

1 **Sexual and temporal variation in New Zealand bellbird song repertoires**

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3 Michelle M. Roper¹, Wesley H. Webb¹, Yukio Fukuzawa¹, Christine Evans^{1,2}, Aaron M.T.
4 Harmer¹ and Dianne H. Brunton¹.

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6 ¹School of Natural and Computation Sciences, Massey University, Albany Campus, Auckland,
7 New Zealand.

8 ²College of Science and Engineering, Flinders University, Adelaide, South Australia,
9 Australia.

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11 *Corresponding author:

12 Email: mmroper@mail.com

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15 **Abstract**

16 How song repertoires vary within species and change over time is well studied in male
17 songbirds. However, variation in female song repertoires remains largely unstudied despite
18 female song being much more common and complex than once assumed. We investigated the
19 song syllable repertoire of the New Zealand bellbird (*Anthornis melanura*), a species where
20 both sexes have complex but sexually dimorphic song. We compared songs at individual and
21 population levels to investigate sex and temporal variation of syllable repertoires. We detected
22 96 syllable types in the population over four years, of which 58% were unique to males, 32%
23 unique to females and 9% were shared between the sexes. The population syllable repertoire
24 of both sexes changed substantially across years with similar turnover rates (Jaccard's
25 similarity coefficients; female 52.9–69.0%; male 58.6–73.7%). Furthermore, many syllable
26 types, unique to each sex, varied in prevalence within the population across years. The syllable
27 repertoire sizes of individuals were higher for males than females (13-32, $n = 7$ and 6-16, $n =$
28 8, respectively). Although these sample sizes were low, the temporal variation in syllable
29 prevalence and turnover for individuals were similar to patterns at the population level. Overall,
30 male and female bellbirds exhibited similarities in temporal patterns of yearly repertoire
31 composition, with rapid changes in syllable prevalence, but females had fewer syllable types
32 than males. We suggest that these similarities and differences are consistent with male and
33 female song repertoires being driven by similar but not identical selection pressures.

34 **Introduction**

35 Until recently, female birdsong was considered a rarity rather than the norm. This was
36 particularly apparent in the northern hemisphere, where in many species females either don't
37 sing or tend to sing less often than males (Arcese et al., 1988; Baptista et al., 1993). As a result,
38 research focused on male song and the still prevailing paradigm that song repertoires are under
39 direct selection by female choice and male-male competition (Catchpole, 1980). Contrasting
40 with this paradigm, significant research has been undertaken showing that female song is the
41 ancestral state for Oscines and is common in extant songbirds (Choe et al., 2021; Garamszegi
42 et al., 2007; Odom et al., 2014; Riebel, 2003; Webb et al., 2016). However, quantitative studies
43 of female song repertoires are still rare and there is a call for more integration of female song
44 in birdsong research to provide a platform for better understanding female song function and
45 evolution (Odom and Benedict, 2018; Riebel et al., 2005; Riebel et al., 2019). The prevalence
46 of female song in species varies from no song, such as the zebra finch (*Taeniopygia guttata*;
47 Zann, 1996), to species where females have comparable song repertoires to males, such as
48 streak-backed orioles (*Icterus pustulatus*; Hall et al., 2010). This variation between species
49 highlights the need to describe female song repertoires across a broader range of species from
50 different geographic regions to explore what selection pressures are acting on the evolution of
51 female song.

52

53 Song repertoires are under selection pressure from both inter- and intra-sexual interactions
54 within species (Catchpole, 1980). Within a species, larger male song repertoires have been
55 found to positively correlate with territory quality (Catchpole, 1986; Mcgregor et al., 1981)
56 and size (Buchanan and Catchpole, 1997; Yasukawa et al., 1980), male parasite immunity
57 (Buchanan et al., 1999), and reproductive success (Catchpole, 1986; Eens et al., 1991;
58 Hasselquist et al., 1996; Lambrechts and Dhondt, 1986; Mcgregor et al., 1981). These

59 correlations suggest that, for some species, song repertoires may be a trait used by a female to
60 choose a mate. Alternatively, females may base mate choice on specific repertoire elements
61 rather than just repertoire size alone, hence males may modify their repertoire to produce songs
62 that are more attractive to females (Eriksen et al., 2011). In male canaries (*Serinus canaria*),
63 particular syllables (an acoustic unit) and their spectral features have been referred to as ‘sexy
64 syllables’; the production of these syllable types increases the number of copulation displays
65 by females (Vallet et al., 1998; Vallet and Kreutzer, 1995). Song repertoire size may also be
66 important in intra-sexual interactions; in experiments where male song is played in unoccupied
67 territories, larger song repertoires can deter encroachment by neighbouring males more
68 effectively than smaller repertoires (Krebs et al., 1978).

69

70 As in males, female song may have a role in both inter- and intra-sexual interactions (Riebel,
71 2003). For example, female red-winged blackbirds (*Agelaius phoeniceus*) have two song types;
72 one produced in the presence of males, particularly their mate, and the other in the presence of
73 females (Beletsky, 1983, 1985). Female song is also used differently in different mating and
74 social systems, for example, cooperative breeders such as superb fairy-wrens (*Malurus*
75 *cyaneus*) sing more towards unfamiliar females (Cooney and Cockburn, 1995). In contrast,
76 socially monogamous breeders, such as New Zealand bellbirds (*Anthornis melanura*), sing
77 more in response to neighbouring females (Brunton et al., 2008). In species with more complex
78 mating systems where females must compete for males, female song is used for mate attraction
79 (Langmore and Davies, 1997; Langmore et al., 1996). Female song has also been linked to
80 reproductive success, for example, higher singing rates towards territorial intruders (Cain et
81 al., 2015), spontaneous female song and song complexity (Brunton et al., 2016) are positively
82 correlated with the number of fledglings females’ produce. Female song may also function in
83 within-pair communication (Rose et al., 2020; Sikora et al., 2021). These studies suggest that

84 different aspects of female song repertoires may be driven by either (or both) intra-sexual and
85 inter-sexual selection pressures.

86

87 Even fewer studies are available that shed light on how female song repertoires are learnt,
88 develop and change over time. Furthermore, most of this research has been done on species
89 where males and females significantly overlap in the song components of their repertoires
90 (shared syllable types). These studies demonstrate that developmental patterns can be similar
91 but not identical to those seen for male conspecifics (Roper et al., 2018). Common
92 developmental patterns include increasing or decreasing song repertoires with age, early
93 attrition of syllables, and varying stability of syllable longevity and prevalence throughout an
94 individual's lifetime. For example, female alpine accentors (*Prunella collaris*) increase their
95 syllable repertoire size with age, particularly between their first and second year of age
96 (Langmore et al., 1996). In contrast, the syllable repertoires of female blue-capped cordon-
97 blues (*Uraeginthus cyanocephalus*) have higher levels of selective early attrition (i.e.,
98 discarding syllables from their repertoire that were learnt prior to song crystallisation) than
99 males (Lobato et al., 2015). Hence while both sexes have a similar syllable repertoire size as
100 juveniles during development, adult female cordon-blues have a significantly smaller syllable
101 repertoire size than males (Lobato et al., 2015). Furthermore, in slate-coloured boubous
102 (*Laniarius funebris*), juvenile females occasionally innovate syllable types during song
103 development, whereas males do not (Wickler and Sonnenschein, 1989). Studies of song
104 repertoires of female European starlings have been inconsistent; Pavlova, Pinxten, & Eens
105 (2010) found female song repertoires decrease with age, whereas other studies have shown
106 female starlings alter and increase their repertoire size with age by adding new and deleting old
107 phrase types (a sequence of syllables) as males do (Pavlova et al., 2010). This research indicates
108 that in some species females can change their song repertoire over time, but few studies (e.g.

109 Graham et al., 2021) have examined species with a high degree of sexual dimorphism in their
110 song repertoires.

111

112 Here, we investigated sexual and yearly temporal variation in the song repertoires of the New
113 Zealand bellbird (*Anthornis melanura*; hereafter bellbird); a species that is exceptional
114 compared to previously studied species with female song, as their song is highly sexually
115 dimorphic (Brunton and Li, 2006). Brunton and Li (2006) found that, on average, females have
116 a smaller repertoire size of 1.9 song types versus 5.4 for males, but this could be an
117 underestimate due to the sampling methods used (the range was from one to six song types for
118 individual females). At the population level, the authors detected 36 syllable types: 17 unique
119 to males, 12 unique to females, and seven syllable types shared by the sexes. Females tend to
120 sing shorter and more variable song bouts than males, but despite both sexes having high year-
121 round singing rates, females sing more than males in the breeding season (Brunton and Li,
122 2006). Both sexes develop their songs in a comparable timeframe (Roper et al., 2018) and
123 possible functions of female song include territory defence, polygyny prevention and sexual
124 selection (Brunton et al., 2008; Brunton et al., 2016).

125

126 The aim of our study was to quantify the full syllable repertoire of male and female bellbirds
127 on Tiritiri Matangi Island at both the population and individual level to compare the syllable
128 repertoire of each sex, the degree of syllable sharing and determine the range of syllable types
129 sung over time. We predicted that we would find more syllable types than Brunton and Li
130 (2006) due to the longer duration of this study and more sampling per individual bird, but that
131 the relative abundance of female to male syllable types and proportion of shared syllable types
132 would be similar. We recorded bellbird song across four years and took both cross-sectional
133 (population level) and longitudinal (individual level) approaches to answer two questions: 1)

134 how does the syllable repertoire of each sex compare and 2) do syllable repertoires change at
135 a similar rate for both sexes. Species where male and female song are largely distinct and
136 complex provide an exciting opportunity to understand the evolution of female song.

137

138 **Methods**

139 *Study site and data collection*

140 We recorded bellbird songs for this study on Tiritiri Matangi Island. Tiritiri Matangi Island is
141 a low-lying 220 ha island in the Hauraki Gulf, 4 km off the coast of the Whangaparaoa
142 Peninsula and 25 km north of Auckland, New Zealand. We visited the island four days per
143 week during the breeding season (August to January) and post-breeding season (March to
144 May), between September 2012 and January 2016. We recorded bellbirds between the hours
145 of 0800 to 1800 while searching for individually colour-banded birds and un-banded birds on
146 territories. This study therefore excludes dawn chorus song, which has only been observed to
147 be sung by males (Roper and Brunton, personal observation). Post-breeding season, bellbirds
148 formed loose flocks near food resources (e.g., kanuka trees, *Kunzea ericoides*, for honeydew,
149 or supplementary sugar water feeders; Roper, personal observation), where we targeted
150 individuals for recording.

151

152 On a regular basis, we colour banded individual bellbirds to allow individual repertoires of
153 adult males and females to be recorded. We captured the adults using mist nets on bellbird
154 territories or at specially modified cages containing sugar-water feeders. The birds were banded
155 with unique combinations of three colour bands, and one metal band. All capture, handling and
156 banding protocols were conducted under permits from the New Zealand Department of
157 Conservation (20666-FAU, 34833-FAU, 2008/33) and the Massey University Animal Ethics

158 Committee (12/32, 15/21). We avoided capturing near nests when we knew a female was
159 incubating.

160

161 *Audio recording and acoustic processing*

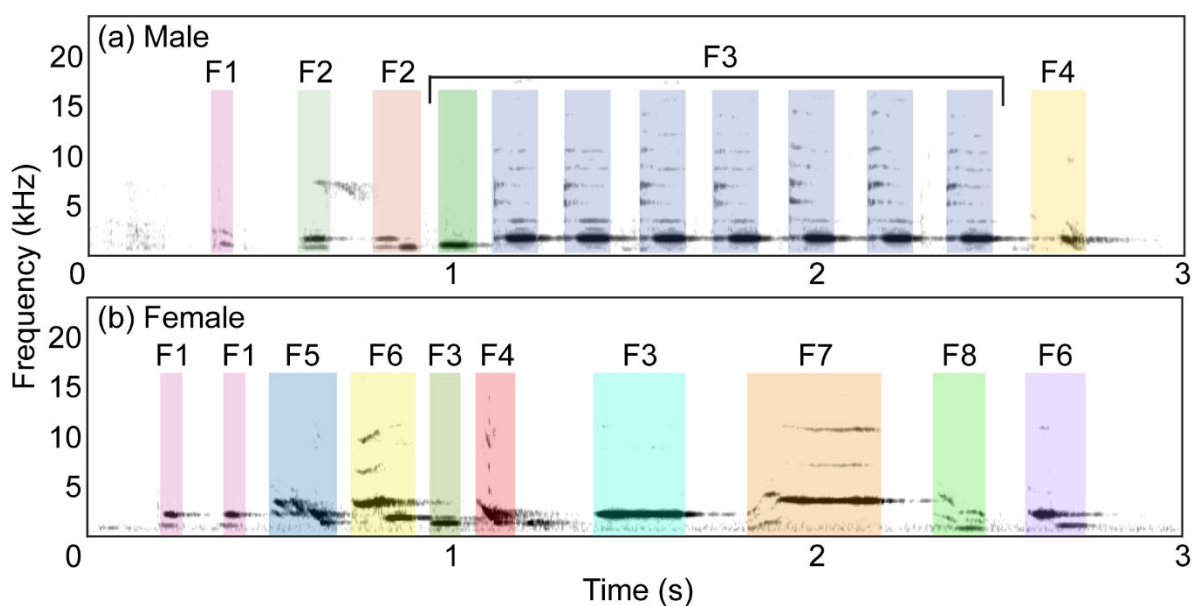
162 We recorded bellbird song using a directional shotgun microphone (Sennheiser ME66,
163 Sennheiser, Germany) and a portable solid state recorder (Marantz Professional PMD 661,
164 Marantz Professional, Cumberland, RI, U.S.A.) with 24-bit sampling precision and 48 kHz
165 sampling rate. Recordings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

174

175 Recordings were processed in Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY) with
176 standardised settings (a bandpass filter of 500 Hz to 22 000 Hz, size 256 samples, time grid
177 overlap 50%, and normalised by amplifying to fill the waveform window). Songs or bouts of
178 singing were selected (hereafter ‘song selection’) from each raw recording. We created Excel
179 (Microsoft Corporation) databases to enter metadata for each raw recording and song selection.
180 The highest quality song selections were then imported into the open-source software Luscinia
181 (Lachlan, 2007).

182

183 We chose syllables as the acoustic unit for measuring repertoire size to compare between the
184 sexes, as males and females sing different song types and the structure of their songs differ
185 (Brunton and Li, 2006). We defined syllables as consisting of one or more elements (i.e., note;
186 a single sound trace on spectrogram) with less than a 15 ms interval between elements or the
187 elements were consistently repeated together within a song type (Kershenbaum et al., 2016;
188 Marler and Isaac, 1961). See Figure 1 for examples of male and female bellbird syllable types.
189 Elements and syllables were selected from spectrograms (FFT algorithm) of song samples
190 using *Luscinia* (Lachlan, 2007). We used the following settings for viewing spectrograms in
191 *Luscinia*, as recommended by R. Lachlan (personal communication): max. frequency 12 000
192 Hz; frame length 10.667 ms; spectrograph points 470; spect. overlap 90.63%; deverbation
193 was set to 100% to reduce echo; dynamic range was altered between 30 and 60 to obtain the
194



195
196 **Figure 1.** Examples of bellbird syllable types (different syllable types are represented by a
197 different coloured box) for (a) male and (b) female bellbirds with syllable family types labelled
198 with the following codes: F1 = stutter, F2 = waah, F3 = pipe, F4 = chump, F5 = down transition,
199 F6 = step-down, F7 = flat-squeak, F8 = down-squeak.

200 best estimation of fundamental frequency when selecting elements; high pass threshold 300
201 Hz.

202

203 The syllables selected in *Luscinia* were then imported into the open-source database program
204 Koe (www.koe.io.ac.nz; Fukuzawa et al., 2020) where syllables were systematically labelled
205 into categories. Syllable types were categorised by eye and ear based on a range of features
206 including shape of elements, fundamental frequency, frequency modulation, harmonics and
207 duration. One experienced observer then used additional syllable ordering information within
208 the song types (i.e., where a syllable type was sung within a song) to ensure consistent labelling
209 of the syllables and agreement was made with an additional experienced observer. For example,
210 if two very similar syllable types were sung with the same syllable order in each song, they
211 were merged together as one syllable type. To verify that the labelling was consistent, machine
212 learning algorithms (supervised and unsupervised) were used to assess how well the syllable
213 labels clustered using the algorithm t-SNE (t-distributed Stochastic Neighbour Embedding; van
214 der Maaten and Hinton, 2008) and determined the accuracy rate using various machine learning
215 algorithms (see Supplementary Methods 1 for additional methods). The syllable labels showed
216 a high degree of clustering (Supplementary Figure 1) and syllables were labelled with $96.6 \pm$
217 1.0% accuracy (Supplementary Table 1). Additionally, syllables were grouped into broader
218 ‘syllable family’ groups, where syllable types with similar spectral characteristics were given
219 a family label (e.g., pure tone syllables were in the family ‘pipe’; see Figure 1 for examples of
220 syllable family types and see Supplementary Table 2 for examples from all syllable family
221 types).

222

223 *Population syllable repertoire size*

224 Using the Koe database, we summarised the number of syllable types and syllable families for
225 the entire study period and between years. A year of recording consisted of both the breeding
226 season months and post-breeding season months, and the four years of recording were
227 numbered consecutively (Year 1 = October 2012 to May 2013, Year 2 = September 2013 to
228 April 2014, Year 3 = September 2014 to March 2015, and Year 4 = September 2015 to January
229 2016). We used simple enumeration to estimate the number of syllable types by plotting
230 cumulative curves of observed syllable types versus number of song selections for each sex
231 across all years and each year with package ggplot2 (Wickham, 2016) in R Studio (R Core
232 Team, 2015). This was done to determine whether the entire population syllable repertoire was
233 captured, determined by whether the cumulative curve approached an asymptote. For syllable
234 types, we calculated the total number of types in the population, number of types sung by each
235 sex and how many types were shared by the sexes, across all years of recording and separately
236 for each year.

237

238 *Variation in population syllable repertoire over time*

239 To determine how the population repertoire changed over time (i.e., yearly turnover rate), we
240 compared the syllable types present each year using Jaccard's similarity coefficient
241 (MacDougall-Shackleton et al., 2009; Podos et al., 1992; Tracy and Baker, 1999), their
242 presence and absence between years, and relative abundance in the population. To measure the
243 similarity of syllable types across years separately for males and female, we calculated
244 Jaccard's coefficient (S_j) following Tracy and Baker (1999) as:

245
$$S_j = s / (x + y + s)$$

246 where s = number of syllable types shared by year X and year Y, x = number of syllable types
247 present in year X but not in year Y, and y = number of syllable types present in year Y but not

248 in year X. To compare the similarity across years between males and females, we used a two-
249 sample t-test. The yearly totals of syllable additions, syllable deletions and shared syllable types
250 was calculated to assess whether any differences in similarity were due to additions or deletions
251 of syllable types from the repertoire or a combination. Since some syllable types may have
252 been undetected in the repertoire due to rarity (and hence were counted as deletions), we
253 calculated the relative abundance of each syllable type. For each syllable type, the total number
254 of individuals singing that type was tallied and we calculated the proportion of individuals
255 singing each type for each year. We used four categories of abundance based on the percentage
256 of individuals singing each syllable type: rare <15%, uncommon 15–45%, common 46–75%,
257 and abundant >75%. To determine if any syllable changes were occurring at small scale (i.e.,
258 within syllable family type) or large/novel scale (i.e., new syllable family additions or old
259 family deletions), we totalled the number of syllable types within each syllable family across
260 each year.

261

262 *Individual syllable repertoire and variation over time*

263 We used the same enumeration method as at the population level to calculate syllable repertoire
264 size for individuals of each sex. We used a subset of individuals for which we had sufficient
265 samples to estimate repertoire size (ten or more song selections). For each sex, we calculated
266 the observed syllable repertoire size range and mean \pm standard error (SE) for this subset of
267 individuals and tested for differences between sexes with an un-paired two-sampled t-test. We
268 also calculated the number of syllable types within each syllable family for this subset to
269 compare the level of syllable diversity between individuals of each sex. We calculated the
270 relative abundance of syllable types for individuals, using the same method as for the
271 population level, to confirm the results found for syllable abundance when using all birds
272 recorded in the population. To compare individual repertoire sizes between years, we selected

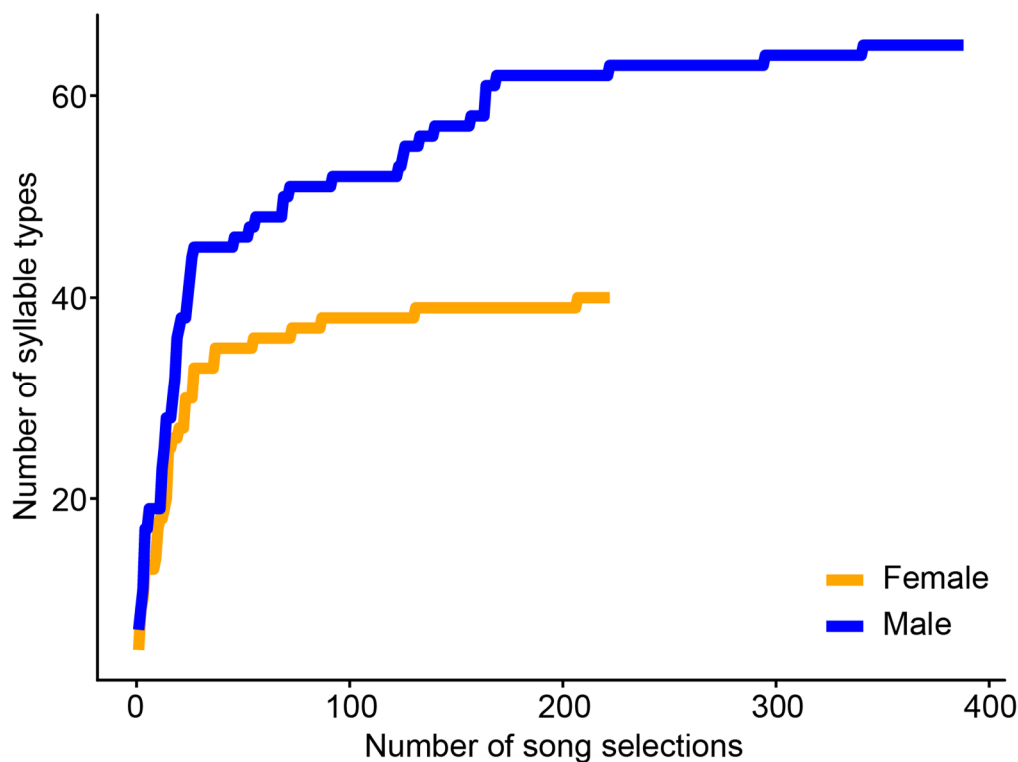
273 individuals that had three or more song selections per year (we did not have the ten selections
274 needed to approach an asymptote for observed repertoire size). As for the population, we
275 calculated Jaccard's similarity coefficient for the syllable types present between years and
276 tallied the number of syllable additions and deletions.

277

278 **Results**

279 *Population repertoire*

280 A cumulative plot of the number of syllable types versus number of song selections approached
281 an asymptote, showing the majority of the population syllable repertoire was captured (Figure
282 2). In total across the four years of the study, we identified 96 syllable types (Table 1). Of these,
283



284

285 **Figure 2.** Cumulative plot of the number of syllable types versus number of song selections
286 for male and female bellbirds on Tiritiri Matangi Island from year 1 (2012–2013) to year 4
287 (2015–2016).

288 58.3% of syllable types were unique to males, 32.3% were unique to females and the sexes
 289 shared 9.4% of syllable types (Table 1). The male population syllable repertoire was hence
 290 almost twice as large as the female population syllable repertoire. The syllable types were
 291 categorised into 20 syllable family types (Table 2). There were six families unique to males,
 292 one family unique to females, and 13 shared between the sexes.

293

294 **Table 1.** Number of syllable types across sexes and recording years (Year 1 = 2012–2013, Year
 295 2 = 2013–2014, Year 3 = 2014–2015, Year 4 = 2015–2016).

	All years	Year 1*	Year 2	Year 3	Year 4
Total	96	60	72	74	71
Male	65	42	48	50	49
(number of individuals)	(110)	(32)	(26)	(31)	(21)
Female	40	21	31	29	28
(number of individuals)	(62)	(10)	(18)	(19)	(18)
Shared	9	3	7	5	6

296 * Note that the female cumulative syllable count did not approach an asymptote in this year.

297

298 *Variation in population syllable repertoire over time*

299 The cumulative plot showed the syllable repertoire approached an asymptote for each year
 300 except for females in year 1 (Supplementary Figure 2). The similarity coefficient (S_j) for
 301 syllable types present between years fell within a narrow range from 52.9 to 73.7% (Table 3)
 302 with no significant difference between the sexes ($t = -1.14$, $df = 9.91$, $P = 0.28$). If the syllable
 303 repertoire changed due to deletions and additions over time, we expected that the further the
 304 years were apart (i.e., temporal distance), the less similar the syllable repertoire would be.
 305 However, we did not find a consistent trend. The average similarity between years with 1-year
 306 difference was 69.4% and 60.2%, 2-years difference 62.9% and 61.0%, and 3-years difference
 307 (not an average as only one sample) 62.5% and 69.0%, for males and females respectively.
 308 This suggests that syllable types may change in their relative abundance (i.e., become rare or

309 **Table 2.** The number of syllable types present within each syllable family in the population
 310 repertoire of each sex for each recording year.

Syllable 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	5	4	4
Flat-squeak	1	1	3	1	1	1	1	1
Peak-squeak	1	2	2	2	1	1	2	2
Pipe	11	12	9	11	5	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	4	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				

311 * Note that the female cumulative syllable count did not approach an asymptote in this year.

312

313 more abundant) between years rather than being permanently deleted from the repertoire.

314 Between most years (except for Year 1), the number of syllable types added and deleted were

315 very similar (Table 3). The changes in syllable types between years were always within the

316 existing family types (Table 2), except for females; although these new family types for females

317 were existing male syllable family types rather than novel family types. For both males and

318 females, the proportion of syllable types that were commonly or abundantly sang by individuals

319 in the population was 14% or lower (Figure 3). Typically, the greatest proportion of syllable

320 **Table 3.** Syllable additions and deletions, number of syllable types shared and syllable
 321 repertoire similarity (Jaccard’s similarity coefficient; proportion) between years, compared at
 322 the population and individual level. See Supplementary Table 4 for the number of song
 323 selections for each individual per year.

Comparison	Sex	Years	Added	Deleted	Shared	Similarity (%)	
Population	Male	1–2*	13	7	35	62.5	
		2–3	9	7	41	71.9	
		3–4	7	8	42	73.7	
		1–3*	16	8	34	58.6	
		2–4	10	9	39	67.2	
		1–4*	14	7	35	62.5	
	Female	1–2*	13	3	18	52.9	
		2–3	6	8	23	62.2	
		3–4	6	6	23	65.7	
		1–3*	9	1	20	66.7	
		2–4	7	10	21	55.3	
		1–4*	8	1	20	69.0	
	Sex	Individual	Years	Added	Deleted	Shared	Similarity (%)
	Individual	Male	1	3–4	2	8	22
2			3–4	5	5	3	23.1
			1–3	0	11	8	42.1
			1–4	3	14	5	22.7
3		1–2	7	7	10	41.7	
Female		1	3–4	0	2	13	86.7
			2	1–2	2	6	3
		2–3		0	1	4	80.0
		1–3		1	6	3	30.0
		3	3–4	0	0	8	100.0
		4	3–4	0	3	8	72.7

324 * Note that the female cumulative syllable count for the population did not approach an
 325 asymptote in this year.

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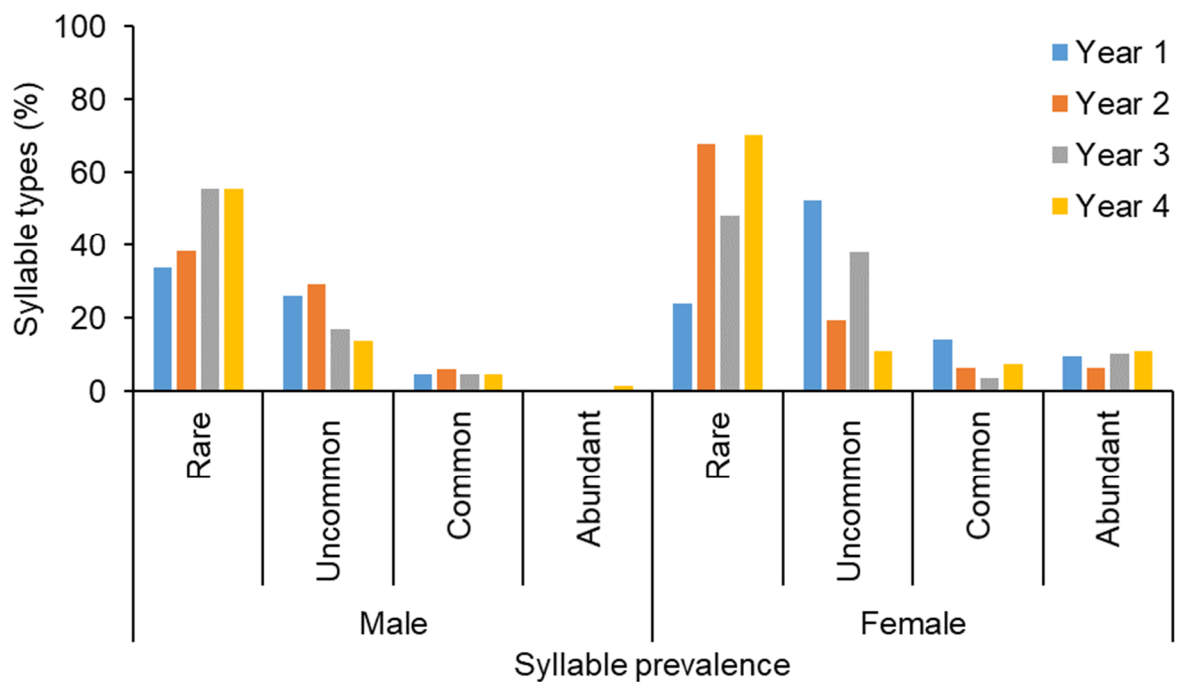
327 types were rare or uncommon among individuals (Figure 3), i.e., most syllable types were only
328 sung by 45% or less of the individuals recorded.

329

330 *Individual syllable repertoire and variation over time*

331 Seven males and eight females had syllable repertoires that either approached or began to
332 approach an asymptote (Figure 4). As the full repertoire size of each individual was potentially
333 not captured, the mean observed repertoire size represents the theoretical minimum mean. The
334 mean \pm SE male syllable repertoire was 19.1 ± 2.5 and ranged from 13 to 32 syllable types
335 (Supplementary Table 3). The mean \pm SE female syllable repertoire size was significantly

336



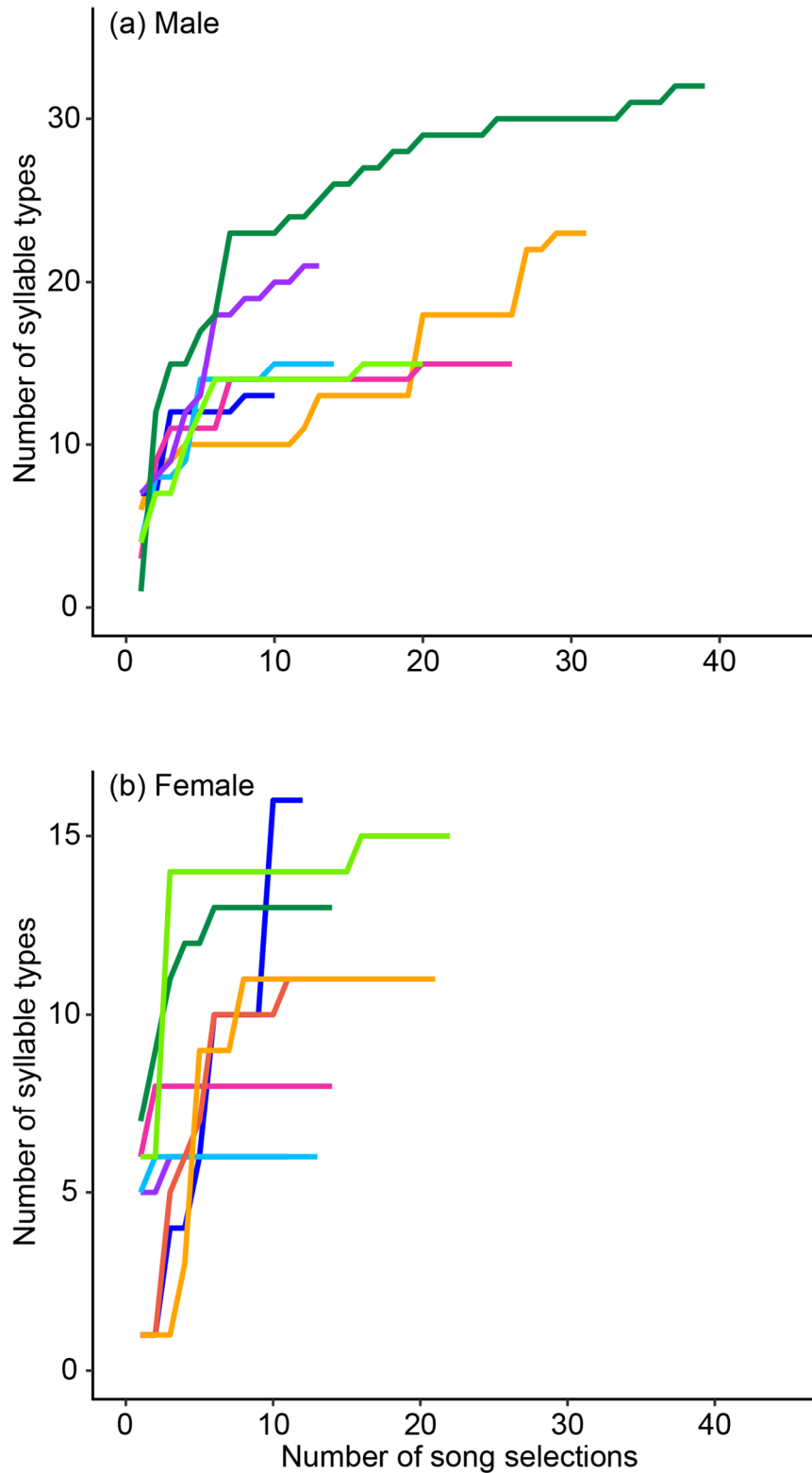
337

338 **Figure 3.** Prevalence of syllable types among the population repertoire compared against the
339 proportion of individuals (rare <15%, uncommon 15–45%, common 46–75%, abundant >76%)
340 singing each syllable type for each recording year (Year 1 = 2012–2013, Year 2 = 2013–2014,
341 Year 3 = 2014–2015, Year 4 = 2015–2016). See Table 1 for the number of individuals within
342 each year.

343 smaller than males at 10.8 ± 1.4 syllable types ($t = -2.91$, $df = 9.26$, $P = 0.02$) and ranged from
344 six to 16 syllable types (Supplementary Table 3). There was variation in the number of syllable
345 family types that individuals sang (Supplementary Table 3). Some syllable family types,
346 however, were only sung by one individual. For example, only one male sang a syllable type
347 in the family ‘stutter up-squeak’ and one female sang a syllable type in the family ‘waah’
348 (which is more commonly sung by males). As for all individuals at the population level,
349 syllable type prevalence among individuals showed similar trends with most syllable types
350 being sung by few individuals (rare and uncommon), and fewer syllable types sung by many
351 individuals (common and abundant; Figure 5).

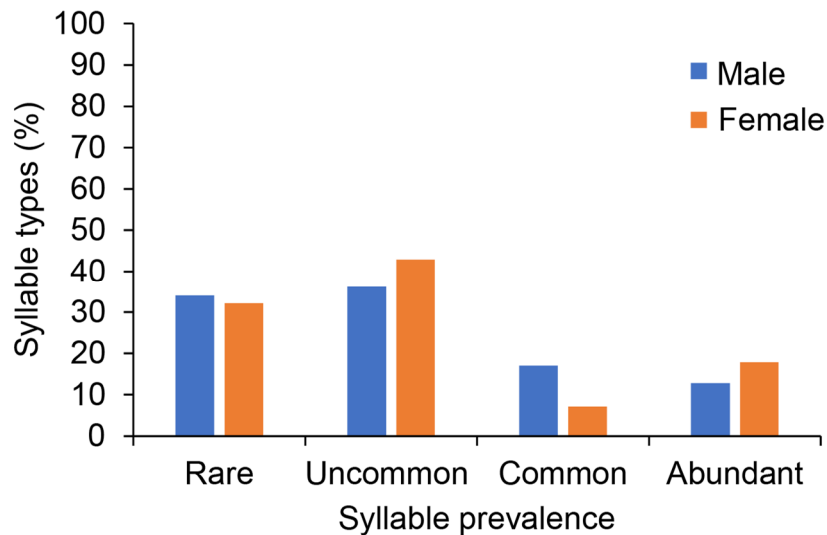
352

353 We were only able to compare three males and four females across years to examine changes
354 in syllable repertoire over time at the individual level (Table 3; see Supplementary Table 4 for
355 the number of song selections). Syllable similarity between years varied from 27.3 to 100% for
356 females and from 23.1 to 68.8% for males. There tended to be more syllable deletions than
357 additions (Table 3), but this may be due to rare syllable types going undetected in years with
358 fewer recordings (Supplementary Table 4) where we may have not captured the full repertoire.
359 For the male (1) and female (1) with the most song selections (where we likely captured most
360 of their syllable repertoires), their syllable similarity between two years was moderately high
361 (68.8% and 86.6%, respectively).



362

363 **Figure 4.** Cumulative plot of the number of syllable types versus number of song selections
364 for individual (a) male and (b) female bellbirds (corresponding to the individuals in
365 Supplementary Table 3) to estimate their total syllable repertoire size.



366

367 **Figure 5.** Syllable prevalence based on proportion of individuals (rare <15%, uncommon 15–
368 45%, common 46–75%, abundant >76%) singing each syllable type for the individuals where
369 the full repertoire was obtained (corresponding to the individuals in Supplementary Table 3).

370

371 Discussion

372 Male bellbirds had a larger observed syllable repertoire than females at both the population and
373 individual levels. The population and individual syllable repertoires were on average almost
374 twice the size in males than in females. There was considerable individual variation in syllable
375 repertoire size, ranging from 15 to 32 in males and ranging from six to 16 in females. Such
376 individual differences in repertoire size can arise for a variety of reasons, for example,
377 differences in nutritional stress during early development (Nowicki et al., 1998), learning
378 abilities (Nowicki et al., 2002), density of the local population (Doutrelant et al., 2000), and
379 the health (Buchanan et al., 1999) and dominance of the individual (Voigt et al., 2007). We
380 found more syllable types each year that were sung exclusively by each sex and a smaller
381 proportion of shared syllable types between the sexes compared to Brunton and Li (2006);
382 however, we acknowledge this could be in part due to differences in syllable labelling. Over
383 half of the syllable families were shared between the sexes, but there were more syllable

384 families unique to males than females, with females having only one unique syllable family.
385 The number of syllable types added, deleted and shared between years was similar for both
386 sexes (except for year 1, 2012–2013, where the female syllable repertoire was not fully
387 captured). Population syllable repertoire turnover between years was similar regardless of
388 which two years were compared for each sex, shown by similarity indices, suggesting that
389 syllable types may vary in relative abundance between years rather than being completely lost.
390 This was supported by our finding that syllable types vary in their prevalence within the
391 population for both sexes. Cross-sectional studies tend to be less informative than longitudinal
392 studies for assessing changes in repertoire over time (Gil et al., 2001). However, our analyses
393 of a smaller number of individuals (longitudinal component) produced similar results as to the
394 population analyses (cross-sectional component). For example, both sexes had similar annual
395 changes in syllable repertoires and most syllable types were sung by only a small number of
396 individuals.

397

398 To date, few studies have identified significant sexual dimorphism in song repertoires for
399 species where both sexes sing complex, highly variable song. The two song types that female
400 red-winged blackbirds sing are different in structure compared to male song (Beletsky, 1983;
401 Catchpole and Slater, 2008), but there is no detail on what syllable types they may share. Some
402 species have similar syllable structure between the sexes but have differences in the overall or
403 particular spectral parameters of their song (Dutour and Ridley, 2020; Hahn et al., 2013;
404 Wilkins et al., 2020; Yamaguchi, 1998). For example, northern cardinal (*Cardinalis cardinalis*)
405 female song has been described as a neotenic version of male song, but it also differs from
406 males in the amplitude of harmonics and syllable stereotypy (Yamaguchi, 1998). Rufous-and-
407 white wrens (*Thryophilus rufalbus*) also have song types that are unique to males and females,
408 with 18 out of 110 song types shared between the sexes over an 11-year study (Graham et al.,

409 2021), whereas bellbird sexes share no song types (Brunton and Li, 2006). A novel finding of
410 our study is that male and female bellbirds also share very few syllable types – a smaller
411 proportion than reported by Brunton and Li (2006). Male and female bellbird syllable types
412 also differ in spectral parameters, such as fundamental frequency, as found in previous research
413 on bellbird song (Roper et al., 2018; Webb et al., 2021). However, they do share common
414 spectral features at the syllable family level. Sharing such features could be due to limits posed
415 by their vocal organ, the syrinx (Suthers and Zollinger, 2004), or for species recognition
416 (Catchpole and Slater, 2008), as their close relative and competitor, the tūi (*Prosthemadera*
417 *novaeseelandiae*), also sings complex song (Hill, 2011; Hill et al., 2017). As the sexual
418 dimorphism in song described in our study is so striking and complex, it is unlikely to be solely
419 for sex recognition. Only small changes in the frequency of the ‘fee’ syllable song of black-
420 capped chickadees (*Poecile atricapillus*), for example, appears to be both a signal of sex and
421 individual identity (Hahn et al., 2013). Bellbirds are highly territorial with strong dominance
422 hierarchies (Craig and Douglas, 1984, 1986), and females tend to be excluded from food
423 resources more often than males (Roper, 2012). This could potentially impact their song
424 sharing with males, as females may not have ample learning opportunities to learn song from
425 males if excluded, or there is a cost to singing male-like song when females are already smaller
426 and submissive. With no duetting described between the sexes of this species (Roper and
427 Brunton, personal observation) and female bellbirds singing more in response to neighbouring
428 females than unfamiliar females (Brunton et al., 2008), we suggest females’ unique repertoire
429 functions more in female intra-specific interactions. Understanding whether such costs or
430 benefits to the amount of song sharing between the sexes is occurring needs further research.
431
432 Sex-based differences in the bellbird syllable repertoires highlights future directions for
433 studying the functions of bellbird song. Deducing from trends in current literature (Catchpole

434 and Slater, 2008), male song is more likely to be under both inter- and intra-sexual selection
435 (i.e., female-mate choice and male-male competition). Perhaps male bellbirds have more
436 unique syllable types and families than females due to their more diverse functions, such as the
437 ‘sexy syllables’ found in male canaries (Vallet et al., 1998; Vallet and Kreutzer, 1995). On the
438 other hand, if female song is under social selection only (i.e., intra-sexual competition for male
439 parental care and resources, such as food), there may be less pressure to develop a larger
440 repertoire size and unique female syllable types. We also found that there was a greater
441 difference in the syllable repertoire size at the individual level than the population level. This
442 may be explained by the individual variation in syllable families sung by females. For example,
443 we only found one female singing a syllable type from the ‘waah’ family and one female
444 singing a syllable from the ‘pipe-down-squeak’ family, suggesting that there are individual
445 females that learn and sing more ‘male-like’ syllable family types, leading to questions on
446 whether female bellbirds can learn from male tutors. European starling females also have
447 considerable levels of individual variation in repertoire size, with some individuals also singing
448 particular phrase type families that in general are sung by all males (Pavlova et al., 2005).
449 Pavlova et al. (2005) suggested these phrase types may be sung in different social conditions
450 or at different population densities, as an earlier study did not find any females singing these
451 phrase types (Hausberger et al., 1995a; Hausberger et al., 1995b). Hence, the different selection
452 pressures acting on song repertoires need further research to tease apart the functions of
453 distinctive male and female repertoires.

454

455 Songbirds can change their song repertoires from year to year (Catchpole and Slater, 2008). At
456 the individual level, we did not capture the full repertoire per individual across multiple years,
457 so we could not address the question of how individual syllable repertoires changed between
458 years. However, for all individuals with sufficient recordings, there were small changes in the

459 syllable types sung between years, regardless of sex. At the population level (cross-sectional
460 analysis), we had the full syllable repertoire for each year (except for females in year 1, 2012–
461 2013) and the difference in syllable repertoires found between each year was within a similar
462 range. This difference did not depend on whether the comparisons were one year or three years
463 apart (i.e., did not vary with temporal distance). This suggests that bellbirds may be changing
464 the relative abundance at which they sing certain syllable types between years (e.g., a syllable
465 type was rarely sung in one year but common in another). There is potential support for this
466 finding in that individuals either commonly or abundantly sang less than 15% of all syllable
467 types and most syllable types were only sung by a few individuals (a trend found at both the
468 population and individual level). This pattern is similar to one found in Darwin's medium
469 ground finches (*Geospiza fortis*) where males appear to prefer singing rare syllable types, hence
470 syllable types may change in abundance over the years, rather than being completely deleted
471 from the population syllable repertoire (Gibbs, 1990). In this case, males singing rare syllable
472 types may improve their reproductive success (Gibbs, 1990; Lemon et al., 1992). Hence, for
473 the bellbird syllable types that were considered as either added or deleted between years, some
474 at least might not have been detected each year due to their low prevalence in the population.
475 Microgeographic variation may also explain why most syllable types were sung by few
476 individuals, as in other songbirds this arises through individuals tending to share more syllable
477 or song types with territory neighbours than individuals on distant territories (Barišić et al.,
478 2017; Briefer et al., 2008). However, further studies will be needed to test this hypothesis in
479 bellbirds.

480

481 The distinctive level of sexual dimorphism in song repertoires and changes over time have
482 several implications for understanding how each sex learns their song repertoire. It has not been
483 tested whether bellbirds are open- or closed-ended learners. However, we suspect they are

484 open-ended learners based on their high levels of dispersal between populations, but little
485 sharing of syllable types between these populations (Webb et al., 2021). We found that
486 individual changes in syllable repertoires between years was similar to the changes found at
487 the population level. This suggests that the change in population syllable repertoire over time
488 is in part due to small changes in individual repertoires between years (a form of selective
489 attrition), versus juvenile recruitment of novel syllable types or immigrating individuals
490 introducing new syllable types not present in this population. However, we cannot exclude the
491 potential that bellbirds are open-ended learners and that they are learning existing syllable types
492 within the population as a contributing factor to this change over time. Our finding that the
493 sexes share a small proportion of syllable types suggests that the individuals may learn, at least
494 to a small extent, from individuals of the opposite sex. Previous research has found that juvenile
495 male and female bellbird songs are more similar to each other in spectral properties than
496 between adult males and females (Roper et al., 2018), also supporting the potential for bellbirds
497 to learn from tutors of the opposite sex, as has been found in a few species (Evans and
498 Kleindorfer, 2016; Geberzahn and Gahr, 2013; Yamaguchi, 2001). Research on tutor choice
499 and learning mode in the species will hence uncover how this species develop their sex-specific
500 song repertoires.

501

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519

520 **Author contributions**

521 Michelle M. Roper contributed to the design of the study, developed the methodology,
522 conducted the fieldwork, managed field assistants, processed recordings, contributed to
523 syllable labelling, performed analyses and wrote the manuscript. Wesley H. Webb imported
524 song selections into the software Luscinia and Koe, and labelled syllables. Christine Evans
525 contributed to syllable labelling. Yukio Fukuzawa developed the new software Koe with
526 Wesley Webb, imported syllable selections into Koe, and performed machine learning
527 algorithms for verifying syllable labels. Aaron M. T. Harmer contributed to methodology and
528 assisted with writing the manuscript. Dianne H. Brunton was awarded the funding, designed
529 the study, developed methodology, assisted with fieldwork, assisted with analyses and
530 contributed to the writing of the manuscript. All authors contributed valuable feedback to the
531 writing of the manuscript.

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