



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

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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 we present results from a field-based cross-sectional study comparing song development in both sexes of New Zealand bellbirds, *Anthornis melanura*. We 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 posthatching and song types crystallizing 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 we 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 we 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. Our study contributes to current knowledge of female song development, a topic important for further understanding the selection pressures driving song evolution in songbirds.

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Female song has been largely neglected in studies of birdsong ontogeny (Riebel, 2003, 2016), primarily as the function of birdsong 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, Stoddard, & Hiebert, 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; 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, 2007; Illes, 2015; Odom, Omland, & Price, 2015; Vondrasek, 2006; Webb et al., 2016), and so it is timely that we 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,

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Z. 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, Brown, & Veltman, 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, intersyllable gap between terminal trills, low and high frequency of terminal trill (Nuttall’s white-crowned sparrow, *Z. l. nuttalli*; DeWolfe et al., 1989), amplitude (nightingales, *Luscinia megarhynchos*; Brumm & Hultsch, 2001), intersyllable 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 nonbreeding 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, Evans, Cope, & Ji, 2008). Females use song to defend their territory against neighbouring females during the breeding season (Brunton

et al., 2008); hence we predicted that both females and males must learn their adult songs by their first breeding season.

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

METHODS

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/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).

Data Collection

The bellbird breeding season occurs during the austral spring and summer, from September to late January. We 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 postfledging 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). We observed a total of 255 nests and banded a total of 282 chicks and 109 hatch-year juveniles.

Audio Recordings

Recordings were made using a directional shotgun microphone (Sennheiser ME66, Sennheiser, Germany) and a portable solid-state

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