



It's complicated: the association between songbird extrapair paternity and within-song complexity



Samuel D. Hill ^{a,*}, Christophe Amiot ^a, Michael G. Anderson ^b, Weihong Ji ^a

^a Human–Wildlife Interactions Research Group, Institute of Natural and Mathematical Sciences, Massey University, Auckland, New Zealand

^b Evolutionary Ecology Group, Institute of Natural and Mathematical Sciences, Massey University, Auckland, New Zealand

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Many songbird species are socially monogamous while exhibiting varying extrapair paternity frequencies. Song complexity, often subject to sexual selection, similarly varies across songbird taxa. Some species form highly complex songs whereas others produce simple songs. The basis of this variability, however, is unresolved. Because selection pressures generally favour the evolution of sexually selected characteristics reflecting male quality, such as song complexity, it should be subject to extrapair mate selection. We therefore predicted a positive association between extrapair paternity frequency and songbird song complexity. In addition, we predicted that broadcast (long-range) rather than interactive songs (short-range) would be more likely to contain sexually selected characteristics, such as higher complexity, especially in species with high extrapair paternity frequencies. This was tested using tui, *Prothemadera novaeseelandiae*, a species with high extrapair paternity frequency. First, analyses on 78 songbird species indicated a significant positive association between extrapair paternity frequency and within-song complexity (the level of complexity within a species-specific song) but not between-song complexity (size of species-specific song or syllable repertoire), while no phylogenetic trait conservation was found. Additionally, our results suggested tui broadcast songs had higher song complexity than interactive songs. The findings in this study indicate extrapair mate selection may play a role in the evolution of within-song complexity in songbirds.

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Birdsong is a learned behaviour and, in some songbirds, complex song is a sexually selected trait (Catchpole & Slater, 2008). Song functions predominantly for mate attraction and territory defence (Andersson, 1994; Leniowski & Wegrzyn, 2013; Searcy & Yasukawa, 1996), and male songs may be assessed by both females and rival males (Illes, Hall, & Vehrencamp, 2006). Evidence suggests unpaired males will sing long, complex songs; in contrast, paired males produce shorter, simpler songs (Catchpole, 1983). Females produce more copulatory displays to males with complex songs (Catchpole, Leisler, & Dittami, 1986). Furthermore, males with more complex songs will be paired earlier within the breeding season, attract larger numbers of females and produce more young (Catchpole, 1986, 1992). Male song also functions to deter rivals from entering territories and copulating with their social partners during the female's fertile period (Catchpole & Slater, 2008).

Song complexity can be measured by calculating the total song or syllable repertoire size and song versatility of individuals (Garamszegi & Møller, 2004; Hasselquist, Bensch, & Von Schantz, 1996; Moore, Székely, Büki, & DeVoogd, 2011), termed 'between-song complexity' (Ballentine, Badyaev, & Hill, 2003). Alternatively, song complexity can be measured using variables such as the mean number of different notes or syllables per song and the number of transitions between different syllable types (Leitão, ten Cate, & Riebel, 2006; Sasahara, Cody, Cohen, & Taylor, 2012; Zhang, Wittenbach, Jin, & Kozhevnikov, 2017), termed 'within-song complexity' (Leitão et al., 2006). Song complexity is likely to be a proxy for male quality in terms of reproductive success, body condition, longevity, low developmental stress, parental care and cognitive ability (Badyaev, Hill, & Weckworth, 2002; Boogert, Giraldeau, & Lefebvre, 2008; Buchanan & Catchpole, 2000; Catchpole & Slater, 2008; Sexton, Murphy, Redmond, & Dolan, 2007; Soma & Garamszegi, 2011; Spencer et al., 2005; Woodgate, Mariette, Bennett, Griffith, & Buchanan, 2012; Woodgate et al., 2011). Degrees of song complexity vary widely across taxa, from simple, monotonous patterns composed of a few syllables (e.g. zebra finches, *Taeniopygia guttata*, Woolley & Doupe, 2008 and

* Correspondence: S. D. Hill, Human–Wildlife Interactions Research Group, Institute of Natural and Mathematical Sciences, Massey University, North Shore Mail Centre, Private Bag 102904, Auckland 1131, New Zealand.

E-mail address: S.Hill@massey.ac.nz (S. D. Hill).

European warblers, *Acrocephalus* spp., Catchpole, 1980) to highly complex songs with a large syllable diversity, organized in nonrandom fashion with discernible patterns (e.g. European starlings, *Sturnus vulgaris*, Moorman & Bolhuis, 2013 and California thrasher, *Toxostoma redivivum* Sasahara et al., 2012). Notwithstanding, song complexity variation also occurs within taxonomic families. In the honeyeaters (Meliphagidae) for example, the repertoires of noisy miners, *Manorina melanocephala*, and New Holland honeyeaters, *Phylidonyris novaehollandiae*, consist of simple single high-frequency notes (Jurisevic & Sanderson, 1994). Tui, *Prosthemadera novaeseelandiae*, on the other hand, sing highly complex songs consisting of many different syllables (Hill, 2011; Hill, Amiot, Ludbrook, & Ji, 2015). The evolutionary basis of phenotypic songbird variation in song complexity levels is somewhat of a conundrum to evolutionary ecologists (Kaluthota, 2016).

Extrapair paternity (EPP) can be defined as 'deviations from genetic monogamy' (Turjeman et al., 2016), where males sire offspring outside their social bond (e.g. Forstmeier, Nakagawa, Griffith, & Kempenaers, 2014). In songbirds, EPP is often directed by a female which will initiate extrapair (EP) mating (Bowers et al., 2015). Extrapair paternity is widespread across songbird taxa (Taylor, Boessenkool, & Jamieson, 2008) despite many species being socially monogamous (Hasselquist & Sherman, 2001; Liu et al., 2015). Extrapair copulations are more likely to occur in species where biparental care is of low importance to chick survival (Petrie & Kempenaers, 1998). Females may attain direct benefits from EP copulations. For example, they may be able to feed on an EP partner's territory, in addition to having EP offspring with lower depredation and starvation rates (Gray, 1997). Moreover, EP mating enhances the inclusive fitness of females beyond the genetic capability of their social partner (Bowers et al., 2015). This is reflected in the increased additive genetic value of offspring, often referred to as the 'good genes hypothesis' (see Reid, Arcese, Sardell, & Keller, 2011). Offspring of EP males may also have greater heterozygosity (Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003).

Extrapair paternity frequency varies within taxa (Spottiswoode & Møller, 2004) and across taxa (Canal, Jovani, & Potti, 2012). For example, previous studies suggest EPP frequency in the Savi's warbler, *Locustella luscinioides*, is 4.1% of all offspring observed (Neto, Hansson, & Hasselquist, 2010) whereas in superb fairy-wrens, *Malurus splendens*, 65% of offspring are a result of EPP (Tarvin, Webster, Tuttle, & Pruett-Jones, 2005). Furthermore, EPP frequency in the great reed warbler, *Acrocephalus arundinaceus*, is 4% (Hasselquist, Bensch, & Vonschantz, 1995) and in a tui population, 57% of offspring observed resulted from EPP (Wells, Ji, Dale, Jones, & Gleeson, 2015).

Selection pressures generally favour the evolution of sexually selected characteristics reflecting male genetic quality (e.g. Garamszegi & Møller, 2004; Kempenaers et al., 1992). This is particularly evident in species with high EPP frequencies, as these males usually do not provide parental care (Møller, 2000). We would therefore predict that song complexity would be more pronounced in species with high EPP frequencies, as males of these species would be under more intense sexual selection pressures. In other words, there would be a significant positive association between EPP frequency and song complexity in songbird taxa. Some evidence supports this prediction and indeed females have been found to select EP males with larger song repertoires and higher levels of song consistency (Hasselquist et al., 1995; Byers, 2007; Read & Weary, 1992). However, other studies including meta-analyses of 65 (Garamszegi & Møller, 2004) and 27 (Soma & Garamszegi, 2011) songbird species found no significant relationship between EPP and multiple song features. Therefore, whether male song traits play a role in EPP mate selection remains uncertain. We tested the prediction that EPP frequency was positively

associated with song complexity in multiple songbird species. To do this, we employed both within- and between-song complexity measures in addition to a larger sample size of 78 species. Advancing from the above-mentioned meta-analyses, we also extracted and analysed song complexity data from song recordings both from the above-mentioned databases, and from field recordings of tui and yellowhammer, *Emberiza citrinella*.

Songbird songs have been categorized into two classes according to audience and transmission range: long-range broadcast songs (BS) and short-range interactive songs (IS; Nolan et al., 2002; Titus, 1998; Reichard, Rice, Schultz, & Schrock, 2013; Rosvall, Reichard, Ferguson, Whittaker, & Ketterson, 2012). Broadcast songs are defined as prominent and nondirectional vocal signals, functioning as advertisements of male reproductive and territorial status (Titus, 1998; Wiley & Richards, 1982). They are directed to no obvious audience; therefore, they probably play an important role in attracting both social and EP mates. Interactive songs, on the other hand, are often initiated and directed towards an observable audience. They are employed in male–male confrontations (Titus, 1998), in addition to courtship and pair bond maintenance (Reichard, Rice, Vanderbilt, & Ketterson, 2011; Titus, 1998). If song complexity is selected in EP mating, BS should contain high complexity in species with high EPP frequencies. Little information is available regarding differences in song classes in the context of mate selection in songbirds.

Previous research suggested IS in the dark-eyed junco, *Junco hyemalis*, a species with moderate EPP frequency (27%, Gerlach, McGlothlin, Parker, & Ketterson, 2012), are more complex than BS in terms of syllable diversity. Using tui, a species with both very high EPP frequency and song complexity, we investigated the role of BS within the context of mate attraction and examined whether BS differ in complexity to IS. We predicted that BS would contain higher levels of within-song complexity than IS.

METHODS

Data Collection: EPP and Song Complexity in Multiple Species

Breeding season songs of males of 78 songbird species were collected, 76 of which were obtained exclusively from online databases: Macaulay Library archive of wildlife sounds and videos of Cornell Lab of Ornithology (Cornell University; www.macaulaylibrary.org) and the Xeno-Canto citizen science project website (www.xeno-canto.org). Songs were extracted from 175 recording files from the Macaulay Library, 53 from Xeno-Canto and four from the field (tui and yellowhammer, Tawharanui Regional Park, New Zealand, using a Marantz PMD620 Solid-State Digital Recorder [Marantz, Kanagawa, Japan], attached to a Sennheiser ME67 shotgun long-range directional microphone [Sennheiser, Old Lyme, CT, U.S.A.]). Xeno-Canto only supports mp3 files and these were converted to wav files using <http://www.audio.online-convert.com/convert-to-wav>. The Xeno-Canto archive has been used to provide compressed sound files in other studies analysing and examining avian song structure (Weir & Wheatcroft, 2011) without having any significant impact on song structural integrity. However, we acknowledge that the recording quality on these files may have been marginally lower than for the other sound samples used in this study. This is, however, unlikely to have had any significant effect on analyses within this study.

All species analysed within our study included 64 of the 65 analysed in a previous meta-analysis by Garamszegi and Møller (2004). The remaining 14 species were chosen to obtain a wider range of EPP frequency and to increase sample size from this previous study. Multiple species within this data set have socially monogamous mating systems with varying EPP frequencies (see

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