, Germany) and a portable solid state recorder (Marantz Professional PMD 661, Marantz Professional, Cumberland, RI, U.S.A.) with 24-bit sampling precision and 48 kHz sampling rate. Recordings were made primarily of adult colour-banded individuals. I had captured these birds for banding as part of a long-term project with mist nets and supplementary feeder cages, or they had been banded as nestlings in the nest. Recordings were processed in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) with standardised settings (a bandpass filter of 500 Hz to 22 000 Hz, size 256 samples, time grid overlap 50%, and normalised by amplifying to fill the waveform window). Syllables were selected from spectrograms (FFT algorithm) of song samples using the open-source software Luscinia (Lachlan, 2007). The Luscinia data were imported into the new open-source database program Koe (Fukuzawa et al. *In prep.*; www.koe.io.ac.nz) where syllables were systematically labelled. Syllables were defined as consisting of one or more elements (i.e. note; a single sound trace on spectrogram) with less than a 15 ms interval between elements or the elements were consistently repeated together within a song type (Kershenbaum et al., 2016; Marler & Isaac, 1961). I then used additional syntax information (i.e. syllable ordering) within the song types to ensure consistent labelling of the syllables and agreement was made with an additional experienced observer. See Chapter 3 for more detailed methods on the acoustic processing and selection of syllables.

A cumulative plot of syllable repertoire size for each sex was plotted for individuals with more than five song selections with package ggplot2 (Wickham, 2016) in the open source statistical software R Studio (R Core Team, 2015). I found seven males and six females where the repertoire curve reached an asymptote. I then calculated the syllable repertoire size range and mean ± standard error (SE) for the individuals of each sex. I determined the frequency range for each sex from measurements of the minimum and maximum fundamental frequency calculated in Luscinia then imported and read in Koe. For species comparisons, I collected data on the zebra finch repertoire size and song frequency range from Zann (1996) and Riede et al. (2010), and for European starlings from Eens (1997), Pavlova et al. (2005) and Jensen et al. (2007). The repertoire size for European starlings, however, is for phrase types. Each phrase type tends to consist of the same repeated syllable type (Pavlova et al., 2005); this makes the phrase type repertoire comparable to syllable repertoire for this study.

4.3.5 SEX AND SPECIES COMPARISONS

I calculated the male to female ratio for body measurements (wing, tail, short tarsus and long tarsus) and the first three bronchial half rings. This was to compare the relative size of the half rings to body size between the sexes. To compare the levels of sexual dimorphism in the syrinx between bellbirds, zebra finches and European starlings, I collated data from this study and previous studies on a range of song and body size parameters, and the size of the first three half rings of the bronchi in the syrinx (Table 4.1). I calculated the male-female ratio for body mass, tarsus length and half ring size. Since I had one male and female bellbird and did not have their body mass, for comparing body size, I used the average body mass and tarsus length for each sex from 67 females and 180 males measured on Tiri (see Appendix C, Table C1 for a summary of the results). The study on zebra finches (Riede et al., 2010) and European starlings (Prince et al., 2011) used different methods to process and measure the half rings. The half rings in these studies used photographs of histological sections of the syrinx to measure the cross-sectional area of 10 points along the dorsal-ventral axis of each half ring. However, since I only compared the male-female ratio between the sexes, this should be comparable between the three

species since it is comparing relative size. With sexual dimorphism being greatest for body mass for all three species (Table 4.1), I adjusted the male-female ratio to account for this. For example, the male bellbird is 1.32 times the mass of the female, and if the half rings scale with body mass, the volume of the half rings should be 1.32 times larger in the male than the female. To account for this, I multiplied the proportion of sexual dimorphism for body mass to each female half ring for all three species (i.e. for the female bellbird, 1.32 times the volume of each half ring). The adjusted male-female ratio for half rings B1, B2 and B3 on each side of the syrinx were plotted to compare between the three species. With a linear regression, I then compared the fundamental frequency bandwidth (maximum fundamental frequency minus minimum fundamental frequency) with body mass and tarsus length for each species and sex to examine the relationship between different aspects of body size (and as a proxy for syrinx size) with the range of fundamental frequencies these species and their sexes can produce.

4.3.6 ANIMAL ETHICS

All research and specimen collection was undertaken with permission from the New Zealand Department of Conservation (DOC; 20666-FAU, 34833-FAU, 2008/33, WA-17590-DOA) and Massey University Animal Ethics Committee (12/32, 15/21). I followed the protocols set out by the New Zealand banding scheme (DOC) for all bird capture, handling and banding. Care was taken to minimise time spent off track and minimise nest disturbance. Handling time for females caught with brood patches was reduced by bypassing body measurements.

4.4 RESULTS

4.4.1 BELLBIRD SYRINX STRUCTURE

The syrinx of each sex consisted of the trachea, tympanum, pessulus, and three enlarged bronchial half rings (Figure 4.1). Both sides of the bronchi contained 13

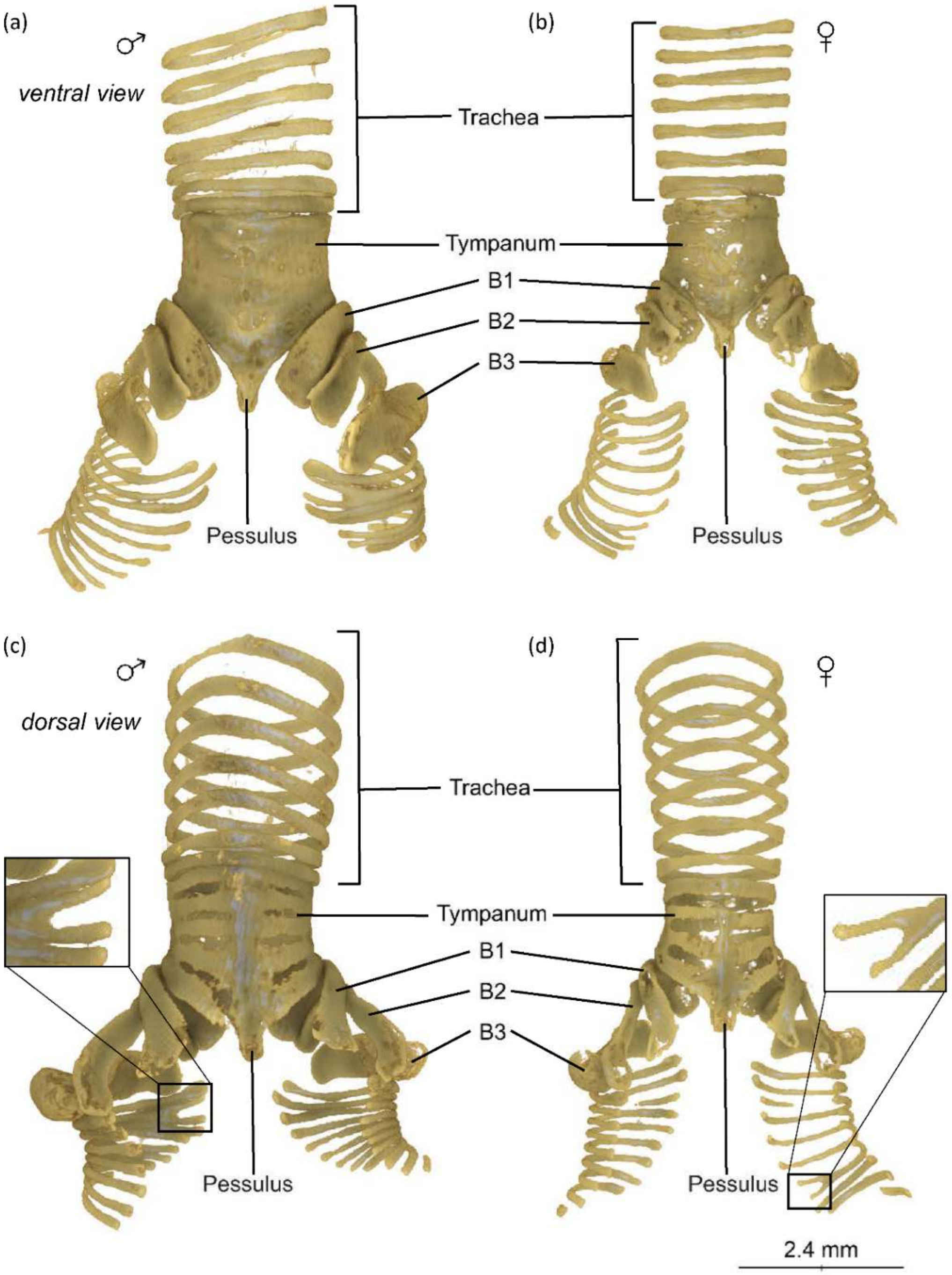


Figure 4.1. Skeletal structure of the (a, c) male and (b, d) female New Zealand bellbird syrinx. Ventral (a-b) and dorsal (c-d) views of 3D renderings based on µCT scans with the trachea, tympanum, pessulus and first three bronchial half rings (B1-B3) labelled. Insets show examples of bifurcating bronchial half rings in the male (c) and female (d).

half rings (although some considerably smaller: female B6 and B13, male B13), except for the male left side which had 11. An unusual finding was bifurcating half rings (see insets in Figure 4.1). These were located on the left side in the male (B5 and B7) and right side in the female (B10). The volumes of the half rings were consistently larger in the male than the female (Table 4.2; Figure 4.2). The left three half rings in each sex tended to be larger than those of the right side (Table 4.2; Figure 4.2). The ratio of sexual dimorphism for the size of the half rings was greater (except for B3 left) than the body size ratio, suggesting no correlation between body size and half ring size (Table 4.2).

Table 4.2. Body morphometrics and volume of the syringeal half rings for the male and female specimens.

	Male	Female	Male-female ratio
Wing length	86.25	76	1.13
Tail length	81.25	64	1.27
Short tarsus length	26.45	23.6	1.12
Long tarsus length	29.65	26.5	1.12
Half ring volume			
B1 - left	0.60	0.36	1.69
B2 - left	0.54	0.31	1.74
B3 – left	0.60	0.55	1.09
B1 - right	0.43	0.25	1.72
B2 - right	0.48	0.22	2.18
B3 - right	0.58	0.33	1.76

Note: length in mm and volume in mm^3

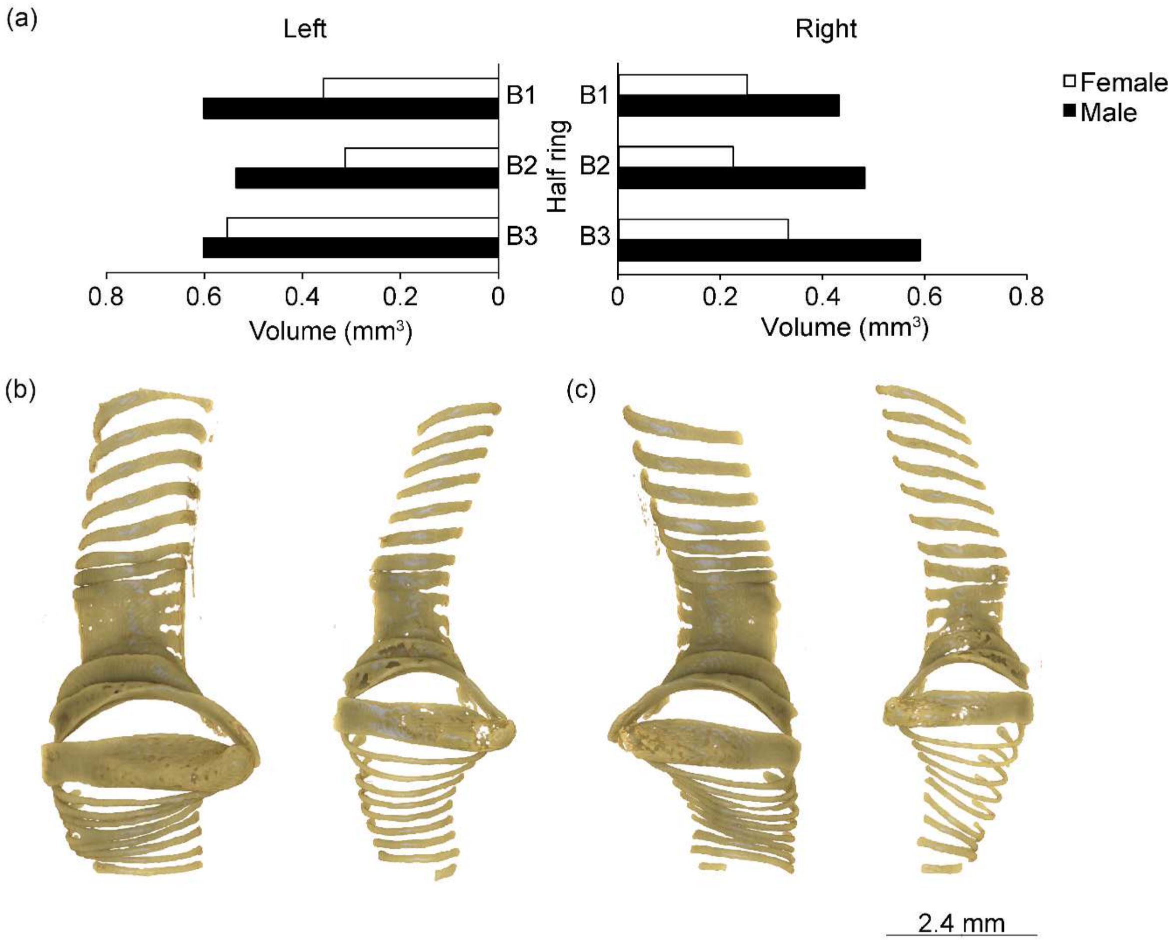


Figure 4.2. Volume of the first three bronchial half rings (B1-B3) for the left and right side of the male and female bellbird syrinx (a). Below are lateral views of 3D renderings of the left (b) and right (c) side of the syrinx for each sex (male on the right, female on the left).

4.4.2 SPECIES SEXUAL DIMORPHISM COMPARISONS

The degree of sexual dimorphism in the bellbird was higher than the zebra finch and European starling. For all half rings, except left B3, the male half rings were between 1.69 and 2.15 times larger than the female (Table 4.1). Only the zebra finches' B1 left had comparable levels of sexual dimorphism and B3 left had comparably low levels of sexual dimorphism between the three species (Table 4.1). The average male bellbird had a repertoire size of 20.6 ± 2.7 (*N* = 7) syllables and this was larger than the female repertoire size of 11.0 ± 1.7 (*N* = 6) syllables. I predicted that the level of sexual dimorphism in the bellbird syrinx would be more comparable to that of European starlings since their syllable repertoire size and frequency ranges are more comparable than that of zebra finches (Table 4.1), but this prediction was not supported. While the females of both European starlings and bellbirds have on average a repertoire size approximately half the size of males, the half ring male-female ratio was much higher in bellbirds, even when adjusted for their sexual

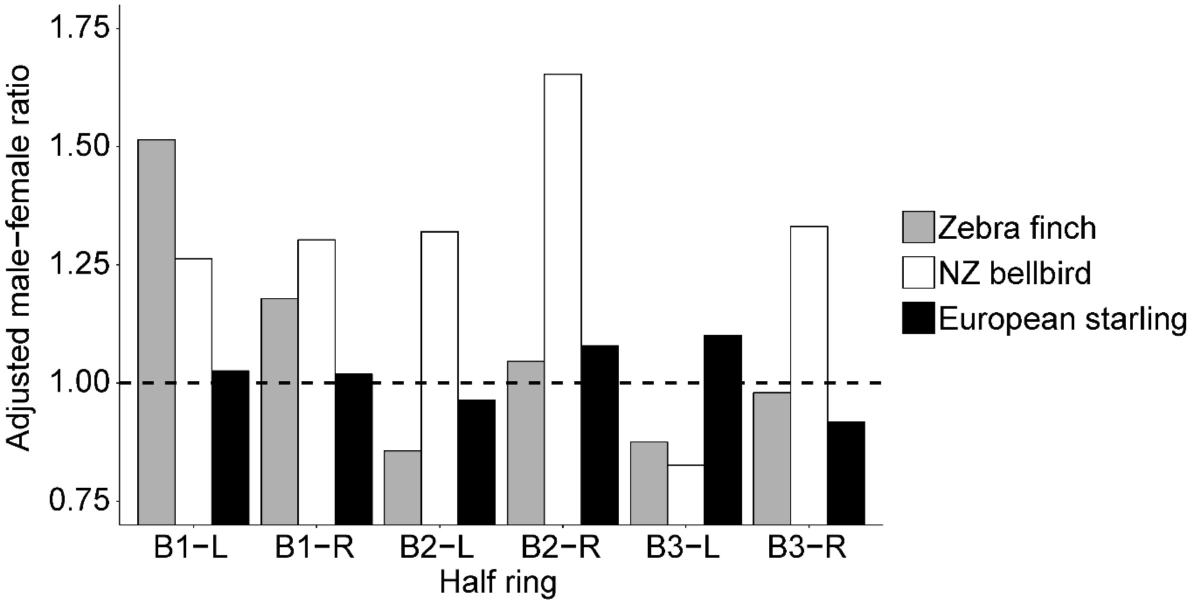


Figure 4.3. Comparisons between the male-female ratio (adjusted for sexual dimorphism in body mass) for the size of the left (L) and right (R) bronchial half rings (B1, B2 and B3) in the syrinx of the zebra finch (Riede et al., 2010), New Zealand (NZ) bellbird and European starling (Prince et al., 2011). The dashed line represents no sexual dimorphism in half ring size for the adjusted male-female ratio.

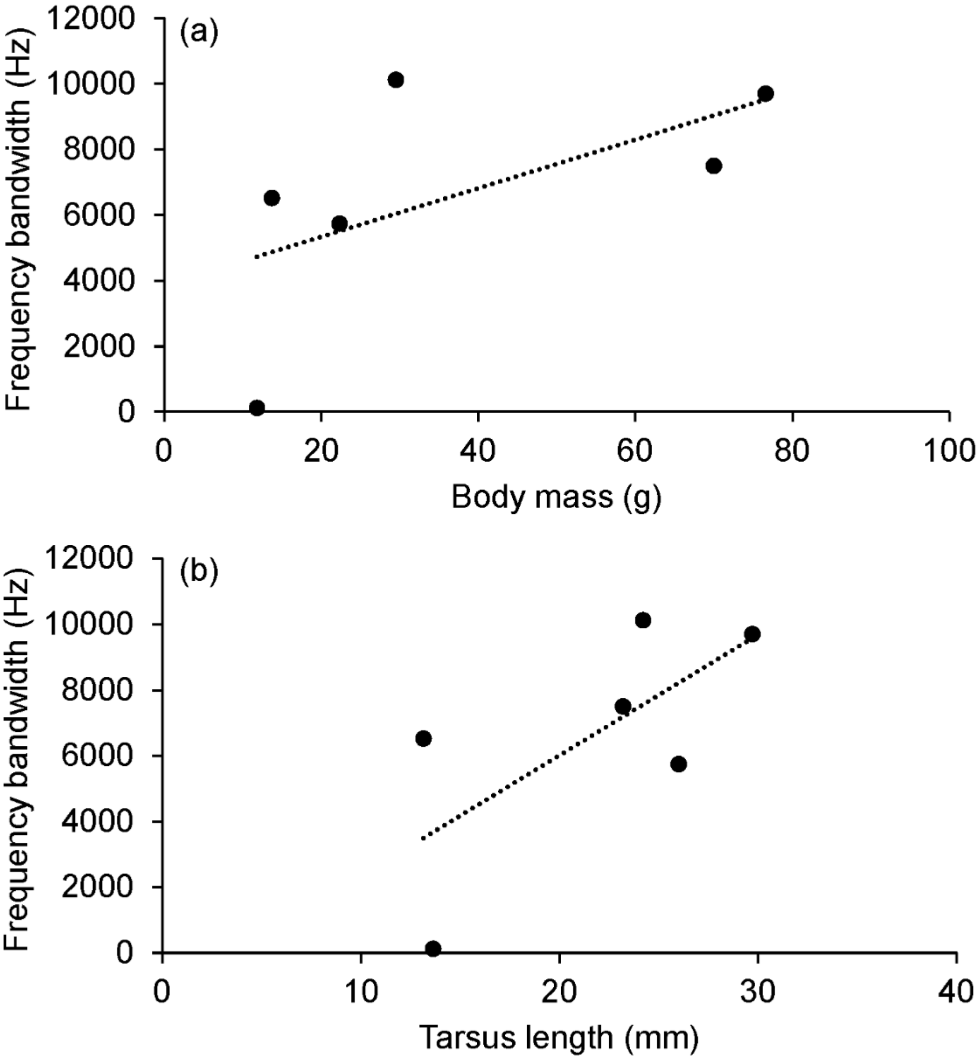


Figure 4.4. Linear regressions to explore fundamental frequency bandwidth's relationship with (a) body mass ($r^2 = 0.34$) and (b) tarsus length ($r^2 = 0.47$) for male and female zebra finches, New Zealand bellbirds and European starlings. See Table 4.1 for references for the data on zebra finches and European starlings.

dimorphism in body mass (Figure 4.3). The bellbird half ring male-female ratio only fell between the range for the other two species for B1 left and a smaller ratio for B3 left (Figure 4.3). Body mass and frequency bandwidth across all three species and sex had a weak positive correlation ($r^2 = 0.34$, $P = 0.22$; Figure 4.4). Tarsus length and frequency bandwidth also had a weak positive correlation ($r^2 = 0.47$, $P = 0.13$; Figure 4.4). Overall, the relative size of the half rings was most similar between the bellbird sexes compared to the zebra finches and European starlings. For example, the bellbird B3 tended to be larger (or similar to B1) than the other half rings on both sides of the syrinx, whereas it tended to be the smallest half ring in zebra finches (Riede et al., 2010) and European starlings (Prince et al., 2011).

4.5 DISCUSSION

In the New Zealand bellbird, I have found sexual dimorphism in the size of the first three syringeal half rings. The size difference was greatest between the right sides of the syrinx and body mass alone could not account for this difference. This coincides with the fact that the right side of the syrinx is known to produce syllables of higher fundamental frequency (Suthers, Goller, & Hartley, 1994). However, the half rings in the left side of both sexes tended to be larger than the right side. The degree of sexual dimorphism in bellbirds does not fit my prediction in relation to the studies on zebra finches and European starlings; therefore, does not support a correlation between sexual dimorphism in syrinx size and syllable repertoire size. Body mass and tarsus length were not strong predictors of frequency bandwidth across the sexes of the three species. While I cannot account for individual variation in half ring size with only one specimen for each bellbird sex in this study and hence the results are not conclusive, the results are intriguing, and I will explore why these results may be significant and worth further investigation.

The degree of sexual dimorphism in the size of the three enlarged syringeal half rings may not be a reliable indicator of repertoire size. While both female bellbirds and European starlings had an average repertoire half the size of males, there was considerably higher sexual dimorphism between the bellbird sexes, particularly for half rings B1 and B2 on both sides of the syrinx. The sexual dimorphism in bellbirds was even greater for most half rings than in the zebra finches, where females do not sing. While the syrinx structure is most conserved within the songbird passerines (Gaunt, 1983; King, 1979), there is still considerable variation in its anatomical structure (Ames, 1971). Selection acting on the vocal performance of each species is therefore likely, which may in turn drive changes within the syrinx structure (although see Gaunt, 1983). Northern mockingbirds (*Mimus polyglottos*), known for being mimics, when trained to sing the song of other species, are not able to replicate the motor production of certain syllables that are unique to those species (Zollinger & Suthers, 2004). Suthers and Zollinger (2006) suggest this supports the hypothesis that selection for increased song diversity is the driver for the evolution of motor patterns within each songbird species. Hence, selection for differences in half ring size may be a mechanism as to how the vocal motor patterns have adapted to producing the unique songs of each species and sex.

Differences in syrinx half ring size may explain differences in some spectral features between species and sexes. While there is consistency between the three species studied with both B1 and B2 tending to be larger in the males, I have found that in bellbirds, the B3 half ring tended to be larger than B1 and B2. However, in both zebra finches and European starlings, B3 was smaller than B1 and B2 (Prince et al., 2011;

Riede et al., 2010). These differences in their half rings may play a role in producing their respective unique song repertoires, as the syrinx is known to have significant control over the fundamental frequency and rapid temporal aspects of a bird's syllables (Elemans et al., 2008; Goller & Riede, 2013; Suthers et al., 1999; Suthers & Zollinger, 2006). The three enlarged half rings are all connected to internal labia (Düring et al., 2013), known for producing a bird's song via the tension that syringeal muscles and corresponding half rings put on these labia (Suthers & Zollinger, 2006). While half ring B2 is the attachment site for the ventral syringeal muscle, known to have the most control over fundamental frequency, B3 is an attachment site for the dorsal tracheobronchial muscle (DTB) which has a small amount of control of fundamental frequency (Goller & Suthers, 1996a). DTB is also activated in the production of some syllables, which may be necessary for the fine control of the syringeal structure in producing these syllable types (Goller & Suthers, 1996b). Hence, differences in the size of B3 and connecting DTB muscle could potentially play a role in differences in vocal production between species. The bellbird sexes produce sexually dimorphic song (Chapter 3), which may explain why we see more sexual dimorphism in the bellbird syrinx half ring size compared to the European starlings, a species with less sexual dimorphism in the syrinx (Prince et al., 2011) and where females are able to sing most phrase types that males sing (Pavlova et al., 2005). The varying sizes and shape (although shape is beyond the scope of this study) of the three enlarged half rings may hence play an important part in the vocal production of differing syllables. Further research on differences between frequency and temporal aspects of the song for each sex in different species will help determine whether the enlarged half rings in males contribute to differences between the syllable repertoires of each sex.

Song features such as fundamental frequency tend to inversely correlate with body mass across species (Derryberry et al., 2018; Mason & Burns, 2015; Wallschläger, 1980). However, I did not find a relationship between the frequency bandwidth and body mass of each species and sex examined. Of the species and sexes that have song, male bellbirds were the outliers, singing a comparable frequency bandwidth to that of male European starlings, which are at least twice the mass of a male bellbird. Within these species, as their body mass increases, there is also an increase in their maximum fundamental frequency. This is not supported by broad scale studies within the tanager (Mason & Burns, 2015) and ovenbird families (Derryberry et al., 2018). The maximum frequency in the song of dusky warblers, *Phylloscopus fuscatus*, is positively correlated with tarsus length (Liu et al., 2017), but I only found a weak correlation between tarsus length and fundamental frequency bandwidth for the species and sexes examined. In some species, the lowest frequency used only in vocal contests has a negative relationship with tarsus length in both males (Hall, Kingma, & Peters, 2013; Price, Earnshaw, & Webster, 2006) and females (Geberzahn, Goymann, Muck, & ten Cate, 2009). This indicates that research on maximum frequency may need to address what maximum frequency is signalling to understand how it may relate to body size. Overall, this suggests the frequency bandwidth of bird song (both high and low fundamental frequency) does not always correlate strongly with body mass and tarsus length. While other aspects, such as habitat, can influence the frequency range birds sing (Baker, 2006; Ryan & Brenowitz, 1985; Slabbekoorn & Smith, 2002), the size of the individual components of the syrinx may also explain inconsistent results for body size and frequency range.

I suggest the relative size of each half ring compared to body size should be further examined to assess the potential impact that half ring size may have on the frequency bandwidth that a bird can sing.

The size of the three enlarged half rings may be a structural adaptation for song diversification. The enlarged half rings provide an important attachment site between the syringeal muscles and sound producing labia (Düring et al., 2013). The larger the syringeal muscles are, particularly in males, the larger the half rings need to be to withstand the forces from the muscles; as the more tension that the muscles can place on the internal labia, the higher the maximum frequencies that can be produced (Riede et al., 2010). Inconsistencies between the size of the labia of each side of the syrinx, within and between species, led Prince et al. (2011) to conclude that size alone of the labia does not relate to the frequency range that a syrinx can produce. This suggests the size of the muscles and corresponding half rings are potentially more critical, as they are necessary to create the tension on labia (Suthers & Zollinger, 2006). Increased muscle mass has also been suggested to be related to the quantity of song produced, as with syrinx muscle mass reducing in syrinx denervation experiments (i.e. cutting the nerves that control the syrinx), this may link why female European starlings who sing less than males, have smaller muscle mass (Prince et al., 2011). While I can only deduce that female bellbirds have a smaller syringeal muscle mass due to their smaller half rings, this trend may not be supported in bellbirds as females with their smaller syrinx, sing more than males during the breeding season (Brunton & Li, 2006). Therefore, the size of the syringeal muscles and half rings may not limit the quantity of song produced but may be adapted to produce a species unique song repertoire.

4.5.1 CONCLUSIONS AND FUTURE DIRECTIONS

The bellbird syrinx is sexually dimorphic with half rings B1 and B2 tending to be larger in the male. This correlates with previous research on the zebra finch and European starling, but the sexual dimorphism between the sexes of each species cannot be explained by their differing repertoire sizes. As pointed out by Gaunt (1983), repertoire size does not simply correlate with the complex structure of the syrinx. However, Gaunt (1983) suggested the syrinx did not adapt under selection pressures to sing diverse song, but current research may suggest otherwise. As more research is carried out, the more we can understand which aspects of the syrinx contribute to the diversity of vocal behaviour. Body mass and tarsus length were not strong predictors for fundamental frequency bandwidth. Adaptations to the size of the three enlarged half rings and corresponding muscles are potentially a key structural feature that allows songbirds to produce wider frequency ranges than body size alone could predict. The bellbird half rings differ in size from zebra finches and European starlings in that B3 tends to be larger than the first two half rings. Further research is needed to examine whether this relates to spectral characteristics of bellbird song that may differ to the other species studied (e.g. why male bellbirds have an increased frequency bandwidth relative to their body size). While there are other structures of the vocal tract (Goller & Riede, 2013) and environmental constraints (Ryan & Brenowitz, 1985) that correlate with the fundamental frequency of syllables, I suggest that the half ring size, along with corresponding muscles and labia, are limiting the frequency bandwidth that songbirds can produce. They are also potentially under indirect selection to increase the diversity of complex singing behaviour, as I found significant sexual dimorphism in the size of the half rings in bellbirds, as well in their song repertoire. Future research is needed to determine what the selection pressures are in the New Zealand bellbird song system to further corroborate this relationship with the structure of the syrinx.

4.6 AUTHOR CONTRIBUTIONS

Michelle M. Roper contributed to the design of the study, developed the methodology, conducted the fieldwork, managed field assistants, contributed to syllable labelling, processed specimens, performed analyses and wrote the manuscript. Wesley H. Webb imported song selections into the software Luscinia and Koe, and labelled syllables. Christine Evans contributed to syllable labelling. Yukio Fukuzawa developed the new software Koe, imported syllable selections into Koe, performed machine learning algorithms for verifying syllable labels. Aaron M. T. Harmer contributed to methodology and assisted with writing the manuscript. Dianne H. Brunton designed the study, developed methodology, assisted with fieldwork, assisted with analyses and contributed to the writing of the manuscript.

5 Reproductive life-history trade-offs demonstrated by long-term changes in the breeding biology of the New Zealand bellbird on an ecologically restored island

The nest of a New Zealand bellbird (photo: Michelle Roper).

5.1 ABSTRACT

Ecological restoration projects provide excellent opportunities to study how animals adapt their life-history strategies in response to a changing environment. A key way an animal can optimise reproductive success in changing conditions is to make trade-offs between particular parameters within their breeding system, for example, clutch size, timing of breeding activities, and degree of parental care. The New Zealand bellbird (*Anthornis melanura*) has a long history on Tiritiri Matangi Island (Tiri), from a degraded agricultural past to recent restoration. I studied the breeding biology of the bellbird to assess how their reproductive life-history strategies have responded over time to the restoration on Tiri. I compared the current breeding biology (2012–2017) of the bellbirds with data from studies between 2001–2010 (including Baillie, 2011; Cope, 2007), and a study from 1977–78 (Anderson & Craig, 2003), prior to the island's restoration. I also explored potential short-term associations between abiotic and biotic factors and key aspects of reproductive success. My main finding was that clutch size reduced over time from a mean of 3.6 to 2.4 eggs per nest and negatively correlated with population density. This is consistent with a density dependent effect, although further data are required to test this idea. Laying dates in early breeding seasons advanced to late August and in delayed years, could extend to January, with all chicks fledged by the end of February. Variation in the timing of breeding onset was likely due to annual variation in food resources. Nest success was 47% across 2012–2016 and fell within a similar range as previous studies. I found little effect of year, weather, or parental age and morphometrics on aspects of reproductive success. I observed directional change in patterns of parental investment between 1977–78 and 2012–16. In 2012–16, parents were persisting with first nests and raising single broods rather than

abandoning early nests and re-nesting. These results and comparisons with the breeding biology of other populations suggest that the bellbirds life-history traits are plastic in response to local conditions and that food resources may be a limiting factor.

5.2 INTRODUCTION

Islands restored to their native habitat and an ecological functioning state are crucial for the conservation of New Zealand's endemic flora and fauna. New Zealand (hereafter NZ) has been a pioneer in island conservation since its mainland forest cover was reduced to as little as 25% following human settlement (Saunders & Norton, 2001). Since then, there has been a significant number of extinctions due to loss and fragmentation of habitat (McGlone, 1989; Veblen & Stewart, 1982), hunting and specimen collecting by humans (Clout & Craig, 1995; Craig et al., 2000), and the introduction of invasive species, which became predators and competitors of the native species (Clout & Craig, 1995; Craig et al., 2000; Veblen & Stewart, 1982). NZ's smaller islands became refuges for the survival of many species such as the hihi (stitchbird, *Notiomystis cincta*) and tuatara (*Sphenodon* spp.). Some islands that did not escape the effects of human settlement have since become the focus for ecological restoration to expand the number of safe havens for endangered and threatened species (Bellingham et al., 2010; Veitch & Bell, 1990).

Monitoring the populations on these restoration islands is essential to understand whether viable populations are being maintained. The aims of these ecological restoration projects are to increase native biodiversity, often with a focus on protecting rare endemic species. Valuable insights come from studies of native species protected on these restoration islands, especially long-term breeding and ecological studies of focal species such as the North Island (NI) robin (*Petroica longipes*) and hihi on the scientific reserve of Tiritiri Matangi Island (Armstrong & Ewen, 2013). The data collected for these species were initially for modelling population growth and how to best manage reintroduced populations. Data on parameters such as reproductive success and survival show that reproductive success is not density-dependent for either species, but the probability of NI robin juveniles surviving after fledging declines with increasing population density on the 220 ha island (Armstrong & Ewen, 2013). This NI robin population was small, starting with 7 breeding pairs in 1992 (with an additional translocation increasing this to 11 breeding pairs in 1993) and population growth halted at around 65 individuals (Armstrong et al., 2000) on this island. Other bird species reintroduced to islands have shown reduced reproductive output with increasing population size, such as tieke, *Philesturnus carunculatus*, on Mokoia Island (Davidson, 1999). This reduction in reproductive output in tieke occurred in just under 10 years for this small island population (Davidson, 1999). However, these studies do not reflect how a species' breeding biology adjusts with not only conspecific density, but also improved ecosystem function. Longer-term data for species on islands with larger carrying capacities will be valuable to assess how a population's breeding ecology can respond to a restoring ecosystem.

Variation in the expression of life-history traits often occurs in species that live in variable environments (Camfield et al., 2010; Martin, Camfield Alaine, & Martin, 2009; Sandercock et al., 2005). Life-history strategies tend to vary on a continuum of high reproductive output but low adult survival, to low reproductive output but higher adult survival (Sæther, Ringsby, & Røskaft, 1996). Such trade-offs between reproductive output and survival are made at the individual level; as parents must decide how to allocate energy to their young and their own future survival (Martin, 1987). These trade-offs are driven by environmental changes that include food availability, climate, and predation (Camfield et al., 2010; Martin, 1987, 1995; Sandercock et al., 2005). Species with life-history traits that are 'phenologically flexible', such as the ability to adjust reproductive timing in response to changing temperature (Moussus, Clavel, Jiguet, & Julliard, 2011), are likely to better adjust and persist in changing environments.

Reproductive trade-offs in life history strategies of birds could occur in restoration populations as the environment and population density will change over time. As the habitat restores, the availability of food and nest sites is expected to increase. This increase in food availability will allow parents to invest energy into producing more or higher quality young (Martin, 1987). However, as the density of a species increases, reproductive output may reduce due to density-dependence (Lack, 1954). Density-dependent reproductive output occurs as birds are either forced into lower quality habitat, or are faced with an increase in competition that causes a uniform decrease in habitat quality (Both, 1998; Ferrer & Donazar, 1996). Competition due to higher densities can lead to an increase in nest failure (Arcese et al., 1992; Both, 1998), reduce territory size and increase parental foraging time (Sillett et al., 2004). To compensate for high levels of competition, reproductive trade-offs are made to ensure an individual’s reproductive output is maximised. For example, birds can first reduce egg volume to conserve energy but produce the same number of offspring (Martin, 1987). However, there is limit to which the egg volume can reduce, as mortality of the young will increase, and thereby a reduction in clutch size will optimise the birds’ reproductive output (Martin, 1987).

Reproductive output is optimised by an individual’s ability to respond to environmental changes, which includes using different strategies regarding timing of breeding, breeding attempts per season, clutch size and parental investment. Breeding is ideally timed so that the periods of highest food demand by chicks coincide with abundant food availability in the environment (Tomás, 2015). To achieve this, for example, birds can alter incubation timing and intervals (Tomás, 2015). Single-brooders (parents raise only one successful brood) must wait for this optimal period before commencing breeding, but if a nest fails, clutches become smaller throughout the breeding season for successive attempts (Crick, Gibbons, & Magrath, 1993). Multi-brooders (parents can raise multiple successful broods) however, can start breeding earlier, which is why there is an observable pattern of increasing clutch size with increasing food availability, then a decline in clutch size over the breeding season as food availability reduces (Crick et al., 1993). Even within species, different populations can show a tendency to be either a single- or multi-brooder, depending on their geographic location and migratory behaviour (Dhondt, Kast, & Allen, 2002; Gil-Delgado, Marco, Paredes, & Vives-FerrÁNdiz, 2005). Low food availability can delay the start of breeding and reduce reproductive output, e.g. by 0.15–0.25 young per female in red-eyed vireos, *Vireo olivaceus* (Marshall, Cooper, DeCecco, Strazanac, & Butler, 2002). On the other hand, in superabundant food years, lesser grey shrikes, *Lanius minor*, have earlier laying dates and an increase in clutch size (Hoi, Kristin, Valera, Hoi, & Sodhi, 2004). Parents must also consider their condition; hence, they could alter clutch size, as a larger clutch size would require more feeding visits (Lack, 1954). When female great tits, *Parus major*, are artificially given a larger brood size, they are less successful at recruiting offspring compared to females that naturally have larger broods, suggesting the females with naturally larger broods are fitter (Pettifor, Perrins, & McCleery, 2001). Parents can also adjust their response to predators by visiting the nest less frequently when there is a higher risk of predation (Kleindorfer, 2007; Olsen, Felch, Greenberg, & Walters, 2008).

The climate and weather events on islands can differ from the mainland and these differences can have significant short-term impacts on reproduction. NZ’s northern islands can be warmer than the mainland (Meurk & Blaschke, 1990) and are more likely affected by extreme weather events, such as drought (personal observation). Total rainfall can have both positive and negative effects on reproduction. Food availability can depend on rainfall during the breeding season, for example in common blackbirds, *Turdus merula*, where higher rainfall increases earthworm availability and in turn increase the mass of chicks (Chamberlain, Hatchwell, & Perrins, 1999). Total rainfall during certain stages of the nesting period can be detrimental to nestling survival and fledging success (Arlettaz, Schaad, Reichlin, &

Schaub, 2010; Fantle-Lepczyk, Taylor, Duffy, Crampton, & Conant, 2016; Öberg et al., 2015), whereas in song sparrows, *Melospiza melodia*, nest survival and length of the breeding season increases with higher rainfall (Chase, Nur, Geupel, & Stouffer, 2005). Past rainfall can also impact the subsequent breeding season, e.g. high rainfall in the previous season leads to an increase in nest success in the puaiohi, *Myadestes palmeri* (Fantle-Lepczyk et al., 2016). Higher temperatures prior to fledging counteract the effect of higher rainfall earlier in the nesting period in hoopoes, *Upupa epops*, with an increase in nestling survival (Arlettaz et al., 2010). Night-time temperatures affect reproductive effort in barn swallows, *Hirundo rustica*, as it affects the day-time energy expenditure of the parents (Spencer & Bryant, 2002). Therefore, understanding how weather events may affect birds' reproductive success on NZ's northern offshore islands could help with species' management plans.

The New Zealand bellbird (*Anthornis melanura*; hereafter bellbird) is a socially monogamous songbird in the family Meliphagidae that has benefitted from restoration projects. The bellbird is a NZ endemic species with a range of more than 1500 km from Three King Islands in the north (36.9029 ° S, 174.7547° E) to Auckland Islands in the south (50.6218° S, 166.1196° E) of NZ. Throughout their range though, bellbirds have undergone local extinctions, such as in the northern third of the North Island (north of Hamilton) by 1870 (Bartle & Sagar, 1987). The exact cause of these local extinctions is unknown but it is likely a combination of disease, presence of invasive predators, and loss of habitat (Bartle & Sagar, 1987; Lack, 1954). The restoration of offshore islands has allowed bellbirds to flourish, in particular, on conservation-managed islands such as Tiritiri Matangi Island (Tiri). The Tiri bellbird population declined to less than 24 birds by the time farming ended in 1972 (Baillie, 2011; Cameron & Davies, 2013), with only 6% native vegetation cover remaining in 1984 (Graham et al., 2013). The bellbird population has since significantly risen after intense habitat restoration, mammalian predator eradication and supplementary feeding (Baillie, 2011; Graham & Veitch, 2002; Roper, 2012). Both the increasing bellbird population, and the reintroduction of other avian species, may have resulted in bellbirds experiencing increasing competition for resources since the island restoration began in 1984. See Figure 5.1 for a timeline of events and bird reintroductions on Tiri. These significant changes to the island make the Tiri bellbird population an ideal system for understanding the plasticity of life-history traits, and how breeding biology can change over time.

I studied the breeding biology of the NZ bellbird to assess how a critical component of life history, clutch size, has changed over time on the restoration island Tiritiri Matangi Island. I compared the current breeding biology of the bellbirds with data in studies from 2001 to 2010 (including Baillie, 2011; Cope, 2007), and a study from 1977/78 (Anderson & Craig, 2003), prior to the island's restoration. I also examined what factors, including environmental and parental morphometrics, could influence aspects of reproductive success. I predicted that during this period where the bellbird population has grown rapidly, that clutch size has declined due to both intra- and inter-specific competition for resources. I also predicted an increase in fledging success over time due to the eradication of mammalian predators and

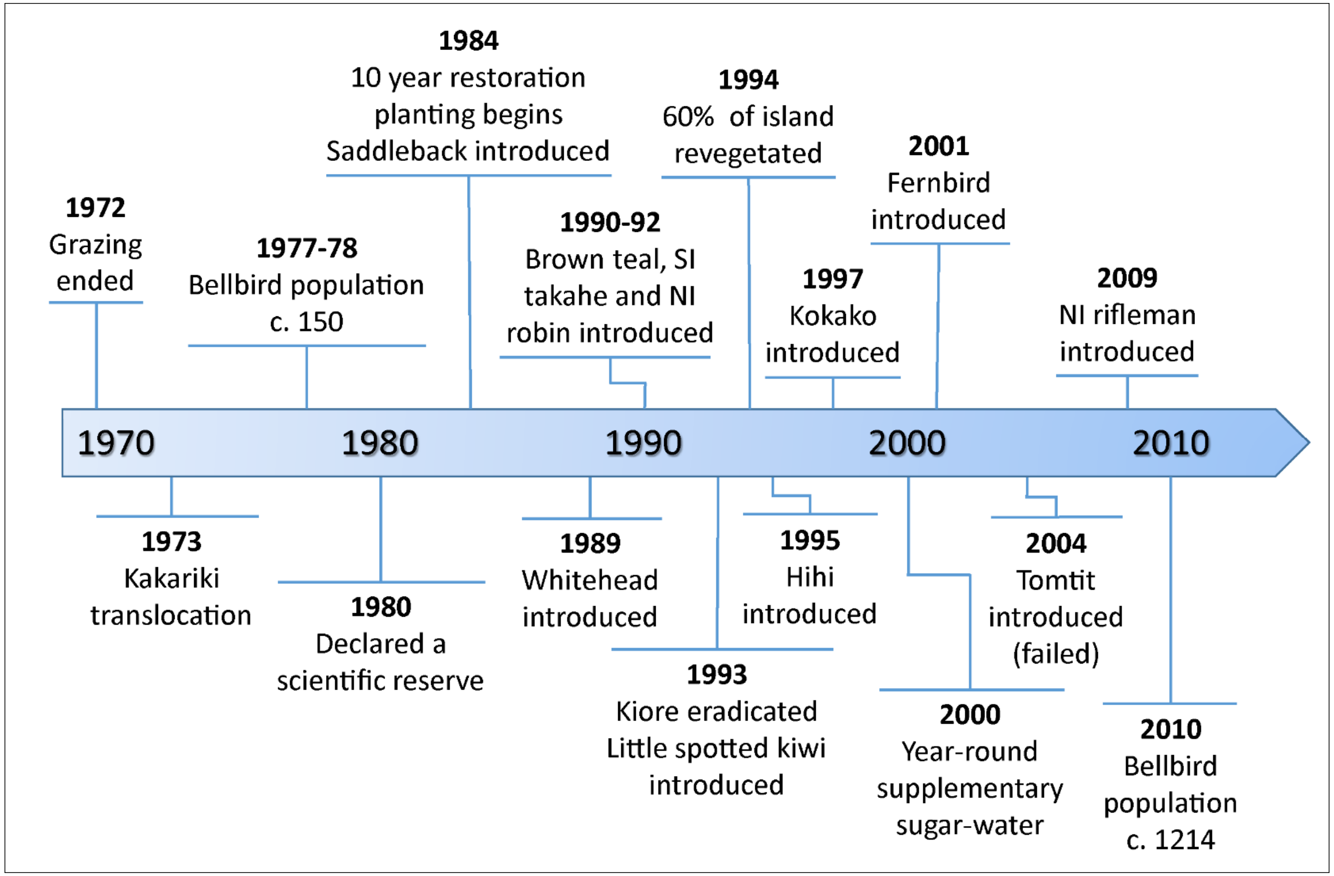


Figure 5.1. Timeline of significant events and avian reintroductions to Tiritiri Matangi Island. Contents of figure compiled from Anderson and Craig (2003), Cameron and Davies (2013), Galbraith and Cooper (2013) and Roper (2012). NI = North Island, SI = South Island.

successful habitat restoration. Finally, short-term variations in nesting success were predicted to be associated with higher rainfall due to greater food abundance.

5.3 METHODS AND MATERIALS

5.3.1 STUDY SITE AND SPECIES BACKGROUND

My study was conducted on the scientific reserve Tiritiri Matangi Island. Tiri is a low-lying 220 ha island in the Hauraki Gulf, 28 km north of Auckland, New Zealand (36.60° S, 174.89° E). Prior to the study in 2010, the island had a bellbird population of approximately 6.3–10 birds per ha (Roper, 2012). Bellbirds have been present on the island for at least 100 years but only in the last 30 years has the bellbird population expanded after intensive replanting and invasive mammal eradication (Rimmer, 2004). The island is now representative of a typical northern New Zealand forest with ephemeral flowering and fruiting plant species providing food resources year round (Gravatt, 1970).

Bellbirds are an endemic New Zealand honeyeater. They are sexually dimorphic in plumage (males are darker olive green and females have a white cheek stripe) and size, with females approximately 20% smaller (Heather & Robertson, 2005). Their song is sexually dimorphic with males tending to sing longer song bouts and females singing single song types with more variable intervals (Brunton & Li, 2006). There are seasonal differences in their singing behaviour with females singing at higher rates than males in the breeding season (Brunton & Li, 2006). The function of song in female bellbirds is possibly for sexual selection and polygyny inhibition (Brunton et al., 2008a). Their diet consists of nectar, seasonably available fruit, and invertebrates (Craig, Stewart, &

Douglas, 1981; Rasch & Craig, 1988; Roper, 2012). There are relatively few studies on their breeding biology (Anderson & Craig, 2003; Cope, 2007; Massaro, Starling-Windhof, Briskie, & Martin, 2008) and no studies have compared changes in nesting biology over time.

5.3.2 DATA COLLECTION

I collected breeding biology data as part of a larger study on bellbird behavioural ecology that began in 2001. I collected data for this study from 2012 to 2017 and compared these data with data collected at various levels of intensity from published and unpublished studies (see Table 5.1). The bellbird breeding season occurs during the austral spring and summer, from late August to late January. Nests were located by finding pairs on territories and observing the birds for nesting behaviours (e.g. carrying nesting material) and searching for built nests. I regularly checked nests (every 2–4 days) to record start and end dates for each nesting period (building, laying, incubation and hatching) to determine nesting timing and variation between the years. I also measured clutch size, brood size and the number of fledged chicks to calculate hatching and fledging success. Nest site selection measures included nest height and nest plant species. I was limited to measuring nests at a maximum height of 8m (but note that the majority of nest were below this limit).

Where possible, I captured the adults using mist nets or specially modified cages containing sugar-water feeders near the nests. The birds were banded with colour and

Table 5.1. Nesting data for bellbirds on Tiritiri Matangi Island from current (2012–2016) and previous (1977–2010) studies.

Year	Total number of nests	Clutch size			Brood size			Hatching success		Fledging success		Apparent nest success		Reference
		N	Mean	Median	*N*	Mean	Median	*N*	%	*N*	%	*N*	%	
1977/78	27	16	3.60 ± 0.10		16	2.56 ± NA		16	75	16	68			Anderson and Craig, 2003
2001	20		3.00 ± 0.10		18	2.40 ± 0.2		18	83	16	64	19	79	Oron, T. and Brunton, D.H. Unpublished
2005/06	54	45	2.75 ± 0.08	3										Cope, 2007
2005	33				20	1.50 ± 0.24		33	85			23	65	Cope, 2007
2006	21				16	1.40 ± 0.29		21	62			20	55	Cope, 2007
2007	20	11	2.91 ± 0.09	3	16	1.81 ± 0.31	2	11	69	10	85	14	64	Baillie, 2011
2009	32	19	2.52 ± 0.12		19	1.20 ± 0.12				13	66			Brunton, D.H. Unpublished
2010	15	15	2.44 ± 0.24		9	1.70 ± 0.24				9	71			Brunton, D.H. Unpublished

2012	52	24	2.63 ± 0.15	3	17	2.35 ± 0.23	2	17	89	17	90	39	77
2013	81	50	2.32 ± 0.10	2	47	2.21 ± 0.12	2	47	95	35	85	58	72
2014	54	26	2.23 ± 0.16	2	25	2.00 ± 0.19	2	25	91	22	80	36	58
2015	68	38	2.45 ± 0.11	3	37	2.24 ± 0.14	2	37	91	23	90	55	62
2016*	112	4	2.00 ± 0.41	2	4	2.00 ± 0.41	2	4	100	4	62.5	103	65

* Smaller sample size occurred for specific clutch and brood sizes due to most nests observed from a distance.

metal bands and as part of our banding protocol I measured weight (g) with Pesola scales, tarsus length (mm) and head-bill length (mm) with Vernier calipers, and wing length (mm) and tail length (mm) with a wing rule. I also collected data on their age (hatch year (HY), second year (SY) or after second year (ASY), determined by plumage and the presence or absence of a wing slot; Craig, 1985), body fat (categorised on a scale of 1–7; Ralph et al., 1993), moult (presence/absence) and parasites (noted if observed). I then collected a blood sample using a capillary tube following venal puncture of the brachial wing vein. All capture, handling and banding protocols were conducted under permits from the New Zealand Department of Conservation (20666-FAU, 34833-FAU, 2008/33) and the Massey University Animal Ethics Committee (12/32, 15/21). I avoided capturing around the nests when I knew the female was incubating, but for females caught with an engorged brood patch, I banded and weighed the bird but bypassed other measurements to reduce handling time.

5.3.3 NEST PARAMETERS AND NEST SUCCESS

I compiled nesting data from 2012 to 2017 into one database. This included timing of nesting, breeding stage of nest when found and ended, nest site parameters (location, nest height, nest plant species), outcome of nest (success/failure), predation of nest, clutch size, number of unhatched eggs, brood size, number of fledglings, age of fledglings if known, and parent's identification if banded, along with their body morphometrics. Weather data (daily rainfall and daily maximum and minimum temperatures) were sourced from a weather station on the island monitored by the Department of Conservation and data from the neighbouring Whangaparoa station on the mainland (approximately 5.65 km away) were used when data were not available on the island (obtained from CliFlow; https://cliflo.niwa.co.nz/). I obtained the bellbird density and population estimates for Tiri from the following sources for each year: 1977 (Anderson & Craig, 2003), 2003 (Kevin Parker, personal communication), 2010 (Roper, 2012), and 2015–2016 from the Supporters of Tiritiri Matangi Island (John Stuart, personal communication).

I investigated the relationship between various abiotic and biotic factors and clutch size, brood size and nest success. Clutch size was analysed from 2012 to 2017 within three time periods over the breeding season to test for changes within the season; the time periods were based on the start date of incubation and defined as: early = 2 September – 13 October; middle = 14 October – 24 November; late = 25 November – 5 January. Mean clutch size was calculated within each period and a Kruskal-Wallis test was used to compare within seasonal variation in clutch size. I tested for differences in clutch size, brood size and plant species used for nest sites between years with Kruskal-Wallis tests. Regression models were fitted to investigate the relationships between clutch size and population size over time in the program Curve Expert Professional (Hyams, 2018). I chose the best regression models based on the smallest standard error (SE), highest r^2 value and smallest 95% confidence interval range. I compared the plant species selected for nest sites between years with a chi-square and nest height was compared between years with a one-way analysis of variance (ANOVA). I compared fledging success, as the mean ± SE number of chicks fledged, against clutch size and brood size with a Kruskal-Wallis test. For all statistical analyses in this study, I used a significance threshold of $P = 0.05$. To assess seasonal reproductive output per female, I calculated the mean ± SE number of eggs laid and chicks fledged per female (only banded females known to have multiple clutches).

I calculated nest success, in terms of a nest successfully fledgling at least one chick, as apparent nest success (number of nests that fledged chicks divided by total number of nests) and a corrected version using daily survival rate (DSR) of nests. DSR was calculated as an adaptation of the maximum likelihood estimator for calculating nest success (Bart & Robson, 1982; Johnson, 1979), which was originally developed in the program MARK (Rotella, 2007; Rotella, Dinsmore, & Shaffer, 2004; Rotella, 2017). This method produces comparable results to other methods of calculating nest success, such as Stanley's method, as these methods take into account exposure days, which reduces bias from the observers missing nests that failed early on, unlike apparent nest success (Jehle, Yackel Adams, Savidge, & Skagen, 2004). DSR of nests (period from first egg laid to fledging) was calculated using the R package RMark (Laake, 2013). I modelled DSR with year, total monthly rainfall, maximum temperature and minimum temperature to investigate what variables may best explain DSR. Nest success from start to finish was then calculated by raising the DSR to the power of the number of days from egg laying to fledging (Rotella, 2017).

Phenotypic traits can also have an effect on reproductive output; this includes the parents' body morphometrics (Baran & Adkins-Regan, 2014; Cain & Ketterson, 2012; Langston, Freeman, Rohwer, & Gori, 1990; McDonald, Olsen, & Cockburn, 2005), and other traits such as age (Bédard & LaPointe, 1985; Forslund & Pärt, 1995; Imlay, Steiner, & Bird, 2017; Jankowiak & Wysocki, 2016; Jarvinen, 1991; Lack, 1954; Nol & James, 1987; Pärt, 1995). To investigate the effects of the parents' morphometrics on clutch size and number of fledglings, I reduced the dimensionality of four morphometric measurements (wing, tail, head-bill and tarsus length) using a principle component analysis (PCA). The PC scores were used in a Pearson correlation in R (R Core Team, 2015) with clutch size and number of fledglings. As some of the parents were measured outside of the breeding season and in moult, they were excluded from the PCA analysis. Hence to increase sample size, I further compared the raw measurements of tarsus and head-bill length (which also had the highest loadings on PC1 and PC2, except for male head-bill; Table 5.2), with clutch size and number of fledglings with ANOVA and Kruskal-Wallis tests. I then compared the parents' morphometrics (wing, tail, head-bill and tarsus length) between the sexes with Pearson correlations to investigate patterns of assortative mating. A Mann-Whitney U test compared second year (SY) first-breeders and after second year (ASY) adults for differences in start date of incubation, clutch size, brood size and number of fledged chicks. See Appendix C Table C1 for summary statistics on the morphometrics for each sex, using R package plyr (Wickham, 2011), with results from a Mann-Whitney U test to test for differences between the sexes for each morphometric using R (R Core Team, 2015).

Table 5.2. Loadings of the four morphometric measures on PC1 and PC2 from the PCA analysis for female and male bellbirds.

		PC1	PC2
Female	Wing	-0.532	0.485
	Tail	-0.574	-0.040
	Tarsus	0.207	0.868
	Head-bill	0.587	0.095
Male	Wing	-0.662	0.001
	Tail	-0.636	0.055
	Tarsus	0.118	0.976
	Head-bill	0.378	-0.212

5.4 RESULTS

5.4.1 TIMING OF BREEDING

A total of 367 nests were observed over the five breeding seasons. The earliest nest building attempts within any given season were observed on 3 September 2013 (Suppl. 5.1), although one nest was found already incubating on 2 September 2013. Where the start date of incubation was not known, it was estimated from the average incubation duration (day all eggs laid to day all eggs hatched) of 12.4 ± 0.3 days (N = 14), with a range of 11 to 14 days. Length of nestling period was 14.4 ± 0.7 days (N = 17) and ranged from nine to 21 days (excluding nests that were force-fledged). Initiation of incubation varied among years (Figure 5.2) with the earliest attempts beginning in early September in 2013–2014 and 2015–2016, which were years of abundant New Zealand flax (*Phormium tenax*) flowering (personal observation). During these early breeding years, there were peaks in the number of nests with eggs in late October/early November and these peaks tended to occur

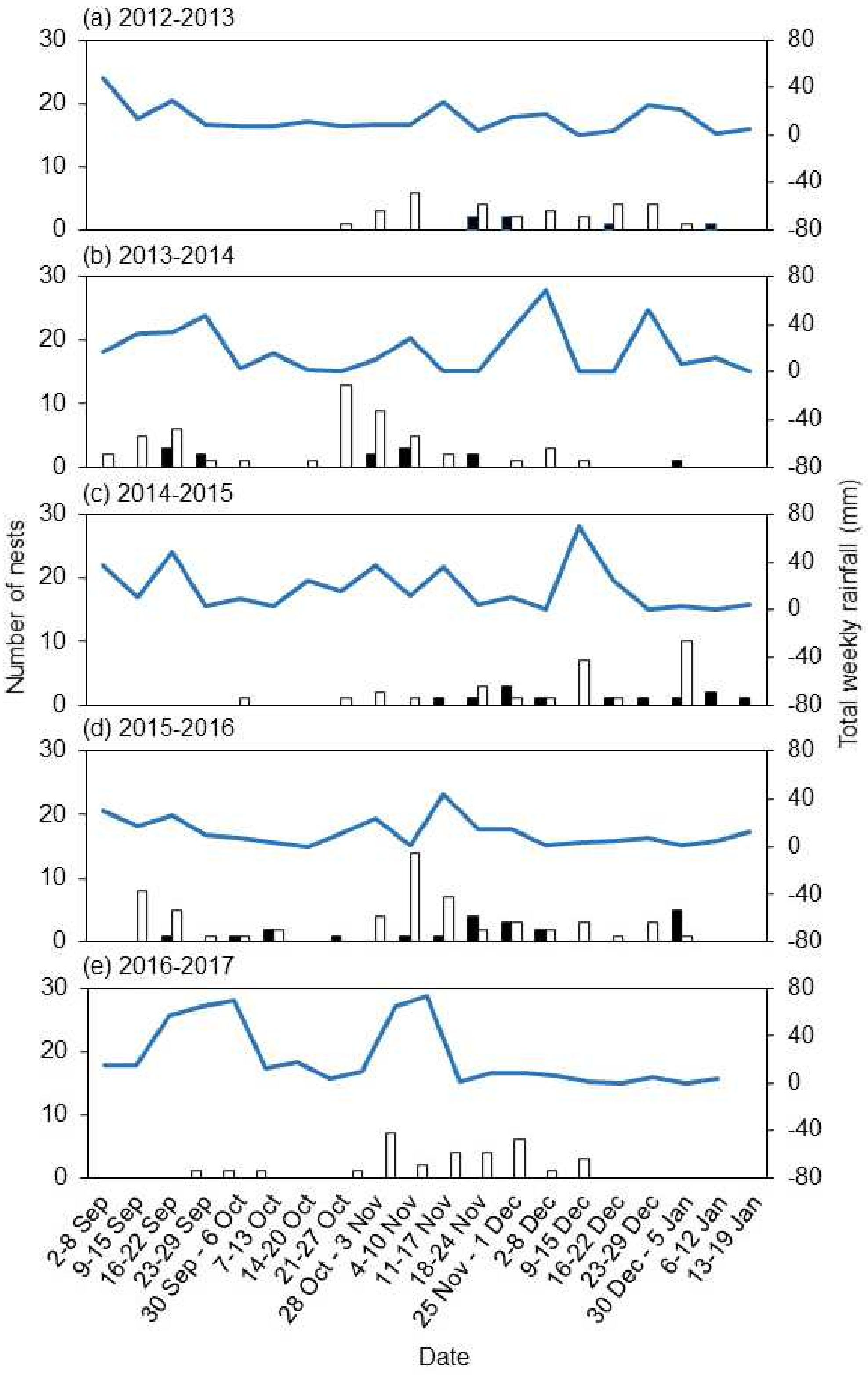


Figure 5.2. Number of nests starting incubation (unfilled bars) and found to have failed (filled bars) for each breeding year (a–e) with total weekly rainfall (solid line).

in weeks of relatively lower rainfall (Figure 5.2). Peaks in incubation start dates were less obvious in 2012–2013, which was a drought year, but the greatest number of nests starting incubation also occurred in early November. In 2014–2015, there were peaks in early December and late December to early January. In 2016–2017, there were smaller peaks in early November and early December. The highest peaks for the start of incubation coincided with weeks of little rainfall but no obvious trends for weather effects on number of failed nests were found (Figure 5.2). However, there was higher rainfall on the 1st and 2nd of January 2016 than the weather station measured (personal observation) and this coincided with the loss of all nests I was observing at the time.

5.4.2 CLUTCH SIZE, BROOD SIZE AND NUMBER OF FLEDGLINGS

From 142 nests that contained eggs and where clutch size was known, median clutch size was 2, with a mean of 2.38 ± 0.06 and range of 1 to 4 eggs. There was no significant difference in clutch size among years 2013–2017 (Kruskal Wallis test, $\chi^2 = 5.59$, df = 4, $P = 0.23$). However, data from previous studies ranging back to 1977 suggests that clutch size has declined over time (Figure 5.3; Table 5.1). Population size on the island grew exponentially over this period ($r^2 = 0.77$, SE = 422.5), whereas clutch size reduced following a Gaussian function ($r^2 = 0.91$, SE = 0.14; Figure 5.4). Clutch size did not significantly vary seasonally between early (2.19 ± 0.12), middle (2.41 ± 0.14) and late (2.46 ± 0.08) incubation start dates (Kruskal Wallis test, $\chi^2 = 3.46$, df = 2, $P = 0.18$). However, a greater number of nests tended to have larger clutch sizes during the middle and later periods of the breeding season

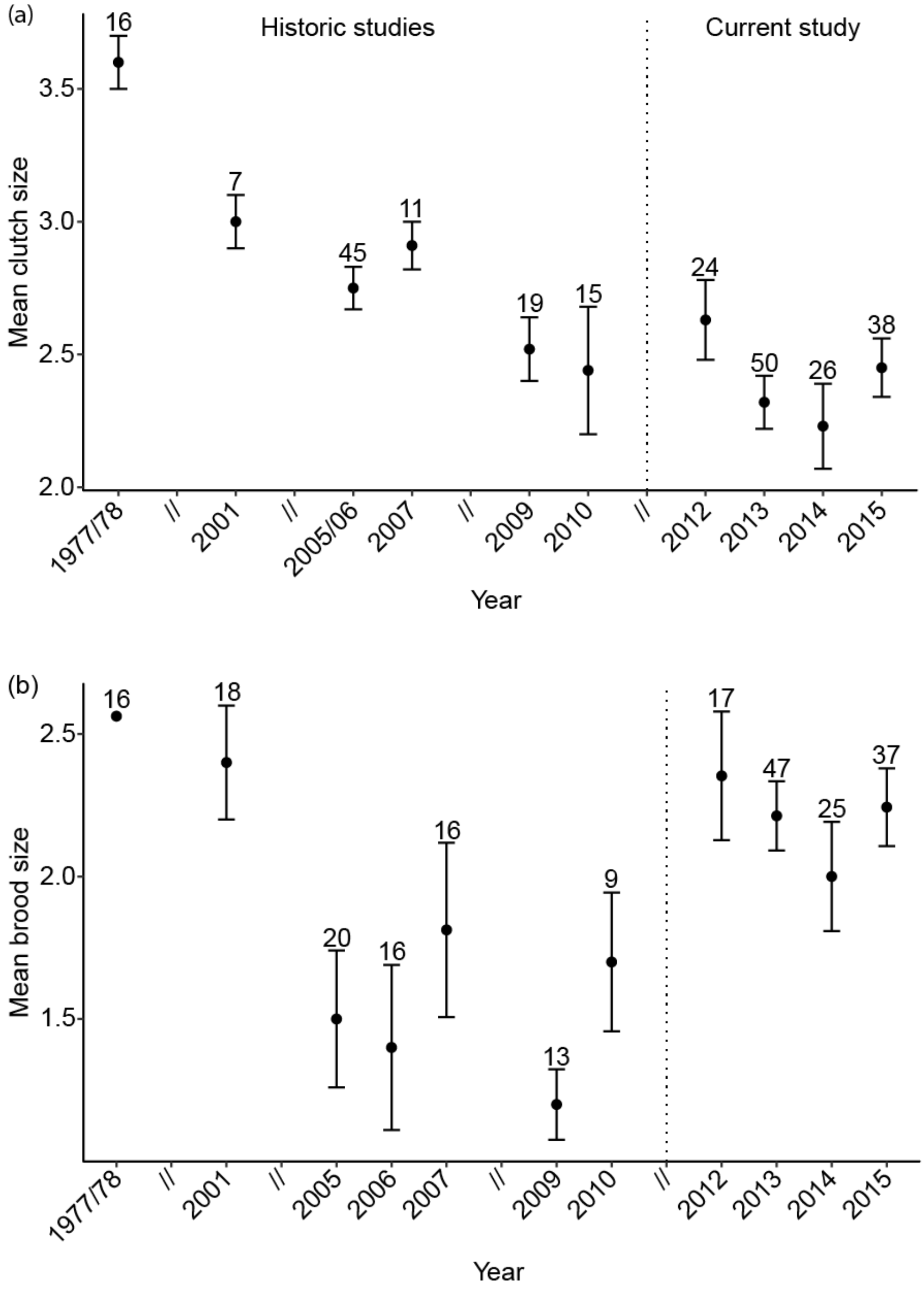


Figure 5.3. Mean clutch size ± SE (a) and mean brood size ± SE (b) with *N* values for bellbirds from current study and studies going back to 1977. See Table 5.1 for references.

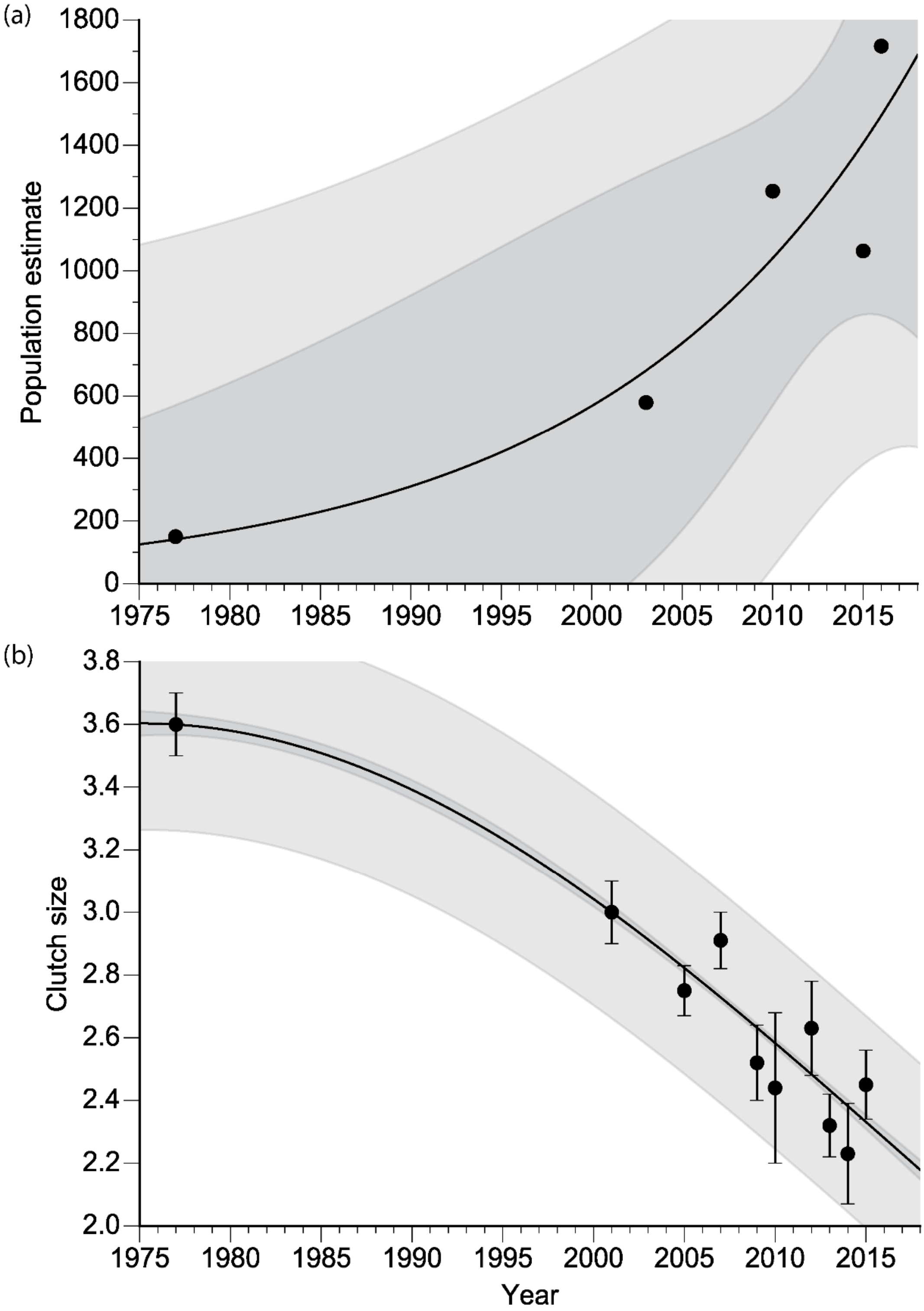


Figure 5.4. Non-linear regression models for (a) population size (exponential) and (b) clutch size (Gaussian model) over time with the 95% confidence interval band (dark grey) and prediction band (95% confidence; light grey).

(Figure 5.5). Hatching success ranged from 89–95% (excluding 2016–2017 due to small *N*) with previous studies ranging from 64–83% (Table 5.1).

For my data set, 130 nests had at least one egg hatch successfully. Median brood size was 2, with a mean of 2.19 ± 0.08 and rang of 1 to 4 chicks. Mean brood size for my data set (no significant difference among years; Kruskal Wallis test, $\chi^2 = 2.57$, df = 4, $P = 0.63$) was relatively high compared to studies from 2005 to 2010 but similar to earlier studies (Figure 5.3; Table 5.1). The mean number of fledglings was 2.10 ± 0.06 with no significant difference between years (Kruskal Wallis test, $\chi^2 = 2.42$, df = 4, $P = 0.66$). Fledging success ranged from 80–90% (excluding 2016–2017 due to small *N*) with previous studies varying from 47–92% (Table 5.1). As clutch size increased for individual females, the rate at which chicks fledged the nest significantly increased (Kruskal Wallis test, $\chi^2 = 6.56$, df = 2, $P = 0.038$) but not for brood size (Kruskal Wallis test, $\chi^2 = 2.81$, df = 2, $P = 0.25$; Figure 5.6). Across multiple broods (banded females only), the mean total number of eggs per female per season was 3.83 ± 0.53 eggs ($N = 12$) and mean total number of fledglings per female per season was 2.45 ± 0.41 ($N = 20$). For hatching success, brood size and fledging success there is the potential for an overestimate of these values for my data set; this could have arisen as for some nests I was unable to identify which nesting period they failed in and the cause of failure. Hence, I cannot determine whether the increase in these parameters is due to this bias, or a change over time in response to the changing conditions on Tiri.

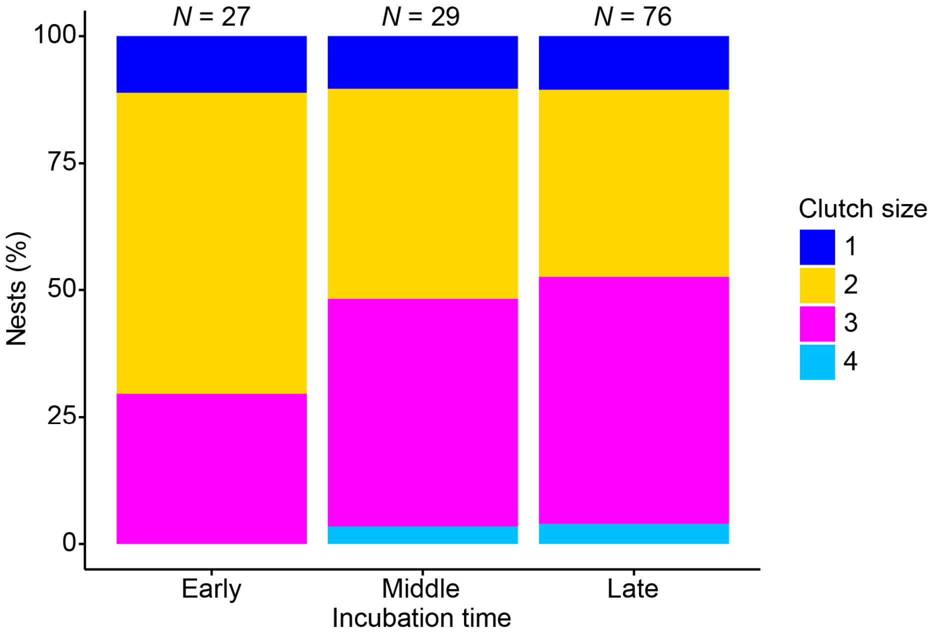


Figure 5.5. Proportion of nests of differing clutch sizes across different incubation periods throughout the breeding season (early = 2 September – 13 October; middle = 14 October – 24 November; late = 25 November – 5 January) from 2012 to 2015.

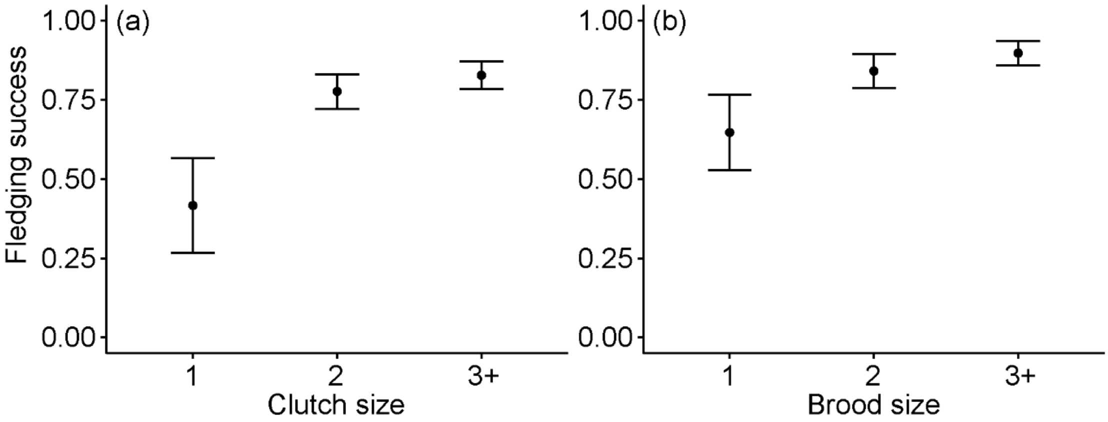


Figure 5.6. Fledging success (proportion of chicks fledging) relative to (a) clutch and (b) brood size (average of the number of chicks that fledged divided by clutch/brood size of nests).

5.4.3 NEST SITE SELECTION

Across 2012–2017, I most commonly found nests in the vines *Muehlenbeckia complexa* and *M. australis* (Table 5.3). This genus often grows on other species, and I found nests most often with this genus in trees such as *Cordyline australis*, *Pittosporum crassifolium* and *Metrosideros excelsa* (Table 5.3). In 2013–2014, nests were most often found in *Cordyline australis* (Table 5.3). I tested whether there was a difference between the proportions of each plant species used for nesting each year with a chi-square test and there was a significant difference between years ($\chi^2 = 1608.60$, $df = 76$, $P < 0.001$). Nest height ranged from 0.3 m to 8.0 m with a mean of 4.08 ± 0.13 ($N = 185$). Nest height did not significantly vary between years (ANOVA, $F(4) = 0.0023$, $P > 0.05$).

5.4.4 NEST SUCCESS

Apparent nest success was relatively high, ranging from 58–77% and was similar to previous studies which ranged from 55–79% (Table 5.1). Daily nest survival rate (DSR) was around 97% for all years (Table 5.4). With all years combined and modelled, year and weather parameters had lower rankings than constant daily survival rate (DSR ~ 1) and did not have an effect on DSR (Table 5.4). Based on average duration of laying, incubation and nestling periods, I calculated that a nest must survive 28 days to survive from the first day of eggs laid to fledging. Nest success was then calculated and varied from 40% to 54% between years and was 47% when calculated across 2012–2015 (Table 5.4). This fell within the range for previous studies from 41–53% (Table 5.4).

Table 5.3. Primary and secondary (host species for *Muehlenbeckia sp.*) plant species used for nest site selection across each breeding season.

Plant species	2012		2013		2014		2015		2016	
Primary	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Muehlenbeckia australis/complexa	22	**42.3**	16	19.8	20	**37.0**	19	**27.5**	31	**27.7**
Cordyline australis	9	17.3	34	**42.0**	10	18.5	7	10.1	24	21.4
Kunzea ericoides	5	9.6	6	7.4	1	1.9	5	7.2	8	7.1
Unknown	5	9.6	0	0.0	0	0.0	4	5.8	20	17.9
Melicytus ramiflorus	3	5.8	6	7.4	7	13.0	5	7.2	10	8.9
Metrosideros excelsa	3	5.8	3	3.7	13	24.1	15	21.7	12	10.7
Knightia excelsa	2	3.8	3	3.7	1	1.9	3	4.3	1	0.9
Phormium tenax	1	1.9	6	7.4	1	1.9	3	4.3	1	0.9
Leptospermum scoparium	0	0.0	2	2.5	0	0.0	0	0.0	0	0.0
Myrsine australis	0	0.0	1	1.2	1	1.9	3	4.3	0	0.0
Dead tree	0	0.0	1	1.2	0	0.0	2	2.9	0	0.0
Other (<2% each)	2	3.8	3	3.7	0	0	3	4.3	5	4.5
Secondary (*Muehlenbeckia sp.* host)										
Pittosporum crassifolium	8	**36.4**	1	7.1	0	0.0	2	14.3	0	0
Metrosideros excelsa	4	18.2	3	21.4	4	**36.4**	3	21.4	0	0
Cordyline australis	2	9.1	7	**50.0**	3	27.3	5	**35.7**	1	25
Kunzea ericoides	2	9.1	0	0.0	2	18.2	1	7.1	0	0
Coprosma sp.	2	9.1	0	0.0	1	9.1	0	0.0	2	**50**
Paraserianthes lophantha	2	9.1	0	0.0	0	0.0	0	0.0	0	0
Melicytus ramiflorus	1	4.5	1	7.1	2	18.2	2	14.3	0	0
Dead tree	1	4.5	1	7.1	0	0.0	1	7.1	1	25
Unknown	0	0.0	1	7.1	0	0.0	0	0.0	0	0
Vitex lucens	0	0.0	0	0.0	1	9.1	0	0.0	0	0

Note: Most commonly used species highlighted in bold for each breeding season.

Table 5.4. Daily nest survival rate (DSR) with model outcomes, and nest success for historic studies (1977–2006) and current study (2012–2015 plus all years combined).

Breeding season	*N*	DSR estimate ± SE	Nest success (%)	Method	Reference
1977–78	17	NA	44	Stanley's	Anderson and Craig, 2013
2001	19	NA	53	Stanley's	Oron, T. and Brunton, D.H. Unpublished
2005	55	NA	45	Stanley's	Cope, 2007
2006	57	NA	41	Stanley's	Cope, 2007
2012	19	0.973 ± 0.011	48	MARK	
2013	40	0.978 ± 0.005	54	MARK	
2014	28	0.973 ± 0.007	47	MARK	
2015	45	0.968 ± 0.006	40	MARK	
2012–2015	132	0.973 ± 0.003	47	MARK	
Model	*k*	AICc	ΔAICc	*wi*	Deviance
DSR ~ 1	1	332.42	0.00	0.36	330.42
DSR ~ year	2	333.58	1.16	0.20	329.58
DSR ~ minimum temperature	2	333.95	1.53	0.17	329.94
DSR ~ maximum temperature	2	334.17	1.75	0.15	330.17
DSR ~ total monthly rainfall	2	334.42	2.00	0.13	330.42

I most commonly found nests predated during the nestling stage compared to laying and incubation (Table 5.5). I could not be certain of other causes of nest failure hence other causes were grouped together (Table 5.5) but included nest hatch failure and coincidence with weather events. There was no consistent relationship across years between nest height and nest failure (Table 5.5). There were no consistent

Table 5.5. Causes of nest failure (proportion of nests) and proportion of nests that failed at different nest height.

Year	Cause of nest failure						Failed			
	Predation			Other	Unknown	*N*	Height			
	Laying	Incubation	Nestling				0-2m	3-5m	6-8m	*N*
2012	0	11.1	0	11.1	77.8	9	37.5	37.5	25	8
2013	0	6.3	12.5	25	56.25	16	0	100	0	1
2014	0	6.7	13.3	6.7	73.3	15	0	33.3	66.7	3
2015	0	0	19	33.3	47.6	21	33.3	33.3	33.3	3
2016	0	0	2.8	5.6	91.7	36	11.7	70.6	17.6	17

relationships across years between reproductive success (measured as average number of fledglings produced per nest) and laying date (Suppl. 5.2).

Comparisons of nest parameters with adult morphometric data did not show any strong correlations. Correlations of PC1 and PC2 with clutch size and number of fledglings showed only a weak positive correlation between female size (represented by PC1) and clutch size (Suppl. 5.3). Comparisons of average head-bill and tarsus length against clutch size and number of fledglings did not show any significant trends (Table 5.6) but males that had nests with three eggs tended to have longer tarsus lengths (Figure 5.7). There was no significant difference between nest parameters of second year (SY) first time breeders and adults over 2 years old (ASY) for both sexes, however ASY birds did tend to start nesting earlier, had larger clutch and brood sizes and more chicks fledged (Suppl. 5.4). There was no correlation between the sexes' morphometrics for each pair (Suppl. 5.5).

Table 5.6. Comparisons between the average head-bill and tarsus length with clutch size and number of chicks fledged for each sex (ANOVA for data following normal distribution and Kruskal-Wallis for non-parametric data).

		Head-bill			Tarsus		
		F/χ^2	df	P	F/χ^2	df	P
Female	Clutch size	1.3	2	0.28	0.09	2	0.91
	Fledglings	1.53	1	0.22	0.15	3	0.99
Male	Clutch size	1.68	3	0.64	2.22	3	0.53
	Fledglings	4.33	3	0.23	0.54	3	0.91

5.5 DISCUSSION

In this study, I examined the current and historical breeding biology of a New Zealand bellbird population, located on an ecological restoration island, to investigate changes in reproductive life-history strategies over time. During the course of this study, I found that the bellbird breeding season start and end dates were variable (although researcher nest searching began later in 2012). There was variation in peak laying dates between years, however the greatest peaks tended to occur in November, as in previous studies on bellbird breeding (Anderson & Craig, 2003; Sagar, 1985). Incubation and nestling periods were similar to that found by Anderson and Craig (2003) in 1977–78 but slightly shorter than found by Cope (2007) in 2005–06. There was little yearly variation in clutch size and brood size from 2012–2016; however, there was a long-term decline in clutch size (but not brood size) from historical records going back to 1977. Nest-site selection tended to be in select plant species, the main preferences for all years being *Muehlenbeckia australis/complexa* and *Cordyline australis*, but the proportion of nests in each type differed between years. This differs from 1977–78

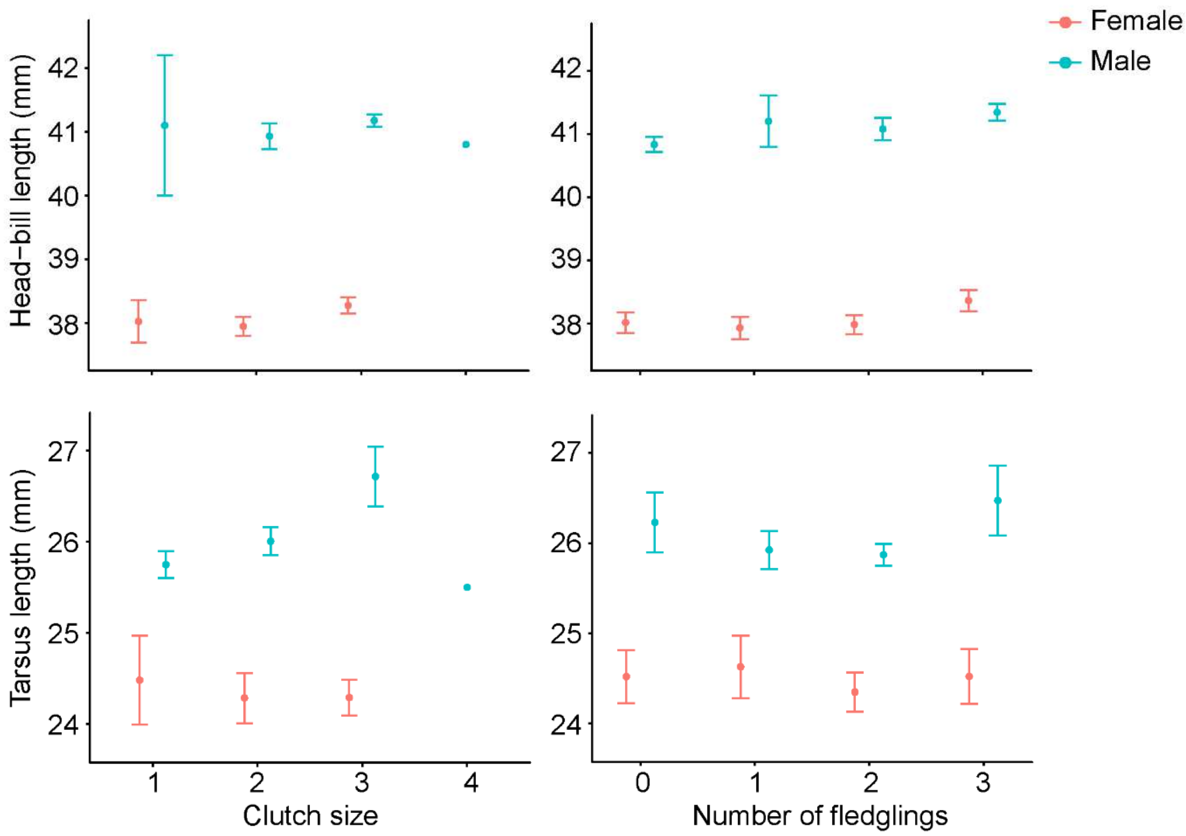


Figure 5.7. Comparison of mean ± SE for head-bill and tarsus length against clutch size and the number of fledglings for male and female bellbirds.

where tree ferns (e.g. *Cyathea medullaris*) were the most common nest site (Anderson & Craig, 2003). However, the availability of different nests sites could be a response to the regeneration of the flora on the island. This suggests that bellbirds were able to adapt to the changing conditions on Tiri but smaller clutch sizes suggest there may be reproductive trade-offs limiting their reproductive output.

I also studied previously unexplored factors, such as weather conditions (rainfall and temperature), that could influence bellbird reproductive success. Nest success was similar between years at 47% with predation and other causes, such as weather events, most commonly causing nest failure. This fell within the range seen in previous studies, but with data missing between 1978 and 2001, I cannot know if nest success initially increased during the early phase of the restoration, prior to the re-introduction of other endemic bird species, which may now be a source of competition. Daily survival rate was also similar across 2012 and 2016 at 97.3% and neither year or weather parameters had a strong effect on DSR. There were no significant relationships between the morphometrics of each parent with clutch size and number of fledglings, however, female body size (PC1 for head-bill, wing and tail) had a weak positive association with clutch size. There was no evidence of assortative mating based on adult morphometrics. Hence, none of the nest parameters measured in this study were effective at predicting reproductive success.

5.5.1 FLEXIBILITY IN BELLBIRD BREEDING ECOLOGY

The mean clutch size of bellbirds on Tiritiri Matangi Island from 2012 to 2016 was the lowest on record. The clutch size on Tiri had not only undergone a decline since 1977 (Anderson & Craig, 2003), but it was also lower than records from other offshore island and mainland sites (Massaro et al., 2008; Sagar, 1985). The bellbird population on Tiri has been on the rise since the eradication of mammalian predators/competitors (e.g. kiore, *Rattus exulans*) and re-vegetation of the island with native flora (Graham & Veitch, 2002). Since 2000, year-round supplemental sugar-water has been available to the bellbirds as part of the recovery plan for hihi, *Notiomystis cincta* (Castro, Brunton, Mason, Ebert, & Griffiths, 2003; Chauvenet et al., 2012), a nectar-feeder slightly larger than the bellbird (Castro et al., 2003; Chauvenet et al., 2012). The bellbird population has grown from about 150 individuals in 1977/78 (Anderson & Craig, 2003) to an estimated 1200–2000 individuals in 2010 (Roper, 2012). The bellbirds on Tiri have likely benefitted from the provision of sugar-water as it used intensively in the non-breeding season (Roper, 2012), which may have reduced winter mortality (as evidenced by hihi mortality reducing during the experimental provisioning of sugar-water on Tiri; Armstrong & Ewen, 2001). While the bellbird breeding density was 4.25 birds per ha in 1977/78 (Table 5.7), the total density may be higher due to other individual bellbirds observed residing in or visiting the study area (Anderson & Craig, 2003). The current average bellbird density was 7.6 birds per ha but may also not be a true reflection of the bellbird density during the breeding season. Although the habitat availability has significantly increased since 1977/78, local densities are likely to be higher in places of abundant resources and lower in areas of poorer quality (such as regenerating monoculture plantations of pohutukawa, *Metrosideros excelsa*). However, this has only been shown for the non-breeding season (Roper, 2012). Despite this, the population has grown exponentially and this large bellbird population is now likely under *K*-selection (Saether, Visser, Grøtan, & Engen, 2016b); where density-dependent mortality of juveniles and adults may be regulating population growth (Saether et al., 2016a; Saether et al., 2016b). This leads to an increase in competition for resources during the breeding season (Evans, Duncan, Blackburn, & Crick, 2005) and females reduce clutch size as a trade-off for optimal fitness (Arcese et al., 1992; Haccou & McNamara, 1998; Murphy, 2000; Pettifor et al., 2001).

While clutch size is known to decrease in density-dependent populations (Lack, 1954; Saether et al., 2016b), the current bellbird density may not be the only factor contributing to the trade-off in reduced clutch size. Aorangi Island (part of the Poor Knights island chain) has a higher population density than Tiri at 11 to 18.1 birds per ha (Sagar & Scofield, 2006) versus 7.6 birds per ha (John Stuart, personal communication; Table 5.7), respectively. Yet, even though Tiri currently has a lower population density than Aorangi Island, it has a smaller clutch size (Table 5.7; Sagar, 1985). (Although the Aorangi bellbird population is recognised as a subspecies, *Anthornis m. obscura*, recent studies suggest there is insufficient evidence to support this; Baillie, 2011.) This indicates there are other factors than high bellbird density resulting in the trade-off in clutch size over time on Tiri. Tiri has a much higher biodiversity of bird species that are likely a source of competition for food resources, particularly invertebrates, but also competition for other resources (e.g. nest sites) from the closely related tui (*Prosthemadera novaeseelandiae*), which are rare visitors to the Poor Knights islands (McCallum, 1981). The Aorangi population, however, has traded-off the ability to have multiple successful broods (Sagar, 1985). Comparing the current Tiri populations' annual number of eggs laid per female at 3.83, Tiri bellbirds potentially have higher annual reproductive output than the Aorangi bellbirds. The different reproductive trade-offs on these two islands may be explained by the duration of the breeding seasons and the number of clutches this allows them to have. Since the Tiri population has a longer breeding season and is able to successfully fledge multiple clutches, they can afford to trade-off smaller clutches while having multiple clutches. Whereas, the Aorangi population can afford to have slightly larger clutches to compensate for only being able to fledge one successful clutch during their shorter breeding season. This could allow these two populations to optimise their reproductive output while using two different life-history strategies to cope with different environments.

Other factors contributing to a decline in clutch size include territory quality and prevalence of predators. Based on the habitat heterogeneity hypothesis, at high population densities, breeding pairs are forced into lower quality habitat which reduces reproductive output in, for example, Spanish imperial eagles, *Aquila adalberti* (Ferrer & Donazar, 1996). I found second year first-time breeders were able to secure a territory and breed on Tiri; however, they do not on Aorangi Island (Sagar, 1985). Aorangi's high bellbird density could be contributing to this observation but Tiri territories may be of lower quality and unable to support larger clutch sizes due to the island having less nutrient availability, compared to the higher nutrient availability that burrowing seabirds provide in forests such as on Aorangi Island (Mulder & Keall, 2001). Higher predation rates can reduce clutch size (Evans et al., 2005; Kleindorfer, 2007) and Tiri has a wider range of predators compared to Aorangi (Table 5.7). However, two mainland bellbird populations in Kaikoura with and without mammalian predator control does not have a significant difference in clutch size (Massaro et al., 2008). Hence, predation rates on Tiri was unlikely to be a significant factor. I recommend future research on the bellbirds breeding biology on Tiri to assess whether second years will still manage to secure breeding territories as the Tiri population grows, and whether changes in predator densities will have an effect on their reproductive strategies.

Table 5.7. Comparison of bellbird breeding characteristics between studies on Aorangi Island and Tiritiri Matangi Island with data on population density and habitat.

	Aorangi Island	Tiritiri Matangi Island	
Year	1978–1982	1977–1978	2012–2016
Density (birds per ha)	11–18.1 [a]	4.25	7.6 [b]
Abundance	1921–4008[a]	150	1390 [b]
Breeding season range	Sept – Dec	Oct – Jan	Aug – Feb
Clutch size	2.87	3.6	2.38
Brood size of 1	NA	No	Yes
Success of early broods	High	Low	Lower except for when there is a change in weather events
SY birds breed	No	Yes	Yes
Predators	Australasian harrier (*Circus approximans*)	Kiore (*Rattus exulans*), Australasian harrier, morepork (*Ninox novaeseelandiae*)	Australasian harrier, morepork, common myna (*Acridotheres tristis*)
Habitat Size	66 ha	<20 ha	195 ha[e]
Dominant habitat	Pohutukawa (*Metrosideros excelsa*) forest[c]	Grassland and fernland[d]	Planted forest e.g.pohutukawa, mahoe (*Melicytus ramiflorus*), kohekohe (*Dysoxylum spectabile*), etc.[f]
Reference	Sagar, 1985	Anderson and Craig, 2003	

[a] Sagar and Scofield (2006); [b] Mean density and population estimate from 2015 and 2016 (John Stuart, personal communication);[c] Onley (1982); [d] Esler (1978); [e] Roper (2012); [f] Cameron and Davies (2013). NA = data not available. SY = second year (age at which bellbirds can first potentially breed).

Timing breeding with peak food availability for chicks is crucial for maximising reproductive success and bellbirds show flexibility in the onset of breeding depending on local conditions. Multi-brooders should ideally start laying so that the timing of nestlings hatching coincides with optimal chick-rearing conditions (Crick et al., 1993). With this strategy, they can start breeding early and over the season, their clutch size will increase before declining with successive broods (Crick et al., 1993). The bellbirds on Tiri appear to use this strategy with an extended breeding season that can start as early as late August and finish in February. However, in some years such as 2014 and 2016, the breeding season had a delayed start and similar timing as found by Anderson and Craig (2003) in 1977–78. The longest breeding seasons (2013–2014 and 2015–2016) coincided with abundant NZ flax flowering years (personal observation) and had moderate levels of rainfall. While our DSR models did not show rainfall to be an important factor for nestling survival, it may be important for other factors such as invertebrate abundance (Chamberlain et al., 1999). Heavy rainfall, however, can be detrimental during certain stages of nesting (Arlettaz et al., 2010; Öberg et al., 2015) and coincided with nest abandonment in my study and by Anderson and Craig (2003). On Aorangi Island, the bellbirds have single-broods and a relatively short breeding season of three months (Table 5.7) that coincides with pohutukawa flowering early in the season, then the fruiting of kawakawa (*Piper excelsum*) and *Coprosma spp.* later on (Sagar, 1985). Other honeyeaters such as the regent honeyeater (*Anthochaera phrygia*) also time their breeding to coincide with certain flowering species (Geering & French, 1998). Anderson and Craig (2003) suggested that the small population of bellbirds and low success of early broods on Tiri in 1977–78 (Table 5.7) resulted in the extended period of breeding, but the current larger bellbird population on Tiri does not support this. Tiri in the 1970's and Aorangi Island have a lower diversity of flowering plants, in particular they have very little NZ flax (Esler, 1978; Onley, 1982) compared to Tiri currently (Cameron & Davies, 2013), but the islands' habitats differ in other areas such as fresh water availability. The abundant NZ flax flowering years and perhaps other changes to the diversity of plant species or habitat modifications on Tiri may be an important factor in allowing bellbirds to extend their timing of breeding and have multiple broods to increase their annual productivity. This shows bellbirds have the flexibility to adapt to local conditions.

5.5.2 BELLBIRD NEST SUCCESS

Various factors can affect nest success, but bellbirds appear to have relatively consistent nest success over time. When kiore were present on Tiri, nest success was 44% (Table 5.4), but since the eradication of kiore, there has not been a marked increase in nest success for bellbirds or other species on the island, such as North Island robins (Anderson & Craig, 2003; Armstrong et al., 2000). This suggests kiore were not a major threat to bellbird nest success on Tiri, in terms of a nest predator or competitor for food resources during the breeding season. In all studies of bellbird breeding biology on Tiri, nest success has remained below 60% (Table 5.4). The Australasian harrier (*Circus approximans*) and morepork (*Ninox novaeseelandiae*) were the most common predators over the time of this study, but I was only able to account for up to 20% of nest failures due to predation. Anderson and Craig (2003) suggested that the marginal habitat on Tiri results in greater exposure of nests to storm events. I also found nests tended to fail after storm events but cannot separate desertion from other causes. Perhaps the regenerating plant growth that covers 64% of the island (Cameron & Davies, 2013) is still more vulnerable to storm damage (particularly on the exterior of the forest edges) than older forest growth.

I was unable to detect any strong relationships between the body morphometrics or age of parents and reproductive success. Body size and age can affect various aspects of reproductive success. It has been suggested that selection should favour smaller female size as smaller females have lower energetic requirements and could hence breed earlier (Downhower, 1976), but in some cases, such as red-winged blackbirds (*Agelaius phoeniceus*), larger females lay earlier and have higher nest success (Langston et al., 1990). However, whether female size has a causal effect on reproductive success is debateable as size can correlate with other traits such as aggressiveness (Cain & Ketterson, 2012; Langston et al., 1990). Female bellbirds only showed a weak positive trend between body size and clutch size. Clutch size can indicate female condition and hence those that can raise larger clutches have higher fitness (Pettifor et al., 2001). However, this weak trend for female bellbirds suggests other factors have more influence on reproductive success, as has been found for the positive relationship between female bellbird song rate and fledging success (Brunton et al., 2016; Appendix A). For male birds, there are also relationships between body size and aspects of reproductive success, for example, barn swallow (*Hirundo rustica*) males with longer tails arrive earlier at breeding sites and have better success at acquiring a mate (Møller, 1990). I only found a slight positive trend between male bellbird tarsus length and clutch size. This could perhaps be due to high levels of extra-pair paternity (Cope, 2007), hence clutch size and fledgling success per nest may not reflect a male's true reproductive output. Age does not have a consistent effect on breeding success but it has been shown for several species that young birds tend to breed later (Bédard & LaPointe, 1985; Conrad & Robertson, 1993; Jankowiak & Wysocki, 2016; Jarvinen, 1991). While older bellbirds in my study tended to have higher reproductive output, the relationship was not strong. More research is needed, including annual reproductive success, extra-pair paternity and larger sample sizes, as success with age could be caused by differences in either competence (Nol & James, 1987; Pärt, 1995) or experience (Jankowiak & Wysocki, 2016).

Whilst I did not find strong evidence for factors that could influence nest success, I observed a changed in parental investment over time. Anderson and Craig (2003) found that bellbirds abandon nests when there is only one chick remaining and never raise single-brood nests. This is likely a result of gaining better reproductive investment by re-nesting than by raising a single chick (Anderson & Craig, 2003). However, I have observed many nests fledging single chicks. Despite finding that fledging success increased with larger clutch sizes in this study, there was not a significant difference between fledging success in brood sizes of one or more. This suggests that conditions have changed in favour of raising one chick over re-nesting, as the costs of egg laying and incubation may be more expensive than once thought, compared to raising chicks to independence (Monaghan & Nager, 1997). I speculate that this may be due to greater competition for resources, particularly invertebrates, which makes producing eggs for re-nesting more costly than raising a single chick.

The increasing number of bird species re-introduced to the island (Figure 5.1) could potentially be increasing inter-specific competition for invertebrates during the breeding season.

5.5.3 IMPLICATIONS FOR SPECIES' MANAGEMENT

Bellbirds show flexibility in their breeding biology, a key component to their life history that influences population viability. Bellbird success on Tiri shows how important restoring islands can be in re-establishing populations to the higher densities seen on islands that remain relatively untouched by human settlement. Similarly, high bellbird densities have been achieved in 'mainland islands' with predator proof fences and where introduced predators are reduced to very low levels, e.g. Tawharanui Regional Park and the Maungatautari Ecological Island Reserve. However, density may not be completely indicative of reproductive success (Vickery, Hunter, & Wells, 1992) as there is relatively high genetic connectivity between bellbird populations (Baillie, 2011) and some sites could potentially act as sink populations. However, species such as the hihi, for example, have not yet reached a self-sustaining population on Tiri, despite having similar life-history traits. Hihi do differ in their reproductive strategies, being cavity nesters (Castro & Robertson, 1997), and rely on artificial nest boxes on Tiri (Armstrong & Ewen, 2013). This suggests that the hihis' life history is less adaptive to early-regenerating habitat, while bellbirds on the other hand perhaps show more plastic life-history traits that allow their success in adapting to regenerating habitat. Monitoring reproductive success is hence a valuable tool in managing species' survival and knowing how flexible their life-history traits are will help identify at what stage of an ecological restoration a population will have the best chance of becoming self-sustaining.

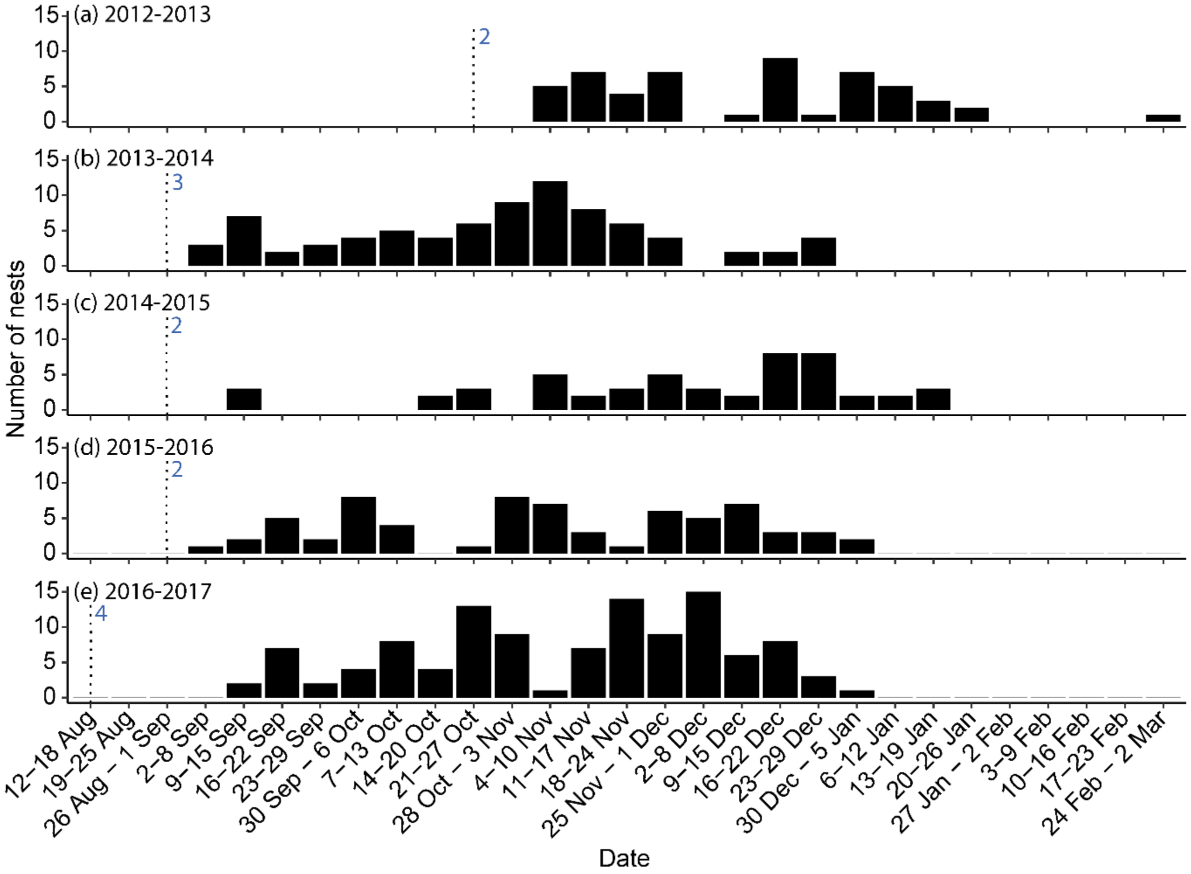
5.5.4 CONCLUSION

The life-history strategies utilised by New Zealand bellbirds show great flexibility that has allowed their population to grow successfully on Tiritiri Matangi Island. They have become self-sustaining, unlike the hihi, which has a comparable life history apart from their reproductive strategies (Castro et al., 2003). Tiritiri Matangi Island has significantly transformed since the first study on bellbird breeding biology in 1977–78. Bellbird breeding biology has responded in ways predicted by K-selection. My major findings are that clutch size has declined over time, as the population is likely becoming density-dependent. The high bellbird density however is not the only contributor, with competition also likely occurring with tui and re-introduced bird species. Such low clutch sizes may also be due to reduced winter-mortality, perhaps from supplementary feeding, causing greater competition for resources during the breeding season, and potentially leading to the occupation of lower quality territories. This current Tiri population has been able to extend its breeding season, possibly in response to the increased diversity of plant species, particularly NZ flax, as its flowering coincided well with the longest breeding seasons. Nest success has remained relatively stable with nest failure still due to avian predation and storm damage, which is possibly high due to the marginal habitat of the restoring vegetation. I observed a change over time in parental investment as bellbirds are now placing more energy in raising single brood clutches rather than abandoning and re-nesting. The size of the parents only weakly predicted the number of eggs laid, suggesting that nesting behaviour may have a larger influence on predicting reproductive success. I have demonstrated the flexible nature of bellbird breeding biology on a restoration island over time. My study also provides baseline information needed to determine the success of conservation management of bellbirds on islands and at mainland sites. This was the first study to show that the bellbirds' reproductive biology involves significant reproductive life-history trade-offs that allows them to adapt to their environment whilst optimising their reproductive success.

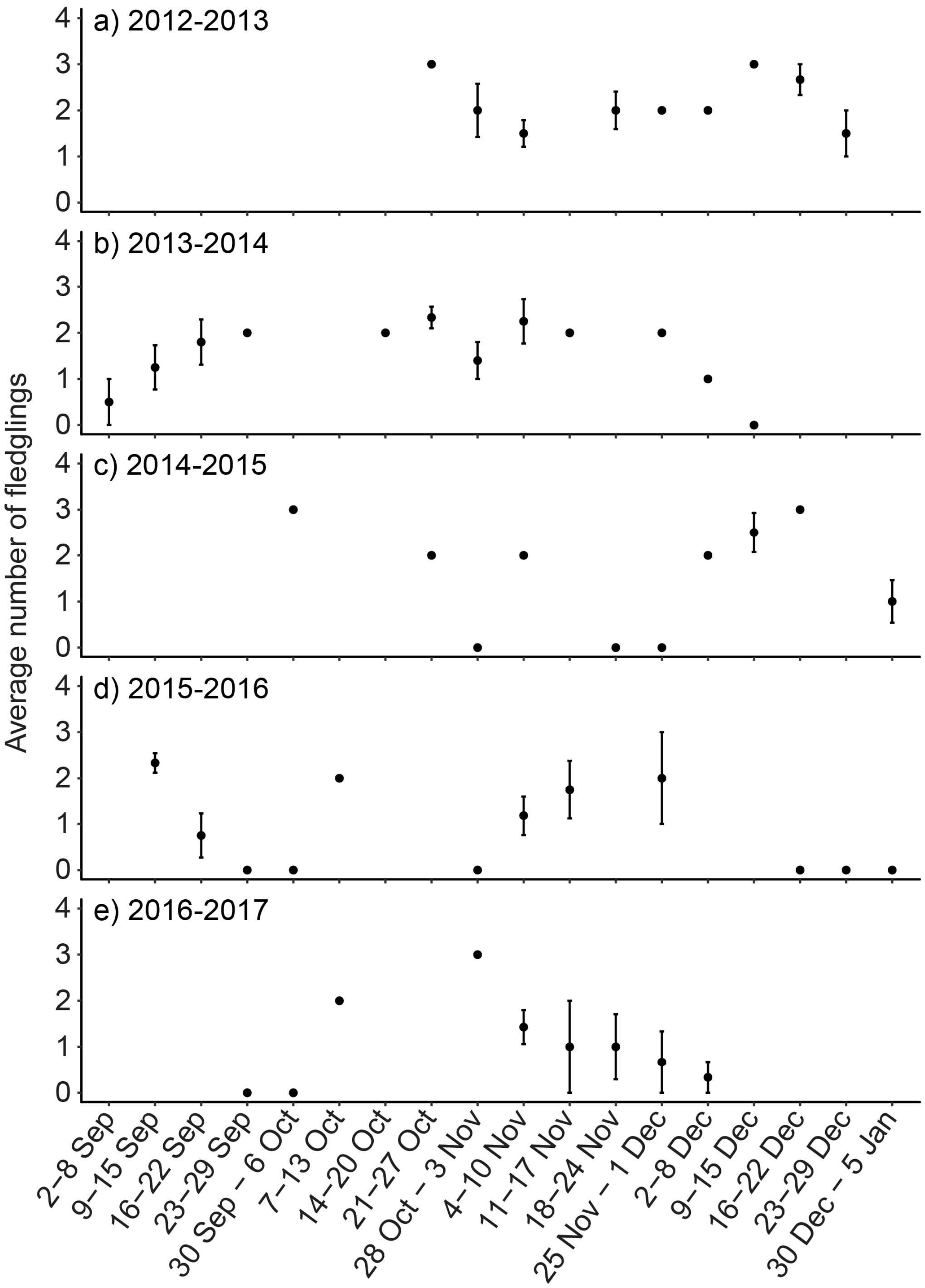
5.6 AUTHOR CONTRIBUTIONS

Michelle M. Roper contributed to the design of the study and development of the methodology, conducted the fieldwork, managed field assistants, performed statistical analyses and wrote the manuscript. Aaron M. T. Harmer assisted with the analyses and writing the manuscript. Dianne H. Brunton designed the study, developed methodology, assisted with fieldwork, assisted with analyses and contributed to the writing of the manuscript.

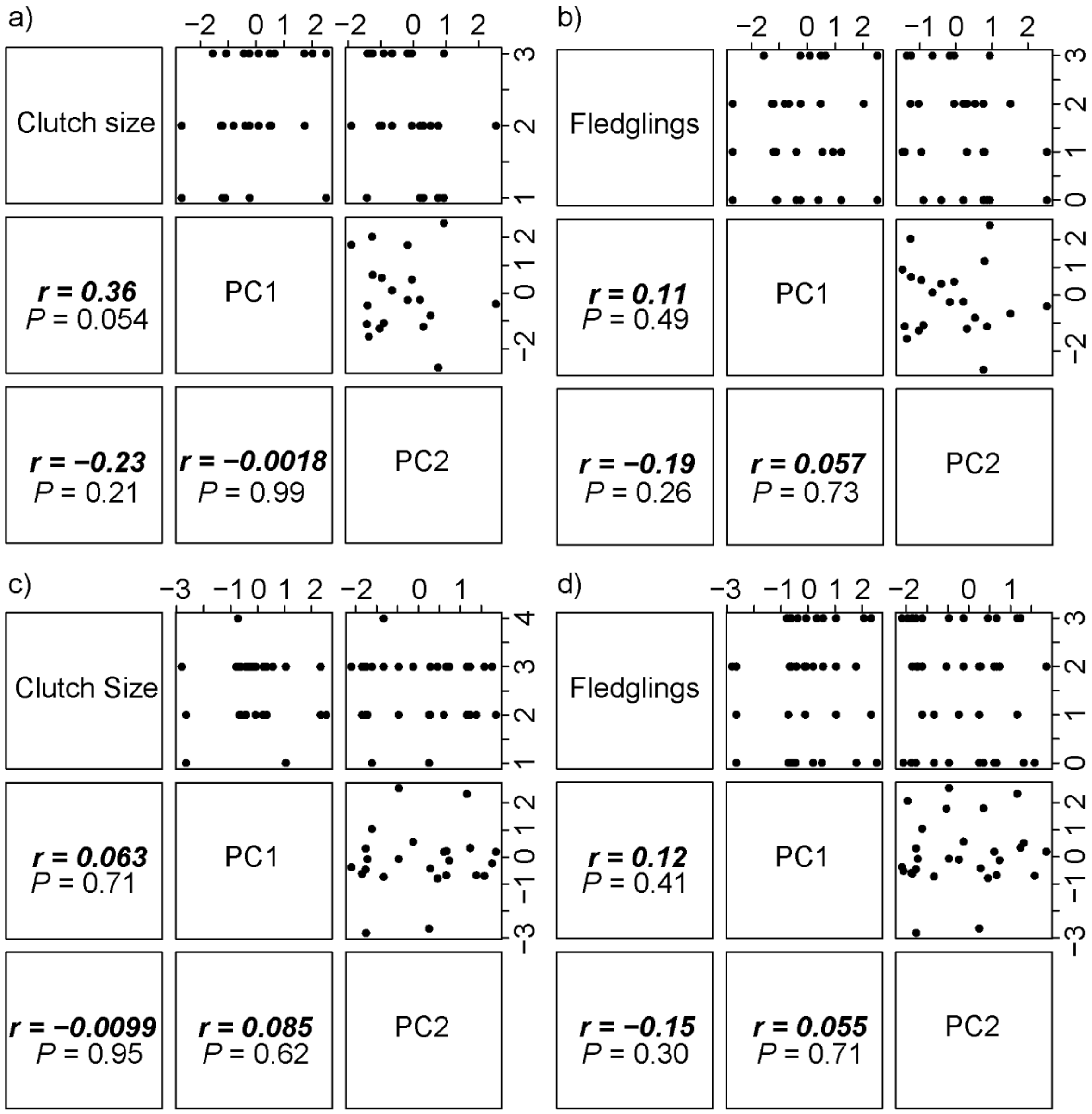
5.7 SUPPLEMENTARY MATERIAL



Suppl. 5.1. Number of new nests found each week in each breeding year (a–e), with the week nest searching began (dotted line) and maximum number of observers conducting nest searchers (next to dotted line).



Suppl. 5.2. Relationship between laying date and reproductive success (average number of fledglings per nest) for each breeding season studied (a–e).



Suppl. 5.3. Correlation matrix for PCA analysis of morphological parameters, clutch size and number of fledglings for female (a, b) and male (c, d) bellbirds. Table 5.2 indicates the loadings of the four morphometric measures on PC1 and PC2.

Suppl. 5.4. Comparison of reproductive performance between second year (SY; first breeding season) and after second year (ASY) for female and male bellbirds with a Mann-Whitney U test.

		SY		ASY		*U*	*P*
		N	Mean ± SE	*N*	Mean ± SE		
Female	Start of incubation (weeks)*	10	11.70 ± 1.13	64	10.03 ± 0.10	260.5	0.35
	Clutch size	7	2.00 ± 0.22	53	2.38 ± 0.10	245.5	0.13
	Brood size	7	2.00 ± 0.22	51	2.12 ± 0.13	201.5	0.57
	Number fledged	10	1.00 ± 0.37	73	1.34 ± 0.13	427.5	0.37
Male	Start of incubation (weeks)*	8	11.25 ± 1.98	67	10.32 ± 0.53	247.5	0.73
	Clutch size	7	2.00 ± 0.31	57	2.49 ± 0.09	268	0.11
	Brood size	7	2.00 ± 0.31	57	2.23 ± 0.12	231.5	0.41
	Number fledged	4	1.00 ± 0.40	81	1.62 ± 0.12	215	0.23

*Number of weeks from first nest found incubating.

Suppl. 5.5. Correlation between male and female morphometrics for pairs where both parents' measurements were known (*N* = 34).

Measurement	Pearson's r-value	*P*
Wing	-0.088	0.62
Tail	0.12	0.51
Head-bill	0.28	0.11
Tarsus	-0.21	0.23

6 Conclusions and future directions

A female New Zealand bellbird (photo: Michelle Roper).

6.1 OVERVIEW

As female song is now recognised as widely spread throughout the songbird lineage and is indeed the ancestral phenotype of songbirds (Odom et al., 2014), it is timely that more research is carried out on all aspects of female song. To date, song development, song repertoire size and vocal production research has concentrated on male songbirds. This has led to our current understanding of, and the development of theory surrounding, the function of song i.e. song is characterised as driven by female mate choice and male-male interactions (Catchpole & Slater, 2008). Here, I synthesise my new findings on female song production and sexual variation in the repertoire size of a wild songbird, the New Zealand bellbird (*Anthornis melanura*; hereafter bellbird). I also speculate how variation in the song repertoire of male and female bellbirds may be linked to sexual dimorphism in the structure of the vocal organ, the syrinx. My study population was unique in that it has persisted on an island that has undergone ecological restoration from a previously highly degraded ecosystem. This has provided the opportunity to assess how trade-offs in bellbird reproductive life-history traits may have facilitated adaptation to the changing environment on this island over the last four decades.

6.2 FEMALE SONG DEVELOPMENT

Our knowledge on the motor phases of song development is founded on research conducted on male songbirds and principally in laboratory studies (Marler, 1970b; Marler et al., 1972; Nottebohm, 1969). Even for male songbirds, there is limited research conducted in the wild and most focuses on tutor choice (Kroodsma, 1974; Liu & Kroodsma, 2006). In this thesis (Chapter 2; Appendix B), I have presented for the first time, comparable results on the motor phases of song development between the sexes of a wild songbird. I showed that female and male bellbirds developed their song through the different motor phases within similar timeframes. This is significant as previous studies on female song have been limited to only identifying the onset of some of the motor phases (Brown et al., 1988; Lobato et al., 2015; Wickler & Sonnenschein, 1989) and tutor choice (Baptista & Petrinovich, 1986; Evans & Kleindorfer, 2016; Price, 1998). Undertaking this study in the wild was also key for obtaining a comparable song development timeframe between the sexes; as this timeframe differs between captive and wild songbirds, for example, in brown-headed cowbirds, *Molothrus ater* (O'Loghlen & Rothstein, 2010).

I further revealed how song structure and syllable diversity differ between the sexes, as this research topic is similarly biased towards male song (Brumm & Hultsch, 2001; DeWolfe et al., 1989; Glaze & Troyer, 2013). Only recently have researchers studied differences in blue-capped cordon-bleus, *Uraeginthus cyanocephalus*, indicating that both sexes have similarities in the early song structure but then diverge in terms of song duration and repertoire size (Lobato et al., 2015). At the song structure level, I found that the bellbird sexes were most similar during the juvenile learning-phases of song development (juveniles singing primarily subsong and plastic song), then the sexes song diverged in both structural and spectral parameters. This likely reflects the adult sexes differing singing behaviour (Brunton & Li, 2006) and the large sexual variation in syllable repertoire (Chapter 3). Like the blue-capped cordon-bleus, both bellbird sexes show a similar reduction in syllable diversity with much tighter groupings of syllable types in adult individuals and adults sang less unique syllable types per 3 s of song. Lobato et al. (2015) suggest that the sexes may have differing song developmental pathways; blue-capped cordon-bleu sexes vary in the degree of selective attrition that occurs by adulthood and the size of the song control regions in the brain differ. The fundamental frequency of syllables was consistently different between the sexes of all age groups and reduced across both sexes from learning-phase to adulthood. Morphological limitations (Ryan & Brenowitz, 1985) and environmental factors (Ryan & Brenowitz, 1985) are likely causes for this difference. Hence, while both bellbird sexes refine their song between the learning-phases and adulthood, aspects of the songs' structure and spectral parameters change between the learning-phase and adulthood as each sex develops their sex-specific songs. Further research needs to examine whether this may result from sexual dimorphism in the developmental pathways within the song control regions of the brain, and what drivers have given rise to such differences between the sexes.

For the first time in a wild songbird, to my knowledge, I have observed that syllables become more consistent from the early stages of the motor phases to adulthood. This is significant, as an increase in syllable consistency has not been observed before in female songbirds. Only in males has there been reports on syllable consistency changing with age (Botero et al., 2009; Brumm & Hultsch, 2001; de Kort et al., 2009; DeWolfe et al., 1989). Such an increase in syllable consistency in male songbirds is associated with an increase in reproductive success, hence syllable consistency may be a signal used in sexual selection (Botero et al., 2009). Female bellbird syllables may also become more consistent over time owing to their song functioning strongly in intra-sexual interactions (Brunton et al., 2008a) and act as a predictor of female reproductive success (Brunton et al., 2016; Appendix A). The bellbird sexes had syllables that varied in their consistency, both within the age groups and across age groups. The most complex syllables (i.e. composed of two elements and longer in duration) were the least consistently produced in the youngest learning-phase age group. This suggests that female bellbirds are also capable of developing complex syllables which likely require both sides of the syrinx (Zollinger et al., 2008), hence more coordination between components of the vocal tract (Nelson et al., 2005; Pytte & Suthers, 2000; Suthers et al., 1999; Veit et al., 2011). Individual learning abilities (Nowicki et al., 2002) and social interactions with tutors (Margoliash et al., 1994; Ritschard & Brumm, 2011) are also able to affect song development; these are aspects beyond the scope of this study but worth further investigation.

I propose several future directions to continue our understanding of female song learning. Studying songbirds in the field posed challenges due to the difficulties of following individuals within a large population and unpredictable weather conditions for recording. Furthermore, local movements and juvenile mortality resulted in the low probability of relocating individuals throughout their first year. Hence my study took a cross-sectional approach and I minimised the potential bias from, for example, phenotypic dependent survival by only including in my analyses individuals that survived to their first breeding season. Given the differences that longitudinal and cross-section studies can detect (Forstmeier et al., 2006; Gil et al., 2001), I would recommend future studies on female song learning in the wild to be longitudinal and use additional technology, such as, RFID (radio-frequency identification) pit tags and/or radio tracking to track and locate individuals. New technology in the development of small backpack microphones (Gill et al., 2016) that could be adapted for use in the field could also advance research by allowing us to continuously record the singing behaviour of individuals and potentially record vocal interactions they have in social interactions, for example, with tutors. Between species, song tutors vary from a chicks mother and social father (Böhner, 1983; Evans & Kleindorfer, 2016; Greig et al., 2012) to their territorial neighbours after dispersing (Beecher et al., 1994; Liu & Kroodsma, 2006; Nordby et al., 2001; Payne, 1981). Research on who the tutors are in bellbirds, however, would allow us to assess why and how bellbirds learn their sex-specific syllables, as a preliminary study has found that juvenile bellbirds share more syllables of the opposite sex's repertoire than in adults (Brunton et al, unpublished).

6.3 SEXUAL AND YEARLY VARIATION IN FEMALE SONG REPERTOIRES

While sexual dimorphism is already known to occur in the song of bellbirds (Brunton & Li, 2006), I discovered considerably more variation between male and female song than previously thought (Chapter 3). Earlier female song research has mainly revealed differences in species where females sing similar song repertoires to males, for example European starlings (Sturnus vulgaris; Pavlova et al., 2005) and streak-backed orioles (Icterus pustulatus; Hall et al., 2010). Female bellbirds had a smaller syllable repertoire size than males, but with considerable individual variation. Similar differences occur in European starlings, and like European starling females (Pavlova et al., 2005), there were individual female bellbirds that had more 'male-like' syllable family types in their repertoire. Pavlova and colleagues (2005) suggest this may arise from female European starlings singing these 'male-like' phrase types (i.e. a sequence of syllables) in differing social interactions or population densities. However, considering my novel finding that the bellbird sexes share few syllable types, and that bellbirds have differing inter- and intra-sexual social rankings (Craig & Douglas, 1986; Roper, 2012), perhaps there are costs and/or benefits to individuals based on the types of syllables sung that are shared with the opposite sex. Certain syllable types do reflect functions in male songbirds, such as 'sexy syllables' (Vallet et al., 1998; Vallet & Kreutzer, 1995), and some species produce different song types for specific inter- or intra-sexual interactions (Byers, 1995, 1996a, 1996b). Hence, further research is needed to tease apart whether differences in male and female song sharing is due to differences in selection pressures acting on the sexes song, and whether female variation in singing more 'male-like' syllables is a result of differing social environments and pressures.

A new finding in my thesis was that female bellbird syllable repertoires can change over time. Very few studies have investigated this for female song, and have been limited to changes with age (Langmore et al., 1996; Pavlova et al., 2010) and between populations, i.e. dialects as a result of cultural evolution and acoustic adaptation (Graham, Heath, Walter, Mark, & Mennill, 2018). At the population level, the syllable repertoire of both bellbird sexes changed at a similar rate. However, similarity between years did not depend on the number of years apart, suggesting syllable types may change in relative abundance rather than being completely deleted from the population repertoire. A similar patterns occurs in Darwin's medium ground finches (*Geospiza fortis*), where males prefer rare syllable types and this hence alters their relative abundance from year to year (Gibbs, 1990). The males that sing rare syllables have higher reproductive success (Gibbs, 1990) and my results leads me to speculate that different male and female syllable types may have different functions. Female alpine accentors change their repertoire, mainly between their first and second year, and their songs function in the attraction of males (Langmore et al., 1996). Therefore, with male and female bellbird repertoires changing at a similar rate, perhaps this suggests that both sexes are changing their syllable repertoire for a shared function, such as, defending resources and territories from competitors (Brunton et al., 2008a; Brunton et al., 2008b; Craig & Douglas, 1984). Female song in bellbirds is important for defending a breeding territory against neighbouring females (Brunton et al., 2008a) and females that sing more complex syllables is linked to higher fledging success (Brunton et al., 2016; Appendix A). While this result is not observed for male bellbirds, this may be due to incomplete quantification of male reproductive success given they have high levels of extra-pair paternity (Brunton et al., 2016; Appendix A). My finding that syllable types also differ in consistency (Chapter2; Appendix B) further suggests that syllables may be used for different functions, with the most consistent syllables functioning as a signal for reproductive quality, as in tropical mockingbirds, *Mimus gilvus* (Botero et al., 2009). I suggest playback experiments be utilised to further test the function of different syllable repertoires and assess whether singing rare, common or more consistent syllable types result in gains in reproductive success, while taking into account the age of the individuals and extra-pair paternity.

For my study on bellbird song repertoires (Chapter 3), I faced similar limitations to the song development study (Chapter 2; Appendix B) and future directions should aim to use longer-term datasets and playback experiments. Ideally, the longitudinal component of this study would have played a more significant role in the song repertoire study (Chapter 3), particularly for assessing year-to-year individual variation in syllable repertoires and to find out whether bellbirds are open- or closed-ended learners. However, due to weather constraints, local movements and mortality of birds and following a large number of breeding pairs (for Chapters 2 and 4), this made it difficult to record the full repertoire of numerous colour-banded individuals over consecutive years. While cross-sectional studies can be less informative than longitudinal studies for assessing changes in repertoire over time (Gil et al., 2001), there were similarities in my population and individual level results which lend support to the cross-sectional results. I suggest that future studies on bellbird song repertoire focus on obtaining the full syllable repertoire of individuals within a single recording year. I also suggest additional information on these individuals is collected, such as their dominance ranking and reproductive success (taking into account extra-pair paternity) to find any correlation between certain syllables types with these factors and why certain females sing more ‘male-like’ syllable types. A playback experiment involving assessing individuals’ responses to songs with common and rare syllables artificially swapped, and control song types, will allow us to test whether there are any costs or benefits to singing certain syllable types. Additional analyses comparing the syllable types present in different regions of Tiritiri Matangi Island (hereafter Tiri) will allow us to test whether the large variation in syllables types is due to individual and/or microgeographic variation.

6.4 SEXUAL DIMORPHISM IN THE SYRINX

Sexual dimorphism of the syrinx has been a relatively under-studied area of research. The syrinx structure is known to vary between species of songbirds (Ames, 1971), but we still know very little about how the separate structures of the syrinx contribute to the production of the unique songs each species produces. I investigated the three enlarged bronchial half rings of the syrinx as these are major attachment points for the syringeal muscles and labia (Düring et al., 2013). These enlarged half rings have a significant role in sound production in songbirds (Suthers & Zollinger, 2006). As for the previous studies on sexual dimorphism in bronchial half ring size (Prince et al., 2011; Riede et al., 2010), I found male bellbirds had considerably larger half rings than females, particularly for the first (B1) and second (B2) half rings on both sides of the syrinx. With both bellbird sexes singing complex song, although smaller repertoire sizes than European starlings (Eens, 1997; Jensen et al., 2007; Pavlova et al., 2005; Prince et al., 2011), I predicted that bellbirds would show a similar level of sexual dimorphism in half ring size if there was a link between syrinx size and repertoire size. However, I found that most of the male bellbird half rings were considerably larger than those of the female, even after adjusting for sexual dimorphism in body size. The proportion of sexual dimorphism in some half rings (e.g. B1) was more comparable to zebra finches (*Taeniopygia guttata*), where females do not sing (Riede et al., 2010), however, the sexual dimorphism for half ring B2 was considerably larger in male bellbirds than either zebra finches or

European starlings (Prince et al., 2011; Riede et al., 2010). The third bronchial half ring (B3) varied in size between each side of the syrinx, with the female's being relatively larger compared to the male on the left side but not the right. Half ring B3 was also relatively the largest half ring in bellbirds, compared to zebra finches and European starlings where it is the smallest, at least in terms of cross-sectional area (Prince et al., 2011; Riede et al., 2010). Female bellbirds have a unique set of song syllables compared to males, but the degree of sexual dimorphism in the syrinx does not completely explain the difference in repertoire size. However, the sexes do share syllable family types (Chapter 2; Appendix B); hence, further research is needed to assess whether their ability to share syllables at the family level is due to their unique syrinx structure, such as a larger B3, compared to previously studied species.

The syrinx is involved in the production of various spectral aspects of song, particularly fundamental frequency (Goller & Riede, 2013; Suthers et al., 1999; Suthers & Zollinger, 2006). However, body size is a common measure used to study the variation in fundamental frequencies between species; body size generally has a negative correlation with song frequencies (Derryberry et al., 2018; Mason & Burns, 2015), but there is contrasting results for maximum frequencies (Derryberry et al., 2018; Liu et al., 2017). For the songbirds in my comparisons of body mass and tarsus length with fundamental frequency bandwidth, I only found a weak positive relationship. The larger half ring size in males is thought to allow males to produce higher fundamental frequencies (Riede et al., 2010) but it contradicts research showing in broader family groups that body size limits maximum frequency that birds can produce (Derryberry et al., 2018; Mason & Burns, 2015). Male bellbirds were an outlier, producing a wider frequency bandwidth for their average size. Considering most of the male bellbird half rings were considerably larger than those of females, even when compared to zebra finches and European starlings, could their larger half rings relative to body size play a role in their wider frequency bandwidth? I suggest further comparisons are needed to explore whether the relative size of the half rings to body size is allowing males to sing a wider range of frequencies.

I was only able to collect naturally deceased specimens and more research is needed to further explore these trends. Only one adult specimen from each bellbird sex was obtained in time for this study and I hence could not account for any individual variation in the size of the half rings. While the syrinx structure is fully developed within the embryo (Ames, 1971) and I had collected a few hatch year specimens, these were not included in this study as the age of these birds was not known. Signs that the syrinx may not be fully developed, at least in terms of size in hatch year specimens, came from Chapter 2 (Appendix B), where I found hatch year birds sang higher fundamental frequencies than birds over 2 years old. Hence, further research on the sexual dimorphism in bellbird syrinxes requires more specimens of each sex, and to utilise the hatch year specimens to observe for any developmental differences between the sexes. More comparable measurements are needed between the species studied, i.e. volume of half rings for the zebra finches and European starlings, and further analyses of their song structure, such as frequency modulation and duration of syllables, is needed to compare the song structure of each species and sex. This will allow researchers to tease apart what aspects of song that half ring size may influence. Additional species added to this research, such as more closely related species like tui (*Prosthemadera novaeseelandiae*), could also allow for further corroboration of these trends. Continued research should also include other syrinx structures such as muscle size, labia size and size of the half rings relative to the body of the individual specimen.

6.5 THE LIFE HISTORY OF A FEMALE SONGBIRD

After hatching, female bellbirds can begin developing their song by 3 weeks of age while still on their natal territory (Chapter 2; Appendix B). The timing of their song development occurs at a similar rate as males, but their song diverges by adulthood into the unique song types that female bellbirds sing (Chapters 2 and 3). Their songs likely function in resource defence (Brunton et al., 2008a; Brunton et al., 2008b) and by their first breeding season, they are singing songs that are similar to adult song (Chapter 2; Appendix B). In the female's first breeding season, she may on average start breeding later, have a smaller clutch and brood size and fledged less chicks, but this was not significantly different from after second year females. Age-dependent effects on song have been reported in other songbirds (Bédard & LaPointe, 1985; Forslund & Pärt, 1995; Imlay et al., 2017; Jankowiak & Wysocki, 2016; Jarvinen, 1991; Lack, 1954; Nol & James, 1987; Pärt, 1995) and perhaps the sample size of first year breeders was too small for my study to show an effect of age. In the short-term, weather variables such as temperature and rainfall did not have a significant effect on nest success (a nest producing at least one fledgling) and there was little relationship between nest success and morphometrics of the parents. Only females had a weak positive trend between tarsus length and clutch size. These results suggest other nesting behaviours may play a larger role in short-term nest success.

For example, the more a female bellbird sings while nesting, the more fledglings she has (Brunton et al., 2016; Appendix A). Aspects of song complexity, such as number of syllable types sung, also have a strong positive relationship with the number of fledglings in female bellbirds (Brunton et al., 2016; Appendix A). With individual variation existing in repertoire size for female bellbirds (Chapter 3), this suggests that their song could be a signal of quality, but further research is needed to assess whether this is a signal used in inter- or intra-sexual interactions.

Bellbirds have a lifespan of at least 10 years (unpublished data), and hence could potentially face changing environments throughout their lifetime. The Tiri population has faced such long-term and short-term changes, including the ecological restoration of the island over the last 34 years and re-introductions of other avian species (Galbraith & Cooper, 2013). Bellbird females have made significant reproductive life-history trade-offs by reducing their clutch size. This is likely due to the population reaching density-dependence as a result of either some birds being forced into lower quality territories or there was a uniform decrease in habitat quality (Both, 1998; Ferrer & Donazar, 1996). However, the Tiri population had a smaller clutch size than the Aorangi Island population, which has a significantly higher density of bellbirds (Sagar, 1985). This may be due to higher competition with other avian species that have been re-introduced to Tiri and a population increase in the closely related tui (Dianne Brunton, personal communication), which are rare on Aorangi Island (McCallum, 1981). Tiri bellbirds, however, seem to be able to compensate for lower clutch sizes as they are able to produce multiple broods, unlike the females on Aorangi Island (Sagar, 1985), and in good years, such as those coinciding with abundant New Zealand flax (*Phormium tenax*) flowering, are able to begin breeding earlier in late August, and extend until February in delayed years. Females on Tiri are also now investing in raising single broods, unlike in 1977/78 (Anderson & Craig, 2003). This suggests food resources, such as invertebrates, may be the limiting factor, as the energy needed to raise another brood likely outweighs the available resources for the females' own survival (Martin, 1987; Monaghan & Nager, 1997). Hence, female bellbirds are flexible with their reproductive life-history traits to adapt to changing environments, but has their song adapted as well?

The next steps in studying female and male birdsong should include a broader examination of their life history traits. Bellbirds have significant geographic variation in the songs and syllables they sing and these dialects exist in the island and mainland populations surrounding Tiri (Webb et al. *In prep*). Habitat and cultural isolation are major factors that can cause this geographic variation in song, including in females (Graham et al., 2018). However, I have found that the syllable repertoire in the Tiri population can change year to year for both sexes (Chapter 3). Hence, in further long-term studies on bellbird breeding biology, analyses of their songs should be included. Parameters to include in future studies are the density of breeding pairs, distance between neighbouring nests, habitat description, extra-pair paternity, song rates, song complexity (including the presence of rare and common syllable types and whether females are singing more 'male-like' syllables) and social interactions such as individuals' positions in the dominance hierarchy. A broad study of these factors could help further untangle what aspects of Tiri's restoration are resulting in significant reductions in clutch size and what aspects of bellbirds' changing habitat may have an influence on their song structure. Including extra-paternity will help reveal what aspects of male song influence reproductive success and whether it is the same between the sexes. Studies such as mine, if done on other species with female song, will ultimately provide the foundations to answer the question of why some female songbirds no longer sing.

6.6 CONCLUSION

My thesis has shown that the challenges of field-based studies on female song can be overcome. While field studies still present challenges, song research in the field gives us more accurate timeframes for song development and comparisons between the sex's songs. The development of new technology could allow future researchers to further understand what social and environmental factors could affect female song development and how their song changes over time in comparison to male songbirds. By including broader parameters on the life-history traits in species with female song, these future studies could also further underpin our knowledge on the function and evolution of female song.

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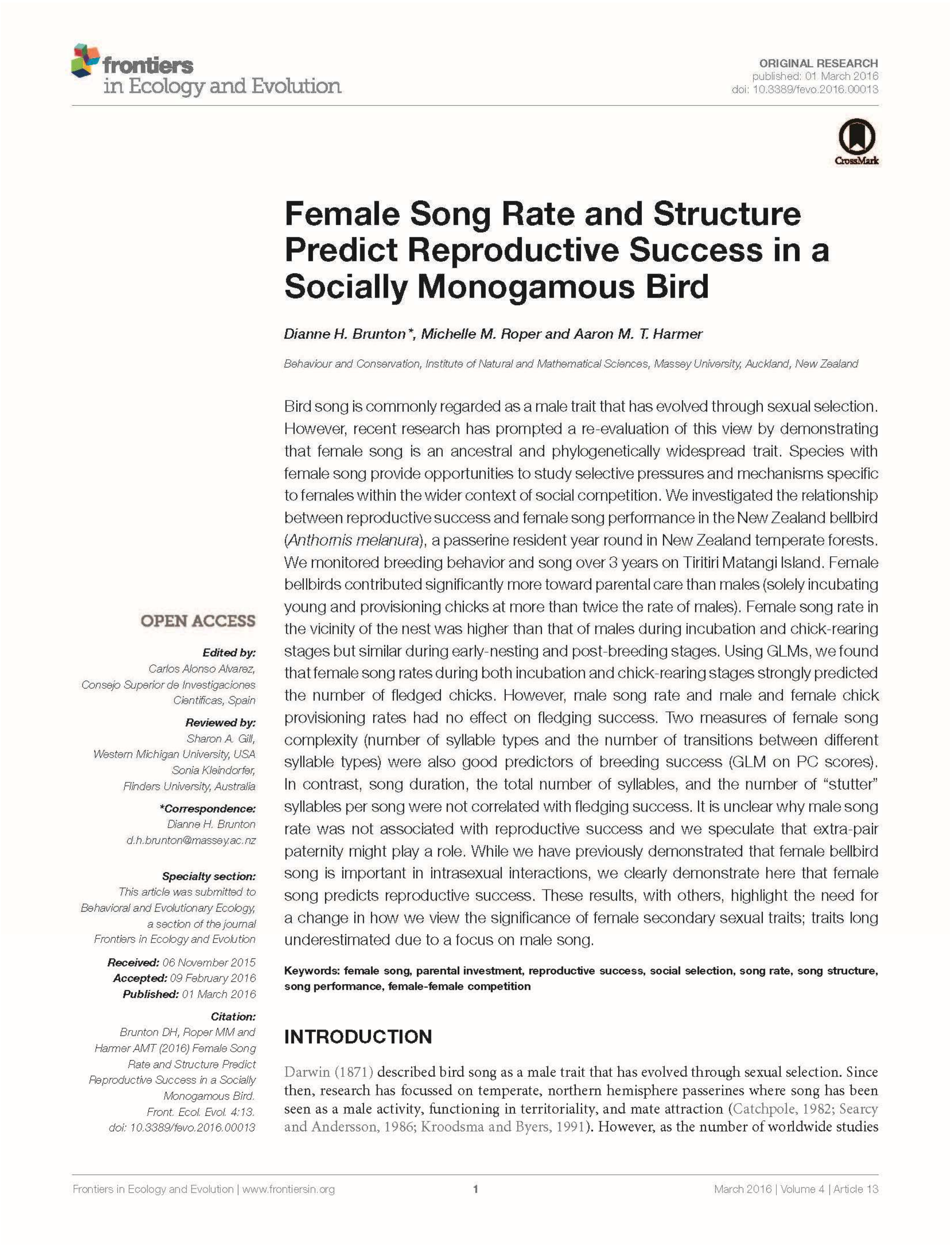
Appendices

A New Zealand bellbird chick (photo: Michelle Roper).

APPENDIX A: REPRINT OF PUBLISHED PAPER

Brunton, D. H., Roper, M. M., & Harmer, A. M. T. (2016). Female song rate and structure predict reproductive success in a socially monogamous bird. *Frontiers in Ecology and Evolution, 4*, 1-11.



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Female Song Rate and Structure Predict Reproductive Success in a Socially Monogamous Bird

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Bird song is commonly regarded as a male trait that has evolved through sexual selection. However, recent research has prompted a re-evaluation of this view by demonstrating that female song is an ancestral and phylogenetically widespread trait. Species with female song provide opportunities to study selective pressures and mechanisms specific to females within the wider context of social competition. We investigated the relationship between reproductive success and female song performance in the New Zealand bellbird (*Anthornis melanura*), a passerine resident year round in New Zealand temperate forests. We monitored breeding behavior and song over 3 years on Tiritiri Matangi Island. Female bellbirds contributed significantly more toward parental care than males (solely incubating young and provisioning chicks at more than twice the rate of males). Female song rate in the vicinity of the nest was higher than that of males during incubation and chick-rearing stages but similar during early-nesting and post-breeding stages. Using GLMs, we found that female song rates during both incubation and chick-rearing stages strongly predicted the number of fledged chicks. However, male song rate and male and female chick provisioning rates had no effect on fledging success. Two measures of female song complexity (number of syllable types and the number of transitions between different syllable types) were also good predictors of breeding success (GLM on PC scores). In contrast, song duration, the total number of syllables, and the number of "stutter" syllables per song were not correlated with fledging success. It is unclear why male song rate was not associated with reproductive success and we speculate that extra-pair paternity might play a role. While we have previously demonstrated that female bellbird song is important in intrasexual interactions, we clearly demonstrate here that female song predicts reproductive success. These results, with others, highlight the need for a change in how we view the significance of female secondary sexual traits; traits long underestimated due to a focus on male song.

Keywords: female song, parental investment, reproductive success, social selection, song rate, song structure, song performance, female-female competition

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INTRODUCTION

Darwin (1871) described bird song as a male trait that has evolved through sexual selection. Since then, research has focussed on temperate, northern hemisphere passerines where song has been seen as a male activity, functioning in territoriality, and mate attraction (Catchpole, 1982; Searcy and Andersson, 1986; Kroodsma and Byers, 1991). However, as the number of worldwide studies of songbirds has increased, the phenomenon of complex, territorial female song has been found to be more widespread than first thought (Arcese et al., 1988; Langmore, 1998; Riebel, 2003; Riebel et al., 2005; Brunton and Li, 2006; Garamszegi et al., 2007; Price et al., 2008, 2009; Geberzahn et al., 2009). Indeed, recent research has prompted a re-evaluation of the assumption that song is a male trait by demonstrating that female song is an ancestral and phylogenetically widespread trait in the oscines (Odom et al., 2014; Price, 2015). These findings raise the issue of why female song may have been lost in some species and the possibility of sex differences in not just the benefits of singing but also in the costs (Kleindorfer et al., 2016).

Male song has been extensively studied and there is evidence that measures of male song quality and performance are related to mating success (Searcy and Marler, 1981; Catchpole, 1987; Lampe and Espmark, 1994; Reid et al., 2004) and reproductive success (Catchpole, 1986; Reid et al., 2005; Nemeth et al., 2012; Taff et al., 2012; Woodgate et al., 2012). Researchers have also found links between male song performance and genetic benefits to females (Hasselquist et al., 1996). It has also been suggested that male song can act as a proxy for age (Botero et al., 2009; Kipper and Kiefer, 2010; Nemeth et al., 2012). However, not all studies of male song have found a relationship with reproductive success (Hiebert et al., 1989; Rivera-Gutierrez et al., 2010; Soma and Garamszegi, 2011), highlighting that plumage and other behavioral traits may play a more significant role in demonstrating male quality.

In contrast to male song, female song performance and structure is a long-neglected field (Langmore, 1998; Riebel, 2003; Riebel et al., 2005). Nonetheless, in some species, females are prolific singers (e.g., Cooney and Cockburn, 1995; Pavlova et al., 2005; Brunton and Li, 2006; Soma and Garamszegi, 2015). In several species where both sexes sing, the responses of territory holders may be sex specific, with same sex interactions being typical (Langmore and Davies, 1997; Langmore, 1998; Brunton et al., 2008b; Kleindorfer et al., 2013; Odom et al., 2015). In general however, the functions of female song are not well understood but have been suggested to parallel those associated with male song (Langmore, 1998), particularly in regard to social competition for resources other than a mate i.e., territorial defense (West-Eberhard, 1983; Illes, 2015). Sexual selection is most commonly defined as a process functioning via intrasexual competition for mates and mating opportunities (Clutton-Brock, 2007). Consequently, traits such as female song that may increase the competitive ability of individuals and be important in female-female competition are not included within this narrow definition of sexual selection. However, female-female competition is covered by the broader approach of social selection (West-Eberhard, 1979, 1983; Amundsen, 2000; LeBas, 2006; Kraaijeveld et al., 2007; Rosvall, 2011; Tobias et al., 2011). In species where females contribute more to rearing offspring than males, female-female competition is arguably highest during breeding activities and in dense populations. If characteristics of female song reflect competitive ability, then we predict an association between female song rate and reproductive success and a positive association between aspects of song performance and female fitness. To our knowledge, just one study has examined female song rates and fitness (Cain et al., 2015), and it found a positive relationship between defense responses to song playbacks during territory establishment and the probability of successful nesting. No study has yet examined how female song complexity and song rate during breeding relates to reproductive success.

Our study uses observational data on patterns of female and male song rates, female song complexity, and amount of parental care to examine the association between these variables and reproductive success (a proxy for fitness). We focused on female song in the vicinity of the nest and spontaneous song rates and song complexity in the New Zealand bellbird (here-after referred to as bellbird); an endemic honeyeater with well-developed female territorial song. For bellbirds, intrasexual aggression is an important component of social interaction for both sexes (Brunton and Li, 2006) and previous playback experiments show that females respond aggressively to female song playbacks that simulate territorial intrusions (Brunton et al., 2008a), particularly to playbacks of their female neighbors (Brunton et al., 2008b). Singing and counter-singing by females occurs frequently throughout the breeding season and females often sing upon leaving the nest after an incubation bout (Li, 2002). We used observations of song and parental investment, and structural analysis of song of individual females to test the hypothesis that female song rates and complex female songs are associated with reproductive success. We suggest that female song performance during the breeding season is crucial in competitive social interactions associated with the defense of resources (including male parental investment), which are essential for breeding activities. Therefore, we predicted a positive relationship between female song rate and/or song structure and reproductive success.

METHODS AND MATERIALS

Study Area and Species Background

Our study was conducted on Tiritiri Matangi Island (Tiri), a 220 ha island in the Hauraki Gulf, 28 km north of Auckland (Lat. 36°60′S, Long. 174.89°E). The bellbird population on Tiri is high-density, with over 10 birds/ha (Baillie and Brunton, 2011; Baillie et al., 2014), and has existed on the island for at least 100 years. Tiri is a wildlife sanctuary with open access to the public and currently has no introduced mammalian predators. The island has been extensively replanted over the last 20 years and a series of avian and reptilian species have been reintroduced for conservation reasons (Rimmer, 2004). Tiri is typical of most northern New Zealand forest ecosystems with year round fruiting and flowering of plant species providing ephemeral, scattered patches of abundant food resources (Gravatt, 1970). Consequently the social behavior and breeding chronology of the avian species and particularly honeyeater species is closely linked to the spatial and temporal patterns of plant breeding phenology (Craig and Douglas, 1986).

Bellbirds are sexually dimorphic in plumage and song (Heather and Robertson, 2000) and easily distinguished in the field (females are approximately 20% smaller and paler gray-green than males, and have a white cheek stripe). Relatively little is known about bellbird breeding biology (Kendrick, 1994; Brunton and Li, 2006; Massaro et al., 2008), although we do know that bellbirds are socially monogamous and that both sexes defend territories and/or resources throughout the year, but particularly during the breeding season (Craig and Douglas, 1986; Kendrick, 1994). The breeding cycle of bellbirds begins in late August and extends until January (Anderson and Craig, 2003). Clutch sizes range from 2 to 5 eggs and several clutches are laid each season. Nest-building activities (2–3 weeks) and incubation (2 weeks) are solely by females, whereas nest-based chick rearing is by both sexes and lasts until chicks fledge at 14–20 days of age. Chick provisioning by both parents can extend past fledging from the nest (Anderson and Craig, 2003). Although only the females incubate the eggs, males feed their mates during this period (Kendrick, 1994).

TABLE 1 | Summary of nest observations over the 3 years of the study.

Breeding stage		Year			Overall
		2010/2011	2013/14	2014/15	
EARLY-NESTING					
Hours	Total	30			30
	Mean ± SE	3.2 ± 0.1			
Nests	ID	1–5			
	n	5			5
INCUBATION					
Hours	Total	30	10	26	66
	Mean ± SE	4.2 ± 0.3	5 ± 0.7	4.1 ± 0.3	
Nests	ID	1–9	11, 14	19–23	
	n	9	2	5	16
HATCHING					
Hours	Total	40	44	32	116
	Mean ± SE	4.0 ± 0.3	5.8 ± 0.4	4.0 ± 0	
Nests	ID	1–10	11–18	19–26	
	n	10	8	8	26
POST-BREEDING					
Hours	Total	22			22
	Mean ± SE	5.5 ± 0.1			
Nests	ID	1–10			
	n	4			4

Bellbird Song

The singing modes of female and male bellbirds differ. Males frequently sing prolonged bouts during dawn chorus and engage in synchronized male chorusing at food sources (Li, 2002). At other times, males sing discrete songs and countersing with other males (Li, 2002). Females sing discrete songs with intervals of at least 3 s between songs (Li, 2002). Although female singing is rarely synchronized, counter-singing by nearby females occurs frequently and females often sing on leaving the nest after an incubation bout (e.g., Li, 2002). Although the number of song types produced by male and female bellbirds is similar (approximately 10 for the Tiri population), this variety is produced in different ways (Brunton and Li, 2006). Females produce song types that have the same basic structure but use different combinations and repetitions of syllables (e.g., ABC, AABC, ABCDE, AABCD, etc.). In contrast, each male song types are structurally distinct and may contain song type-specific syllables. Because of this difference between males and females in song type structure, and the low rate of singing by males in the vicinity of the nest, we were not able to obtain a large enough sample of male song and could not include measures of male song complexity. We based all syllable and song type definitions on previous bellbird studies (Li, 2002; Brunton and Li, 2006).

Data Collection

We collected the data used in this study as part of a larger study of bellbird behavioral ecology that has been running since 2007. The breeding season is during the austral summer, from October to late January. We monitored 26 nests (all first clutches of the season) by color banded males and females on Tiri over three breeding seasons 2010/2011, 2013/14, and 2014/2015 for a total of 216 h ($\bar{x}$ = 8.6 ± 0.2 h/nest; **Table 1**). We checked nests regularly (every 2–4 days) to determine clutch size, and hatching and fledging success. We captured adults using mist-nets or specially modified catching cages containing sugar-water feeders (each cage had multiple trap door entrances that we released manually when a target bird entered the cage). As part of our regular banding protocol we measured weight (g), wing length (mm), tarsus length (mm), tail length (mm), head-bill length (mm), body fat (0–3), and molt score (presence/absence), then we applied color-bands and collected a blood sample (all handling, banding, and blood sampling was performed under permits from the New Zealand Department of Conservation and the Massey University Animal Ethics Committee).

We compiled two independent datasets to examine female song and reproductive success. The first dataset involved direct observations of banded females and males in the vicinity of the nest to determine female and male song rates and behaviors associated with nesting activities (see below). Where possible, observations of song rates were also conducted 2 weeks prior to nesting and 2 weeks post-breeding. The second dataset used opportunistic audio recordings of color-banded females collected during breeding attempts and with known outcomes, to investigate the relationship between song structure and reproductive success.

Observations of Song Rate (Songs per Hour) and Nesting Behavior

Nests were observed continuously for durations of 1 h from clear vantage points at a distance of 5–10 m using binoculars. All activities within 15 m of the nest were generally visible. Incubation and chick-rearing stages were analyzed separately, and only nests with at least 3 h (max 8 h) of observation in a given stage were included (**Table 1**). Nests were not observed twice in the same day, observations started from approximately 8 a.m., and time of day was randomized. Observations for each nest spanned the entire nesting cycle but were not done systematically with regard to development stage. Behaviors recorded during 1 h observation periods for males and females included song bouts, and three parental investment behaviors: male and female chick provisioning, and male feeding the incubating female. All rates are reported per hour (averaged per nest per stage). Only nests that successfully hatched (but not necessarily fledged) at least one chick were included in the analysis of song rates and nesting behavior. Due to small sample sizes during early-nesting and post-breeding stages, overall comparisons of male and female song rates across breeding stages were compared using Wilcoxon signed-rank tests.

Female Song Recordings

We made song recordings of color-banded females using a Marantz PMD661 sound recorder and a Sennheiser ME66 K6 shotgun microphone (frequency response 50–22,500 Hz ± 2.5 dB). The microphone was hand-held using a Rycote shock-mount with a pistol grip. Songs were analyzed using spectrograms and waveforms generated in Raven Pro 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY). Spectrograms were created using the Hann algorithm (Filter bandwidth 500 Hz, size 256 samples, and time gird overlap 50%). Five song measures (**Figure 1**) were taken from each of three songs per female and an average for each female was calculated. Three of the measures represented aspects of duration: song length (s ± 0.01), total number of syllables, and the number of "stutter" syllables ("stutter" syllables are short syllables that distinctively start and end female songs; Brunton and Li, 2006). The other two measures were proxies for song complexity: number of syllable types, and the number of transitions between syllable types.

Statistical Analysis

We investigated the effects of female and male song rate and parental investment on reproductive success (number of chicks fledged) using Poisson regression with a log-link function. Average hourly song rates per nest per stage were calculated and included in the models. Incubation and chick-rearing stages were analyzed separately, with female song rate, male song rate and the rate of male feeding the incubating female as predictors during the incubation stage, and female song rate, male song rate, female chick provisioning rate, and male chick provisioning rate as predictors during the chick-rearing stage. Males only feed females during the incubation stage. Analysis showed that during the incubation stage, female song rate, and male feeding rate were correlated (**Figure 2A**) and so a reduced model was fitted with male feeding rate removed. For the chick-rearing stage, there was a correlation between female song rate and male provisioning rate (**Figure 2B**), and so again a reduced model was fitted with male provisioning rate removed. There were no significant interactions in either analysis and so interactions were excluded from the models.

The effect of each of the song measures on nesting success (1) or failure (0) was examined using a Mann-Whitney U test. The relationship between female song structure and reproductive success (number of chicks fledged) was also investigated using Poisson regression with log-link function. However, the five song structure measures (song length, total number of syllables, number of syllable types, transitions between syllable types, and number of stutter syllables) were not independent and so a principle components analysis (PCA) was performed to reduce dimensionality of the data and generate independent predictor variables. Principle components one and two accounted for approximately 80% of the variation in the data, approximately evenly distributed between the two. Principle component loadings (**Table 2**) indicated that PC1 was composed mainly of

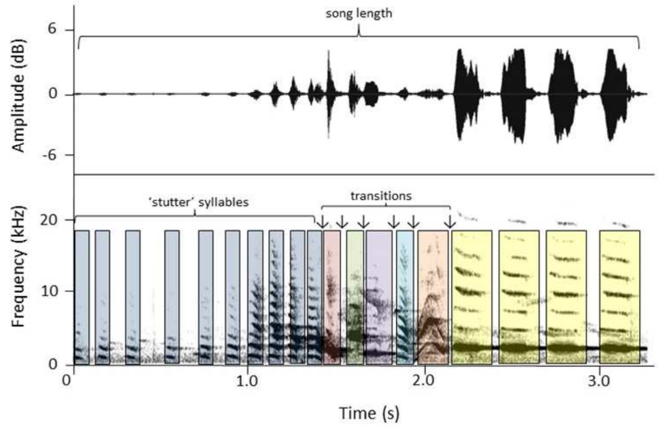


FIGURE 1 | An example of a female song (waveform above, spectrogram below) and the song parameters calculated for each song: song length (s), total number of syllables, syllable types (colors represent different type), number of transitions between syllable types (↓), and number of stutter syllables. Measures for this song example are: # syllables = 19, song length = 3.19 s, # syllable types = 7, # stutter syllables = 10, # syllable transitions = 6.

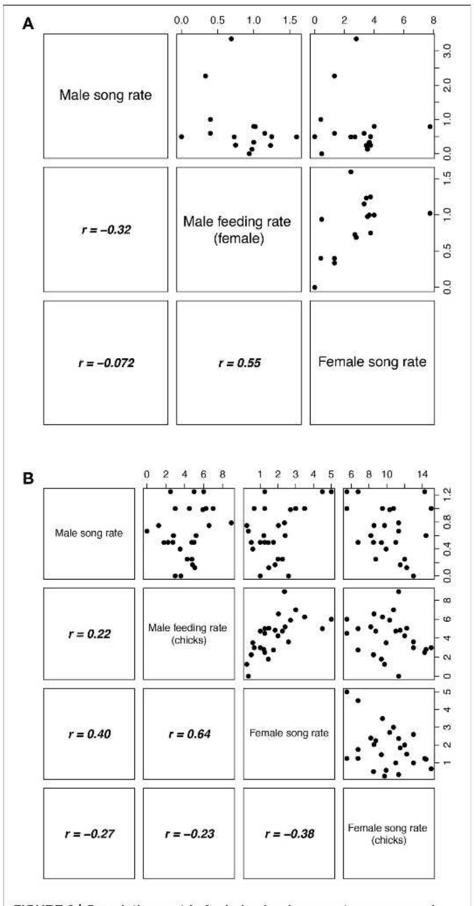


FIGURE 2 | Correlation matrix for behavioral parameters measured during (A) incubation and (B) chick-rearing stages. The four behavioral measures are on the diagonal, the upper triangle shows scatter plots, and the lower triangle shows the respective Pearson's *r*-values. All values were measured as frequency per hour. Dataset based on means per nest (incubation, 16 nests; chick rearing, 26 nests).

total number of syllables and stutters per song, while PC2 was composed of the number of syllables types and the number of transitions per song. The principle component scores for PC1 and PC2 were then used as predictors in the Poisson regression. All analyzes were performed using the programming environment R (R Core Team, 2015). Where reported, means are presented with standard errors (± SE) and a significance level of $\alpha = 0.05$ was used for all statistical tests.

TABLE 2 | The loadings of the five song measures on PC1 and PC2 from the PCA analysis.

	PC1	PC2
Song length	−0.474	−0.239
Number of syllables	−0.625	0.192
Number of syllable types	−0.191	−0.646
Number of stutter syllables	−0.583	0.297
Number of syllable transitions	−0.089	−0.633

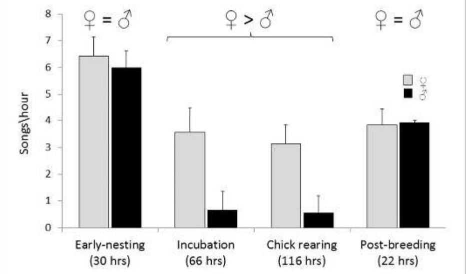


FIGURE 3 | Spontaneous song rate (songs per hour) by males and females on nesting territories (< 15 m from the nest site) based on 234 h of observations of 26 nests. Wilcoxon signed-rank tests were used to compare song rates of males and female within each breeding stage. For early-nesting and post-breeding stages the differences were non-significant, and for incubation and chick-rearing stages female song rates were significantly greater than male song rates, $W = 0$, $P < 0.05$.

RESULTS

Female Song Rates and Reproductive Success

Song rates (per hour) on nesting territories varied with breeding stage and were not significantly different between males and females during early nesting and immediately post-breeding (Wilcoxon signed-rank test, $W = 0$; **Figure 3**). In contrast, during incubation and chick rearing stages female song rate was significantly higher than male song rate (*Wilcoxon signed-rank test*, $W = 7$ and 8, respectively, $P < 0.01$; **Figure 3**).

Observations of 16 nests during incubation (66 h) and 26 nests (the 16 incubation nests plus 10 additional nests) during chick-rearing (116 h) showed that female bellbirds contribute significantly more parental care than males (solely incubating young and provisioning chicks at more than twice the rate of males; *paired t-test:* $t = 8.22$, $df = 26$, $P < 0.0001$; **Figure 4**). Female song rate during both incubation and chick-rearing was a significant predictor of the number of chicks fledged (**Table 3**; **Figure 5**), but male song rate was not (**Table 3**). Female chick provisioning was not a significant effect in our model (**Table 3**).

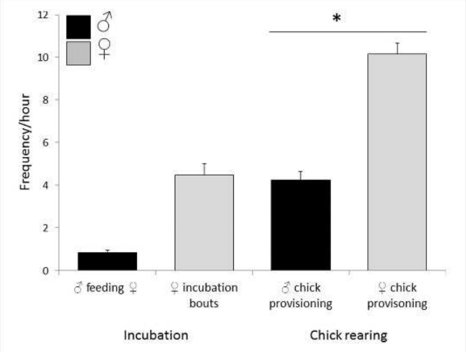


FIGURE 4 | Relative parental investment (PI) by male and female bellbirds. During incubation PI included the male feeding incubating female and female incubation bouts (16 nests, 66 h). During chick-rearing PI included male and female provisioning chicks (26 nests, 116 h). Female chick provisioning rate was significantly greater than male chick-provisioning frequency (*paired t-test:* $t = 8.22$, $df = 25$, $P < 0.0001$, indicated by *). Only nests that hatched at least one chick were included in the analysis.

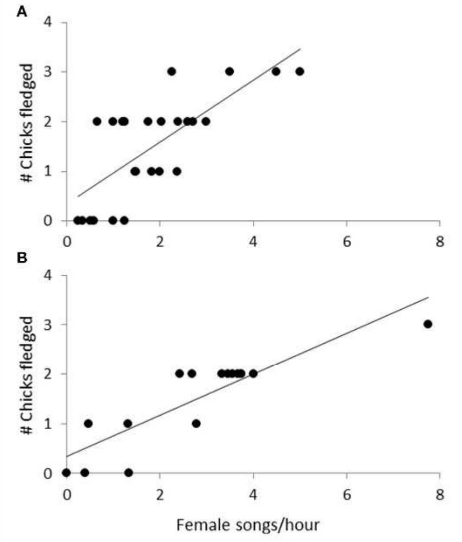


FIGURE 5 | The relationship between the number of chicks fledged and female song rate during (A) incubation ($n = 16$, 66 observation hours), and (B) chick-rearing ($n = 26$, 116 observation hours). The line is from a regression.

TABLE 3 | Results of generalized linear models relating fledging success to song and provisioning rates, and song structure.

	Effects	Estimate ± SE	*P*
Fledging success (incubation)	Female song rate	0.23 ± 0.1	0.016
$\chi^2 = 5.79$, $n = 16$, $P = 0.055$	Male song rate	−0.19 ± 0.3	0.559
Fledging success (chick rearing)	Female song rate	0.46 ± 0.2	0.006
$\chi^2 = 9.57$, $n = 26$, $P = 0.023$	Male song rate	−0.1 ± 0.5	0.830
	Female provisioning rate	0.84 ± 0.1	0.269
Fledging success (song structure)	PC1	−0.12 ± 0.2	0.458
$\chi^2 = 17.33$, $n = 19$, $P < 0.001$	PC2	−0.86 ± 0.3	0.001

Chi-squared values calculated by comparing final model with null model.

Female Song Structure and Reproductive Success

Fifty-seven high quality recordings (low noise to signal ratio) of single songs by 19 females (three songs per female), where nesting outcome was known, were included in the analysis. We first examined breeding success as a binary response (failed vs. one or more fledglings) for the five song structure measures, and found that only song complexity (number of syllable types and number of transitions between syllable types) were significantly different (*Mann-Whitney U-tests:* $U = 4$, $P < 0.05$, and tests $U = 18$, $P < 0.05$, respectively; **Figure 6**). We then included fledgling number (0–3) and applied our GLM model using PCA scores from the five song measures and found that PC2 was a predictor of the number of chicks fledged (**Table 3**) and PC1 was not (**Table 3**). The number of different syllable types and the number of transitions between different syllable types were both associated with PC2 (**Table 2**; **Figure 7**). Hence, the more syllable types and syllable transitions in a female's song, the greater number of chick fledged (**Figure 8**). The duration of the song, the total number of syllables, and the number of introductory stutter syllables did not predict nesting success.

DISCUSSION

We examined the relationship between reproductive success and measures of song structure in females and found that spontaneous song rate during breeding positively correlated with reproductive success and that measures of female song complexity (number of different syllable types and number of transitions between different syllable types) predicted greater breeding success in bellbirds. This contrasts somewhat with other studies where female territorial defense behavior in response to a simulated female intruder (but not spontaneous song), predicts reproductive success (Cain et al., 2015), and where higher rates of female song at the nest increases predation risk (Kleindorfer et al., 2016).

It is known that female song in bellbirds has an important role in female competition (Brunton et al., 2008b) and here we found that higher female song rate during both incubation and chick-rearing were positively correlated with male provisioning rate (**Figure 2**). In northern cardinals (*Cardinalis cardinalis*),

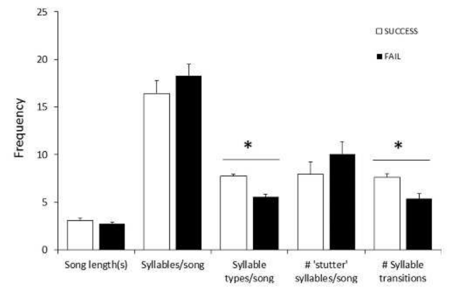


FIGURE 6 | Differences in female song measures (song length, number of syllables, number of syllable types, number of transitions between syllable types, and number of "stutter" syllables; averaged using three songs per female) between nests that successfully fledged chicks (□, $n = 10$) and nests where eggs hatched but no chicks fledged (■, $n = 9$). Data included nests from 2013/14 ($n = 9$) and 2014/15 ($n = 10$), all by different females. There was no difference between years in the proportion of successful or failed nests (2013: 5 successful, 4 failed; 2014: 4 successful, 5 failed). Significant differences (Mann-Whitney U-test) are indicated (*).

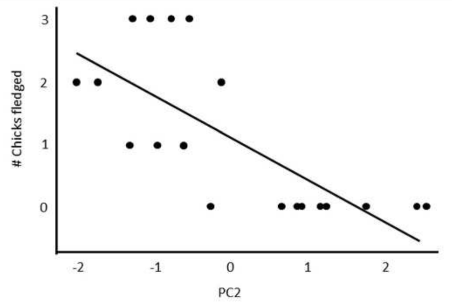


FIGURE 7 | The relationship between the PC2 scores of a PCA analysis and reproductive success. Table 2 indicates the loadings of each of the five song parameters on PC2.

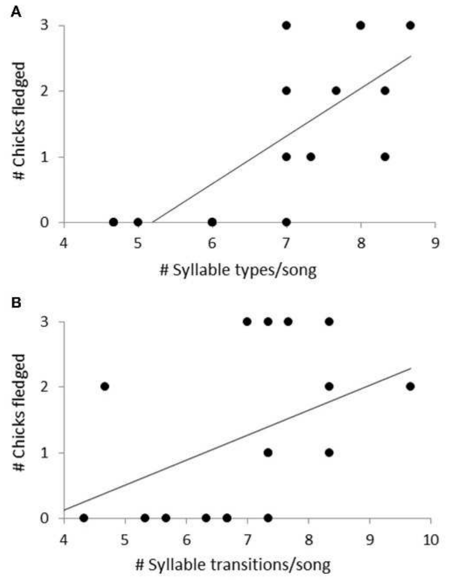


FIGURE 8 | The relationship between the number of chicks fledged and (A) the number of syllable types per song, and (B) the number of transitions between syllable types per song. Linear regression lines show direction of the relationship. These two parameters were associated with the PC2 scores of a PCA analysis looking at the effect of five song parameters on female reproductive success.

males were more likely to come to the nest when the female sang in the vicinity of the nest than when she did not (Halkin, 1997). In contrast, Kleindorfer et al. (2016) found in superb fairy wrens that female song in the nest incurs a significant cost in terms of increased risk of predation and they suggest this may provide a strong selective pressure for reduced female song during breeding. In our study, without manipulating female song rate or male provisioning rate, it is not possible to infer a causal relationship between these factors and chick fledging success. We cannot of course exclude the possibility of other correlated factors, for example, if female song rate is an honest signal of quality (Gil and Gahr, 2002), males may preferentially invest more in females with higher song rates. Furthermore, higher female song rates may secure better access to resources needed for chick-rearing; a possibility supported by our previous playback experiments that found high levels of aggression by territorial females to song playbacks of female neighbors (Brunton et al., 2008b). The lack of a significant effect of chick-provisioning rates and reproductive success was unexpected and is in part due to the strong effect of female song rate, and in part due to our imprecise measure of feeding rate: we were unable to determine quantity or quality of food being delivered to the chicks. Future experimental studies will be needed to test whether females may be increasing fledging success by soliciting higher male attentiveness at the nest.

For males, the literature provides mixed results for the relationship between song performance measures (repertoire, rate, and complexity) and fitness. Positive relationships between repertoire size and annual reproductive success have been demonstrated in great reed warblers, *Arcocephalus arundinaceus* (Catchpole, 1986; Hasselquist et al., 1996), song sparrows, *Melospiza melodia* (Hiebert et al., 1989; Reid et al., 2005), European starlings, (Eens et al., 1991), willow warblers, *Phylloscopus trochilus* (Gil and Slater, 2000), and zebra finches, *Taniopygia guttata* (Woodgate et al., 2012). In contrast, song is often not a reliable indicator of male quality and reproductive success [e.g., in great reed warblers (Forstmeier and Leisler, 2004), collared flycatchers, *Ficedula albicollis*, (Garamszegi et al., 2007), and rock sparrows, *Petronia petronia,* (Nemeth et al., 2012)]. The variation found in empirical studies of the relationship between male song quality and reproductive success, even within a single species, highlights the multimodal nature of sexually selected signals. Although varying song qualities may influence male song function and mating success, other traits such as plumage and behavior may provide stronger and/or alternative mechanisms for mate attraction, resulting in the absence of a link between song quality and reproductive success (Tobias et al., 2012).

Female Song and Social Selection

Because territorial song is so well-entrenched in the literature as a sexually selected male trait involved in competitive processes, many questions remain unanswered as to the nature of selection for song and other ornaments in females (Langmore, 1998; Riebel et al., 2005; Tobias et al., 2012). What are the selective drivers of female song performance and why should female song matter? In year-round territorial species such as bellbirds, where predators are limited, access to resources is likely to be the main predictor of reproductive success. Our study population is located on a conservation island where the main predators are native avian species (the diurnal, open country hunting Australasian harrier, *Circus approximans*, and the nocturnal morepork, *Ninox novaseelandiae*). The bellbird population is dense and likely to be at carrying capacity; therefore we expect that resources probably constrain reproduction and survival. Under such competitive conditions, aggressive social interactions are important and frequent. In general for birds, female reproductive success is not constrained by the number of mates, but by access to resources and parental investment (Bateman, 1948; Trivers, 1972).

If female song is linked to reproductive success but not via classical sexual selection (male attraction), then social selection may provide an alternative hypothesis (i.e., females use song and other competitive indicators to compete for ecological resources). Hence, female territorial song and traits involved in female competition may fit better within the concept of social selection (West-Eberhard, 1979, 1983; Amundsen, 2000; LeBas, 2006; Kraaijeveld et al., 2007; Rosvall, 2011; Tobias et al., 2011). Social selection (defined in West-Eberhard, 1979) focuses on the role of social interactions as drivers of selection, regardless of whether the interaction is sexual or non-sexual (Lyon and Montgomerie, 2012; Tobias et al., 2012). Although still not widely embraced and somewhat controversial, social selection predicts that the strength of social interactions may determine how aggressive traits such as vocalizations, coloration, weapons, and ornaments correlate with measures of reproductive success (McComb et al., 1994; Friedman et al., 2009; Cornwallis and Uller, 2010; Santana et al., 2012; Tobias et al., 2012; Morales et al., 2014).

Our study and several studies of superb fairy wrens (Kleindorfer et al., 2013, 2016; Cain et al., 2015) examine female song and reproductive success in free-living populations. In both bellbirds and superb fairy wrens, females sing complex songs year round at rates comparable to males and in the context of competition between females (Cooney and Cockburn, 1995; Brunton and Li, 2006; Brunton et al., 2008b; Kleindorfer et al., 2013). Aspects of the life history of these two species differ: superb fairy wrens are insectivores and cooperative breeders, whereas bellbirds are primarily nectarivores and exhibit social monogamy (Baillie et al., 2014). However, both species exhibit female dispersal and are non-migratory (Cockburn et al., 2008; Baillie et al., 2014). For these and other species with female song, it is likely that female song traits may convey information about competitive ability such as body condition and age could therefore influence the outcome of non-sexual social interactions and ultimately breeding success and survival.

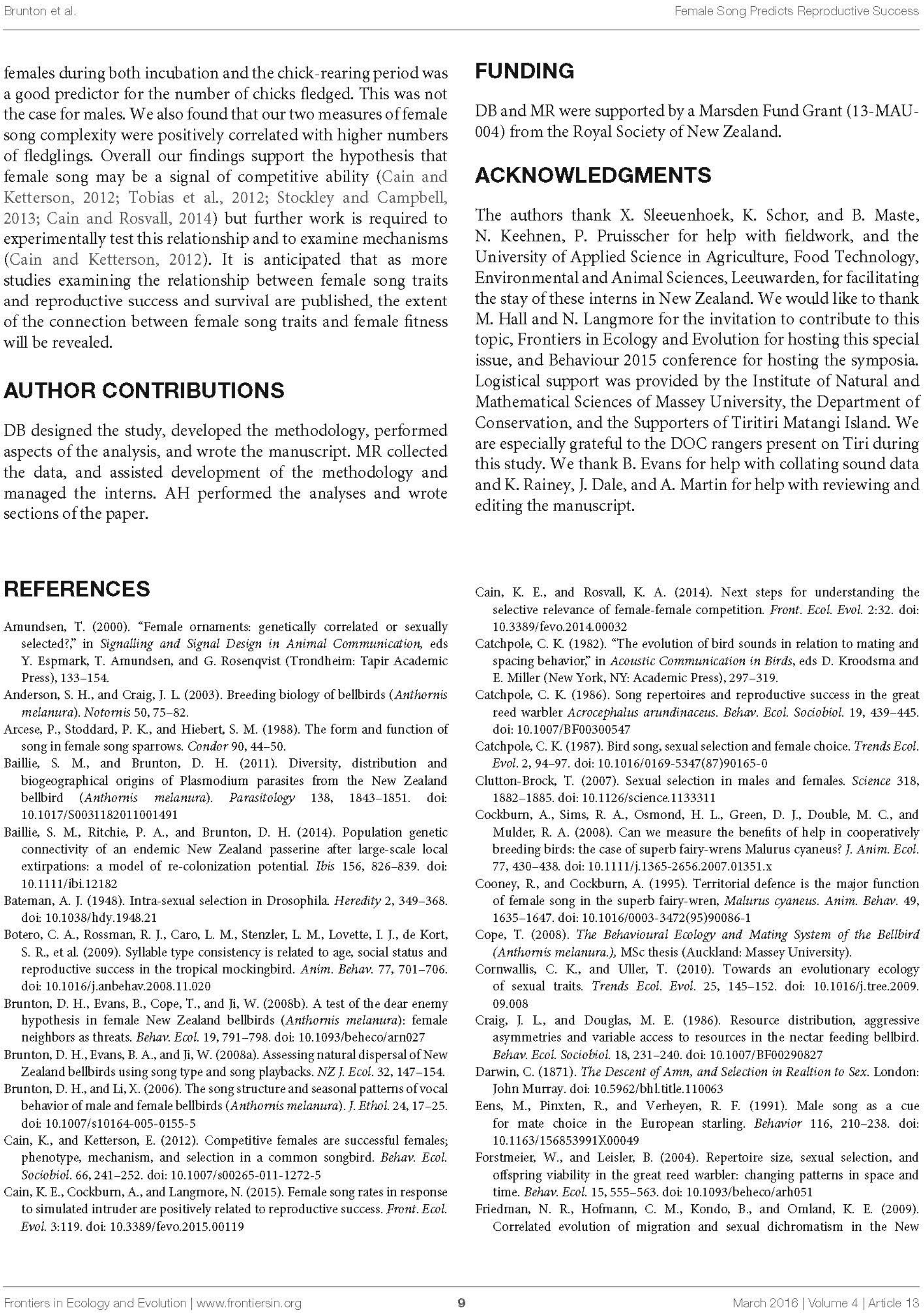
It is unclear why male song rate does not predict the number of chicks fledged. We were unable to collect a sufficient number of male songs to be able to analyse male song structure and it is possible that song complexity rather than rate may be important in male song performance. Alternatively, part of the answer may be extra-pair paternity. Cope (2008) found high levels of extra-pair paternity in the Tiri bellbird populations and Wells et al. (2015) found high extra-pair paternity rates in a closely related New Zealand honeyeater, the tui (*Prosthemadera novaeseelandiae*). Taff et al. (2012) found that male plumage features were associated with within-pair mating success while song consistency was associated with extra-pair paternity in the common yellowthroat (*Geothlypis trichas*). Male song rates and song structure need to be explored further in order to understand how they relate to both mating success and parental investment in bellbirds.

Although our study was observational and we used a single measure of reproductive success, we found that female song rate and structure were good predictors of breeding success. Indeed, because the birds used in the behavioral observation dataset were independent of those used to analyze song structure, our findings are strengthened as analyzes of both datasets showed relationships between female song and breeding success.

The relationships reported here between female song structure, song rate, and reproductive success are based on correlational data. Future work should focus on experimental evidence to confirm the function of song performance in either increasing male provisioning or in social competition. Female song playbacks, clutch size manipulations, and genetic hereditability studies may help us tease apart correlative factors. In addition, how other phenotypic characteristics (e.g., size, body condition, and plumage), female age, and mate quality influence female song structure and rate needs to be explored.

CONCLUSIONS

Although this study is among the first to find a relationship between female song and reproductive success, there is a growing literature on the subject of female song and many species with territorial female song have yet to be studied. We used two simple approaches, observations of song rates and measures of song complexity to measure female song quality in relation to breeding success. We found the rate of spontaneous song by



females during both incubation and the chick-rearing period was a good predictor for the number of chicks fledged. This was not the case for males. We also found that our two measures of female song complexity were positively correlated with higher numbers of fledglings. Overall our findings support the hypothesis that female song may be a signal of competitive ability (Cain and Ketterson, 2012; Tobias et al., 2012; Stockley and Campbell, 2013; Cain and Rosvall, 2014) but further work is required to experimentally test this relationship and to examine mechanisms (Cain and Ketterson, 2012). It is anticipated that as more studies examining the relationship between female song traits and reproductive success and survival are published, the extent of the connection between female song traits and female fitness will be revealed.

AUTHOR CONTRIBUTIONS

DB designed the study, developed the methodology, performed aspects of the analysis, and wrote the manuscript. MR collected the data, and assisted development of the methodology and managed the interns. AH performed the analyses and wrote sections of the paper.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

APPENDIX B: REPRINT OF PUBLISHED PAPER

Roper, M. M., Harmer, A. M. T., & Brunton, D. H. (2018). Developmental changes in song production in free-living male and female New Zealand bellbirds. *Animal Behaviour, 140*, 57-71.

APPENDIX C: TABLE C1

Table C1. Morphometrics (in mm) of adult bellbirds for each sex. Mann-Whitney U tests compare differences between the sexes for each measurement.

Morphometric	Sex	*N*	Mean ± SE	Median	Q.1	Q.2	Q.3	Maximum	Minimum	*U*	*P*
Wing	Female	73	74.05 ± 0.30	73.75	72.50	73.75	75.00	87.25	70.00	240.00	< 0.001
	Male	183	84.46 ± 0.26	84.75	82.50	84.75	86.38	96.25	58.00		
Tail	Female	69	67.61 ± 0.41	67.75	65.25	67.75	69.75	77.50	61.50	511.20	< 0.001
	Male	183	82.70 ± 0.45	84.00	80.00	84.00	86.25	94.75	58.25		
Tarsus	Female	74	24.19 ± 0.11	24.15	23.43	24.15	24.75	27.90	21.65	732.00	< 0.001
	Male	183	26.03 ± 0.06	26.05	25.55	26.05	26.48	29.75	23.75		
Long tarsus	Female	74	27.77 ± 0.21	27.70	26.85	27.70	28.38	40.65	24.95	437.00	< 0.001
	Male	183	29.97 ± 0.08	29.90	29.50	29.90	30.35	41.55	26.55		
Head-bill	Female	71	38.14 ± 0.13	38.30	37.83	38.30	38.65	40.00	30.75	45.00	< 0.001
	Male	183	41.36 ± 0.06	41.35	40.90	41.35	42.00	43.25	38.65		
Mass	Female	67	22.27 ± 0.29	22.00	21.00	22.00	23.50	29.00	17.50	282.50	< 0.001
	Male	180	29.49 ± 0.18	29.50	28.00	29.50	31.00	35.50	21.50		

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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Michelle Mary Roper

Name/Title of Principal Supervisor: Professor Dianne H. Brunton

Name of Published Research Output and full reference:

Original research article.
Brunton, D. H., Roper, M. M., & Harmer, A. M. T. (2016). Female song rate and structure predict reproductive success in a socially monogamous bird. Frontiers in Ecology and Evolution, 4, 1-11.

In which Chapter is the Published Work: Appendix A

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate 50%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Michelle M. Roper collected the data, and assisted with development of the methodology and managed the interns.

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Original research article.
Roper, M. M., Harmer, A. M. T., & Brunton, D. H. (2018). Developmental changes in song production in free-living male and female New Zealand bellbirds. Animal Behaviour, 140, 57-71.

In which Chapter is the Published Work: Chapter 2

Please indicate either:

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  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Michelle M. Roper contributed to the design of the study, developed the methodology, conducted the fieldwork, managed field assistants, performed statistical analyses and wrote the manuscript.

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