

1 Sexually distinct song  
2 cultures in a songbird  
3 metapopulation

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## 17 **Abstract**

18 Songbirds learn their songs culturally, through imitating tutors. The vocal culture of a  
19 songbird population changes as new song units (syllables) are introduced through  
20 immigration, copying errors, and innovation, while other syllables fall out of use. This  
21 leads to a diversification of the syllable pool across the species, much like the  
22 diversification and spatial patterns of human language. Vocal cultures have been well  
23 studied in male songbirds but have been largely overlooked in females. In particular, few  
24 studies compare spatial variation of male and female song cultures. Here we undertake  
25 one of the first comparisons of male and female song culture in birds, analysing song data  
26 from a metapopulation of New Zealand bellbirds *Anthornis melanura*, spanning an  
27 archipelago of six islands. Having classified 20,700 syllables, we compare population  
28 syllable repertoire sizes and overlap between sites and sexes. We show that males and  
29 females—both with complex songs—have distinct song cultures, sharing only 6–26% of  
30 syllable types within each site. Furthermore, male and female syllable types can be  
31 statistically discriminated based on acoustic properties. Despite diverse syllable  
32 repertoires within sites, very few syllable types were shared between sites (both sexes  
33 had highly distinct site-specific dialects). For the few types shared between sites, sharing  
34 decreased with distance only for males. Overall, there was no significant difference  
35 between sexes in degree of site–site repertoire overlap. These results show different  
36 cultural processes at play for the two sexes. We discuss the implications for future  
37 research on female culture.

## 38 **Introduction**

39 Culture is shared information or behaviour acquired through social learning from  
40 conspecifics (Dawkins, 1976), involving the transmission of *memes* (units of culture) by  
41 behavioural imitation. Vocal culture—the social learning of acoustic memes—has so far  
42 been observed in songbirds (oscines; Passeri), some suboscines (*Procnias* spp.,  
43 Cotingidae), parrots, hummingbirds, cetaceans, elephants, seals, bats, and humans (Paton  
44 et al., 1981; Baptista and Schuchmann, 1990; Janik and Slater, 1997; Poole et al., 2005;  
45 Sanvito et al., 2007; Catchpole and Slater, 2008; Kroodsma et al., 2013). In these taxa, the  
46 vocal repertoire of a population changes as new memes are introduced through  
47 immigration, copying errors, and innovation, while other memes fall out of use (Catchpole  
48 and Slater, 2008). This leads to a diversification of the meme pool across the species, much  
49 like the diversification of human language—resulting in dialects (Podos and Warren,  
50 2007). Geographic dialects have been documented in most vocally learning taxa, but very  
51 extensively in songbirds (Jenkins, 1978; Whitehead and Rendell, 2014; Aplin, 2019).

52 Despite the high volume of studies on male song culture and dialects, virtually nothing is  
53 known about female song culture. This is partly due to a northern-hemisphere-biased  
54 view of sexual selection that emphasises male-male competition and female choice in  
55 driving elaborate traits in males (Darwin, 1871), but which does not provide a framework  
56 for understanding elaborate female traits (Riebel et al., 2019). Female song (and other  
57 elaborate female traits) have been overlooked as non-functional aberrations, resulting  
58 ‘accidentally’ from shared genetic architecture with males (Darwin, 1871; Lande, 1980;  
59 see Tobias et al., 2012 for review). This view has now been roundly discounted. Female  
60 song is present in 64% of surveyed songbird species (Webb et al., 2016), has been  
61 recovered as the ancestral state (Odom et al., 2014), can evolve independently of the male

62 song phenotype (Price, 2015) and has female-specific functions in territory and resource  
63 defence, mate attraction, mate defence, and pair bonding (see Austin et al. 2021 for  
64 review).

65 Overlooking female song culture has impeded development of a more general theory that  
66 accounts for both sexes. For instance, the possibility that females could have song cultures  
67 distinct from conspecific males, with different geographic patterns of song sharing, has  
68 hardly been investigated at a population level (Graham et al., 2017a).

69 Studies have reported a wide degree of sexual song dimorphism in songbirds, from  
70 identical repertoires for males and females at one extreme [e.g. forest weaver *Symplectes*  
71 *bicolor* (Wickler and Seibt, 1980), magpie lark *Grallina cyanoleuca* (Hall, 2000)], to  
72 completely non-overlapping repertoires at the other [e.g. many duetting wrens; (Brown  
73 and Lemon, 1979; Levin, 1996; Mann et al., 2009)]. However, studies comparing the sexes  
74 have mostly focused on within-pair repertoires in duetting species. To our knowledge,  
75 only four studies have compared spatial variation of male and female songs at a  
76 population level.

77 First, Mennill and Rogers (2006) examined the songs of duetting male and female eastern  
78 whipbird *Psophodes olivaceus* across their geographic range. While male whipbird song  
79 was highly consistent over space, female song showed pronounced variation, with  
80 multiple distinct song types. The authors suggest eastern whipbirds have undergone a  
81 decoupling of male and female song learning strategies in response to different sex-  
82 specific selection pressures.

83 Three later studies on rufous-and-white wrens (Graham et al., 2017a, 2018, 2021)  
84 showed that song cultures of males and females can be similar in complexity, and appear  
85 to evolve in similar directions via acoustic adaptation and cultural drift. However, males

86 and females differ in the relationship between dispersal distance and song-sharing with  
87 parents (Graham et al., 2017a), the speed of cultural change, and the relationship between  
88 immigration rate and cultural diversity (Graham et al., 2021).

89 We know of no other studies to examine spatial variation in song culture at a population  
90 level, comparing both sexes.

91 The New Zealand bellbird *Anthornis melanura*—hereafter ‘bellbird’—provides an ideal  
92 system for comparing male and female song cultures over space. The bellbird is a non-  
93 duetting endemic honeyeater (Family Meliphagidae) with complex, geographically  
94 diverse song in both sexes, and probable open-ended learning (Roper, 2018). Bellbird  
95 populations occur across a network of islands and peninsulas in the Hauraki Gulf,  
96 northeastern New Zealand. Population connectivity is substantial, and regulated by  
97 geographic isolation (Baillie, 2011; Baillie et al., 2014). Females disperse more frequently  
98 than males, resulting in higher female connectivity between sites (as typical for songbirds:  
99 Greenwood, 1980; Clarke et al., 1997; Paris et al., 2016).

100 In this paper, we seek to advance understanding of female birdsong culture by comparing  
101 the patterns of male and female meme sharing across a network of six island and  
102 peninsula populations (Figure 1). Our questions are:

103 (1) *Are there sexual differences in population syllable repertoire size?*

104 (2) *How much do male and female population repertoires overlap?*

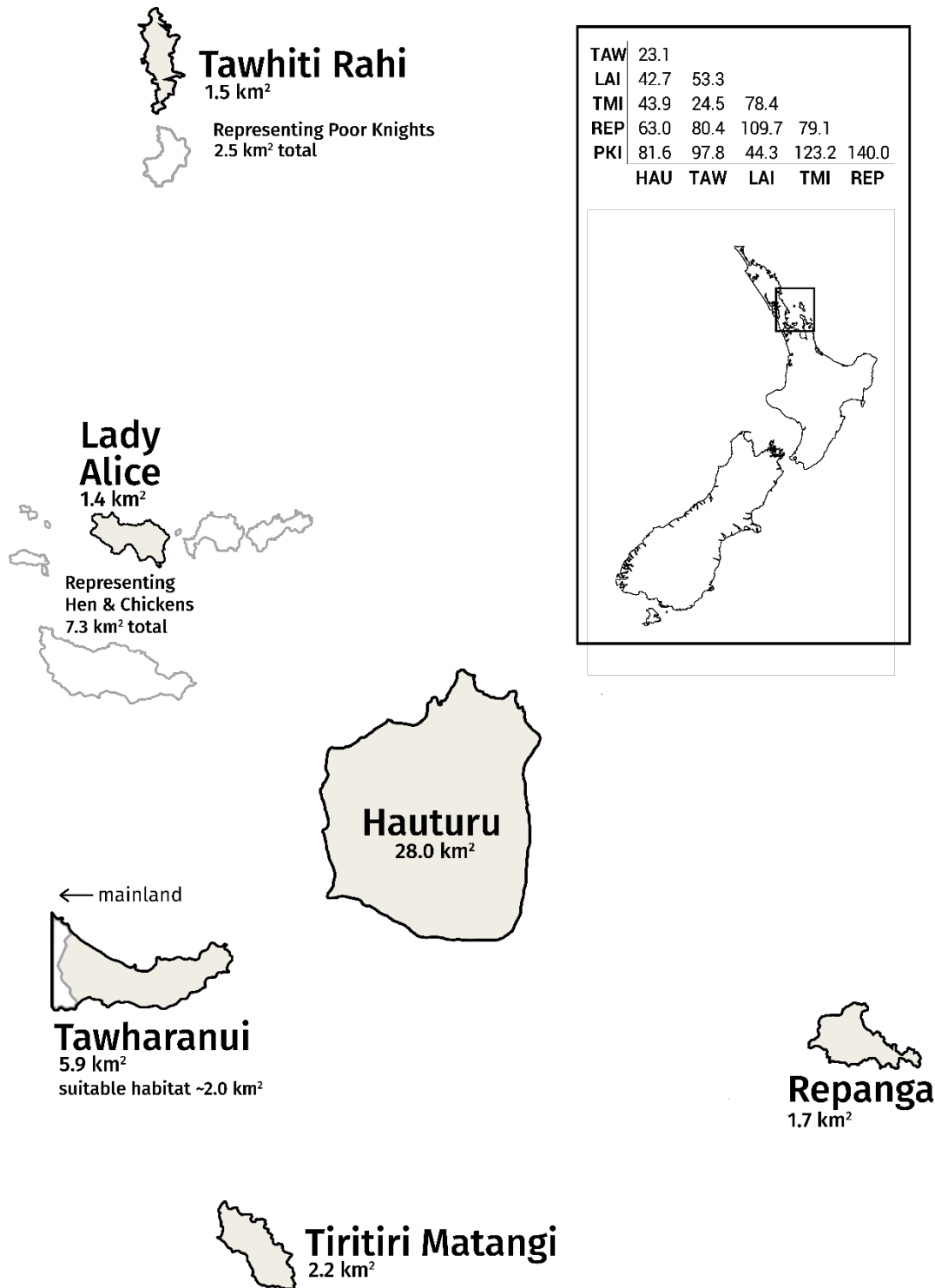
105 (3) *What is the pattern of syllable type sharing between sites?*

106 If geographic proximity drives cultural connectivity between islands, we expect sites that  
107 are closer together will share more memes (i.e. an isolation-by-distance pattern in vocal

108 culture). We also expect higher female dispersal frequency will result in higher sharing of  
109 syllable types between sites than for males.

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113 **Figure 1—Simplified map of the Hauraki Gulf archipelago, home to a metapopulation of bellbirds.**

114 Tawhiti Rahi represents the Poor Knights Islands group; likewise, Lady Alice Island represents the Hen

115 and Chickens Islands group. The other islands of these wider groups are shown in white. The distance

116 matrix between sites (measured in km) is provided (HAU, Hauturu; TAW, Tawharanui; LAI, Lady Alice;

117 TMI, Tiritiri Matangi; REP, Repanga, PKI, Tawhiti Rahi). Distances not to scale on simplified map.

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## 119 **Methods**

### 120 **Creating the song database**

#### 121 **Recording bellbird song**

122 Recording trips were conducted to six island and mainland peninsula sites in the Hauraki  
123 Gulf 2013–2017 (Table 1), with iwi consent (Ngatiwai, Ngati Manuhiri) and permits from  
124 the New Zealand Department of Conservation (47948–FAU, 34833–FAU, 41756–FAU,  
125 48000–FAU) and Massey University Animal Ethics Committee (permit number 15/21).  
126 The sites were chosen based on their large bellbird populations (good return for sampling  
127 effort) and their variety in connectivity. A team of 1–5 recordists per site collectively spent  
128 a total of over 1,000 recordist-hours actively tracking and recording wild bellbirds (per  
129 site: Tawhiti Rahi, 108; Lady Alice, 110; Hauturu, 140; Tawharanui, 132; Repanga, 260;  
130 Tiri, many hundreds of hours), with Marantz PMD661 portable solid-state recorders  
131 paired with handheld Sennheiser ME-66 shotgun microphones. Recordists coordinated  
132 movement to sample sites systematically and with maximal coverage, gathering 2,137  
133 high-quality recorded songs (discrete vocalisation bouts) by adult individuals of known  
134 sex, during daylight hours. During recording, metadata including identity, age and sex of  
135 the focal bird was spoken into the microphone for later transcription.



**Table 1—Geographic and sampling information for the six study sites.**

Tawhiti Rahi represents the larger Poor Knights Islands group; likewise, Lady Alice Island represents the larger Hen & Chickens Islands group. Elevation data from [www.topomap.co.nz](http://www.topomap.co.nz). In the Sample size column, M=male and F=female.

Sites	GPS Coordinates	Area (km <sup>2</sup> )	Elevation	Recording dates and number of recordists	Sample size
Tawhiti Rahi (representing Poor Knights Island group)	35°28'06"S 174°44'13"E	1.5 (2.5 including neighbouring island, Aorangi)	191 m (216 m for Aorangi)	Single trip 23/02/2017–27/02/2017 3 recordists	Birds: 128 M, 48 F Songs: 309 M, 61 F
Lady Alice (represents larger Hen and Chickens Islands group)	35°53'23"S 174°43'41"E	1.4 (7.3 including entire Hen and Chickens group)	158 m (417 m for Hen)	Single trip 27/05/2015–30/05/2015 4 recordists	Birds: 149 M, 116 F Songs: 181 M, 126 F
Hauturu	36°11'57"S 175°04'53"E	28.0	722 m	Single trip 05/04/2016–09/04/2016 4 recordists	Birds: 57 M, 63 F Songs: 67 M, 98 F
Tawharanui	36°22'20"S 174°50'30"E	5.9	91 m	20/04/2016, 18/08/2016, 01/09/2016–07/09/2016, 22/09/2016 1–3 recordists	Birds: 66 M, 26 F Songs: 206 M, 37 F
Repanga	36°26'11"S 175°46'16"E	2.0	214 m	Single trip 03/11/2016 – 09/11/2016 5 recordists	Birds: 122 M, 141 F Songs: 328 M, 196 F
Tiritiri Matangi	36°36'01"S 174°53'24"E	2.2	80 m	Frequent recordings in non-winter months 2013–2015 1–2 recordists	Birds: 91 M, 58 F Songs: 389 M, 138 F

## 136 **Segmenting songs into syllables**

137 Songs were imported into a database and manually segmented into syllables in *Koe*  
138 bioacoustics software (Fukuzawa et al., 2020) by visually inspecting the spectrogram and  
139 setting syllable start/end points. Bellbirds mostly sing in discrete units that are easy to  
140 demarcate as syllables based on a gap either side. Occasionally there are fast-paced bursts  
141 where it is not clear where one unit ends and another begins; in these cases sounds were  
142 grouped together as a syllable if they were separated by less than 15 ms of silence. This  
143 value was chosen through trial and error for the best consistency of syllable groupings.

## 144 **Classifying syllables**

145 To prepare for classification, the 20,700 segmented syllables were ranked by acoustic  
146 similarity in *Koe*. Similarity was calculated by extracting all available acoustic features  
147 for each unit and applying the UPGMA method (Sokal, 1958); see  
148 <https://github.com/fzyukio/koe/wiki> for details of extracted features and similarity  
149 index calculation.

150 WHW then compared syllables visually and aurally to classify them into types based on  
151 just-noticeable differences in pitch, timbre, and duration of the playback and visual  
152 appearance of the spectrogram. Manual perception-based classification is considered  
153 excellent for acoustic classification (Sayigh et al., 2007; Duda et al., 2012) and allowed  
154 finer scale than automated classification methods, such as multi-dimensional scaling  
155 (MDS) or principal component analysis (PCA). The high acuity of bird hearing relative to  
156 humans (Dooling, 2004) justifies a fine-scale classification approach. We validated our  
157 classification by having 74 inexperienced judges independently label a subset of  
158 syllables. Average match with our own labels was 89.6% (median 95.6%); see Fukuzawa  
159 et al. (2020) and Article S1A for more details.

## 160 **Sex differences in population-level repertoires**

### 161 **Male and female syllable diversity**

162 The raw number of syllable types recorded at each site are not directly comparable, due  
163 to the inevitable confounding of different sampling effort. To account for this, we used the  
164 statistical software *EstimateS* (Colwell, 2013) to produce syllable type accumulation  
165 curves and extrapolate the true number of syllable types at each site (Article S1B).

### 166 **Repertoire overlap of male and female population sectors**

167 For each site we calculated the percentage overlap between male and female population  
168 repertoires, using the Jaccard similarity index (Hamers et al., 1989): the number of shared  
169 types divided by the total number of types.

170 Next, the acoustic feature measurements of all syllables (previously extracted to aid  
171 classification in *Koe*) were normalised by mean-centering and dividing by standard  
172 deviation. To test whether male-only, female-only, and shared syllable types form three  
173 distinguishable clusters in acoustic space, we classified syllables using a linear  
174 discriminant analysis (LDA) on the data, with leave-one-out cross-validation. If male-only,  
175 female-only, and shared syllables are randomly interspersed in acoustic space, then the  
176 LDA classification results will be similar to random assignment of groups. If the three  
177 groups occupy more distinct ranges, then the LDA classification will perform much better  
178 than random assignment.

### 179 **The pattern of syllable type sharing between sites**

180 We calculated repertoire overlaps between sites, for all pairwise combinations of site  
181 lists—comparing males against males, females against females. For each sex we tested for  
182 an isolation-by-distance pattern in repertoire overlaps between sites, in two ways.

183 First, we conducted a Hauturu-centric analysis. The large size and geographic centrality  
184 of the Hauturu population make it likely to be a substantial source of dispersing bellbirds  
185 to other sites in the Hauraki Gulf archipelago. We calculated Spearman rank correlation  
186 between *population repertoire overlap with Hauturu* against *geographic distance from*  
187 *Hauturu*.

188 Next, to test for an overall isolation-by-distance pattern, we calculated Spearman rank  
189 correlation between *percentage of site–site repertoire overlap* against *site–site geographic*  
190 *distance* for all pairwise combinations of sites in the archipelago. In this case, to account  
191 for non-independence of points (being pairwise combinations), we used the RELATE  
192 routine in *PRIMER* (version 7, Clarke and Gorley, 2015) with 9999 permutations.

193 To test whether males or females share more syllables between sites overall, we used a  
194 two-tailed Sign Test (Dixon and Mood, 1946), with null hypothesis: the degree of site–site  
195 sharing is equal between sexes (Article S1C).

## 196 **Results**

### 197 **Sex differences in population repertoires**

#### 198 **Male and female syllable diversity**

199 Across the metapopulation we recorded a total of 702 syllable types: 337 male-only, 203  
200 female-only, and 162 shared. See Data S1 and Table S1 for a complete catalogue.

201 For each site and sex, the syllable type accumulation curve levelled off nearly or  
202 completely by 500 songs (i.e. approximating the true number of syllable types present),  
203 allowing meaningful comparison of syllable diversity (Figure S1).

204 There was no evidence of a difference in repertoire size for males versus females within  
205 sites; 95% confidence intervals overlap for males and females in all cases (Table 2). There  
206 was high variability between sites for both sexes, with male point estimates ranging from  
207 80 (Repanga) to 186 (Hauturu) and females from 81 (Repanga) to 186 (Hauturu).

## 208 **Repertoire overlap of male and female population sectors**

209 Male and female population sectors had largely separate repertoires, ranging from 6%  
210 total units shared at Tawhiti Rahi to 26% shared at Hauturu (Figure 2, Table S2). In other  
211 words, 74–94% of syllable types at each site were sung by one sex only.

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### 213 **Table 2—Extrapolated estimates of male and female syllable diversity within sites.**

214 Estimated number of syllable types at 500 songs, for male and female population sectors at each site.  
215 Ninety-five-percent confidence intervals are in brackets. Calculated with the statistical software *Estimate*  
216 *S* (Colwell, 2013).

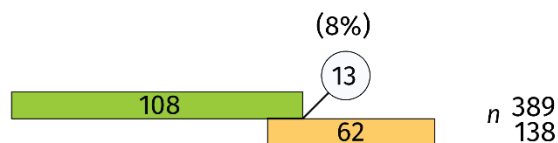
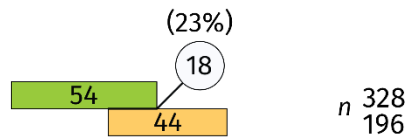
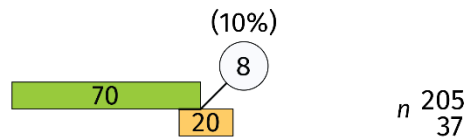
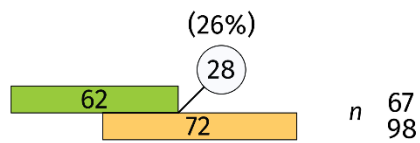
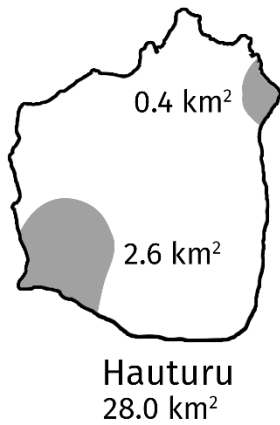
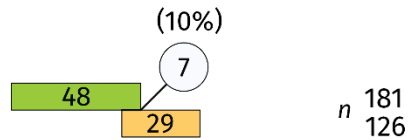
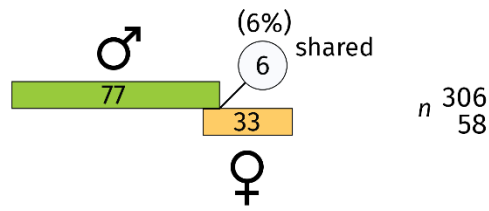
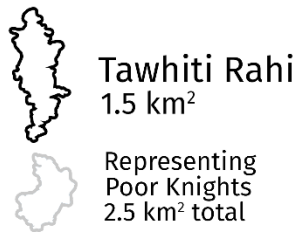
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Site	Male	Female
Tawhiti Rahi	<b>135</b> (121–149) <i>n</i> =306 songs	<b>119</b> (68–169) <i>n</i> =58 songs
Lady Alice	<b>143</b> (118–169) <i>n</i> =181	<b>128</b> (93–163) <i>n</i> =125
Hauturu	<b>186</b> (139–234) <i>n</i> =67	<b>186</b> (151–220) <i>n</i> =98
Tawharanui	<b>116</b> (103–129) <i>n</i> =204	<b>89</b> (48–130) <i>n</i> =37
Repanga	<b>80</b> (72–89) <i>n</i> =328	<b>81</b> (65–97) <i>n</i> =196
Tiri 2013, 2014, 2015	<b>165</b> (152–178) <i>n</i> =389	<b>145</b> (115–175) <i>n</i> =138

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## Syllable types



219 **Figure 2—Overlap of male and female population syllable repertoires.**

220 Each diagram indicates the recorded number of male (green bar) and female (orange bar) syllable types,  
221 and the number of types common to both sexes (circle). The percentage overlap is given above the circle,  
222 calculated as the Jaccard similarity index: number shared divided by total number of types. For  
223 robustness, repertoires exclude types with fewer than three occurrences within that site-and-sex group.  
224 Bar length is proportional to the number of syllable types, and overlap length is proportional to the  
225 number of shared syllable types. Sample sizes (number of songs) for the male and female bars are given to  
226 the right of the bars. Note that repertoire sizes are recorded values, not extrapolated, and therefore are  
227 not directly comparable due to differing sample sizes. However, relative overlap percentage is more  
228 robust to differing sample sizes and thus meaningful to compare.

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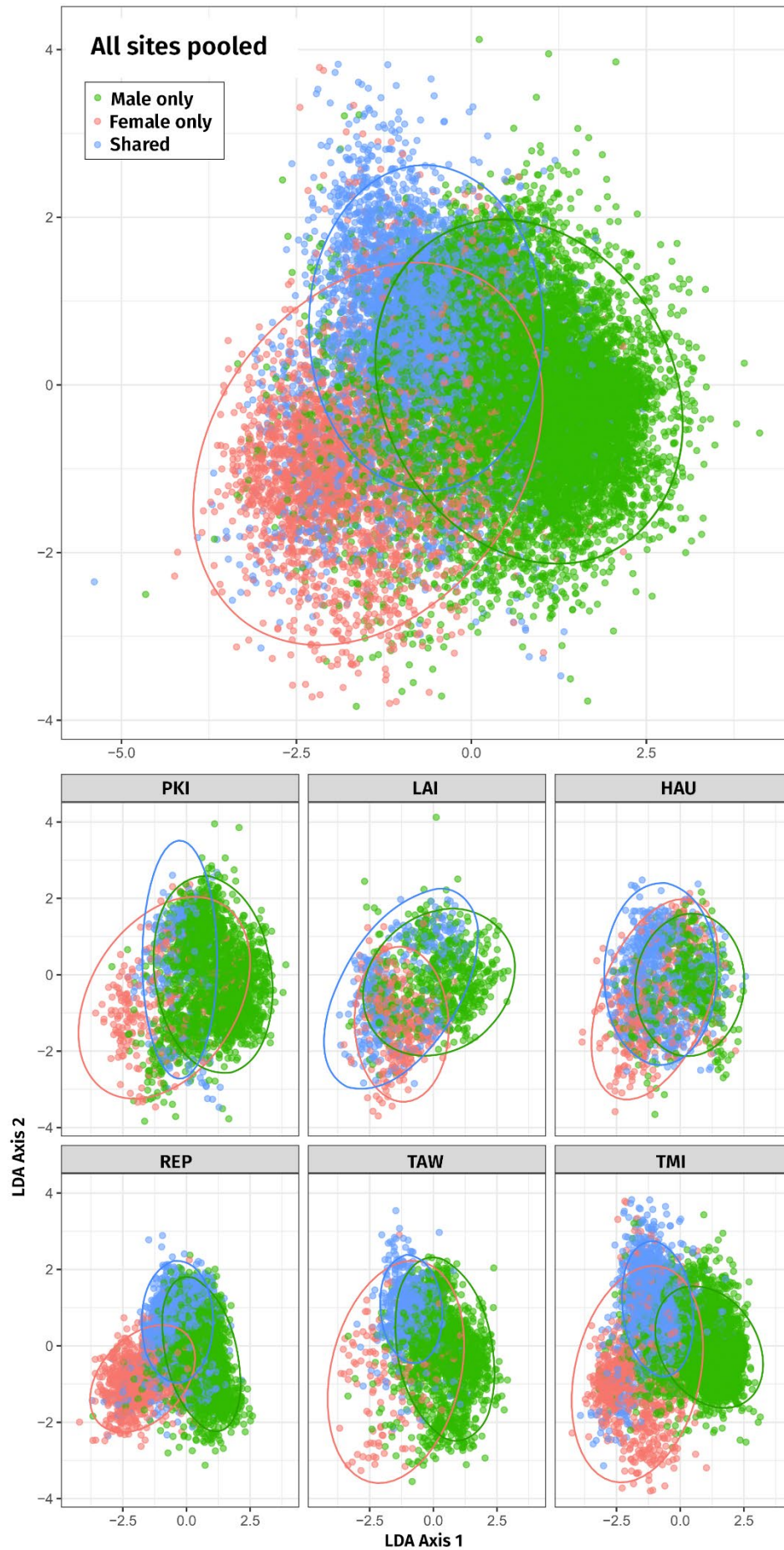
230 In the Linear Discriminant Analysis (LDA) ordination, male-only and female-only syllables  
231 form two clear, partially-overlapping clusters, with shared syllables in between, when  
232 data from all sites are pooled. For individual sites the configuration of the three clusters  
233 varies but shows a tendency for female-only syllables to occur at lower LD1 values, male-  
234 only to occur at higher LD1 values, with shared syllables in between.

235 Success of the LDA leave-one-out classifier had an overall *lift* of 1.78; that is, the LDA  
236 assigned labels (male-only, female-only and shared) to syllables overall 1.78 times better  
237 than random allocation of labels. Lift was 1.51 for male-only syllables, 3.99 for female-  
238 only syllables, and 2.15 for shared syllables. P values for all lift tests were <0.001; i.e. in  
239 all cases none of the 4999 null distributions had a lift as large as the observed lift.  
240 Therefore, male-only, female-only and shared types can be separated on the basis of  
241 acoustic features.

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246 **Figure 3—Two-dimensional linear discriminant analysis (LDA) of male-only, female-only, and**  
247 **shared syllables for all sites combined (top) and each site separately (bottom).**

248 Ellipses represent the regions covering 95% of the data (according to the fitted normal). Each site is  
249 plotted using the same axes to be comparable. Site abbreviations are as follows: PKI, Tawhiti Rahi,  
250 representing Poor Knights Islands; LAI, Lady Alice Island, representing Hen & Chickens; HAU, Hauturu;  
251 REP, Repanga; TAW, Tawharanui; TMI, Tiri (2013, 2014, 2015).

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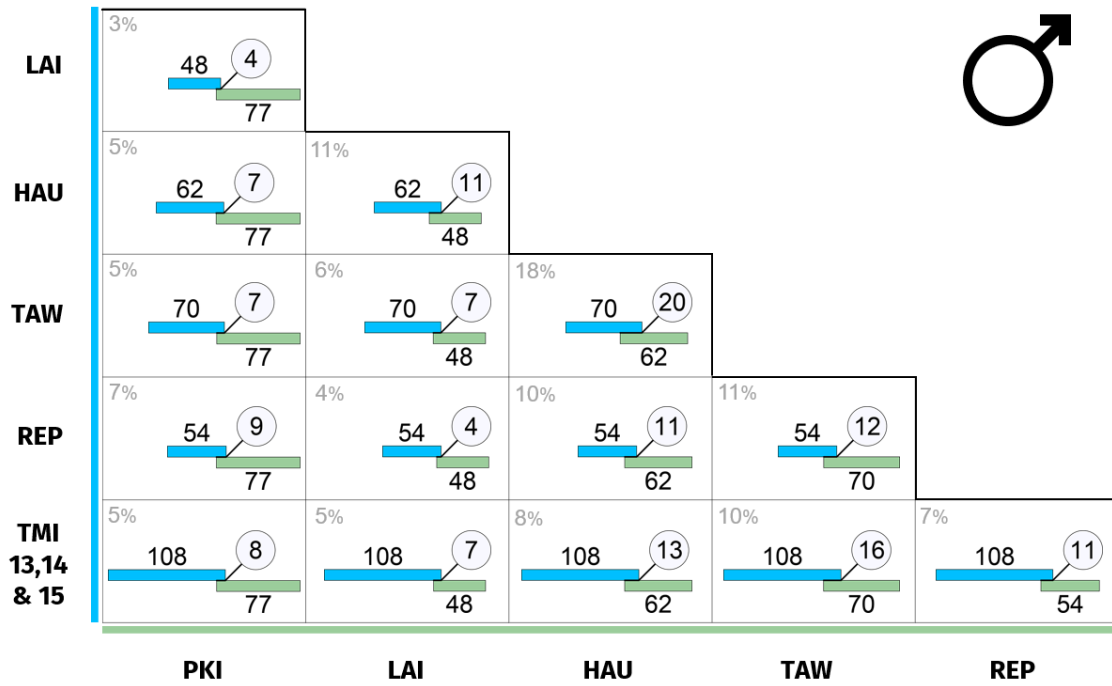
## 254 **The pattern of meme sharing between sites**

### 255 **Site–site repertoire overlap**

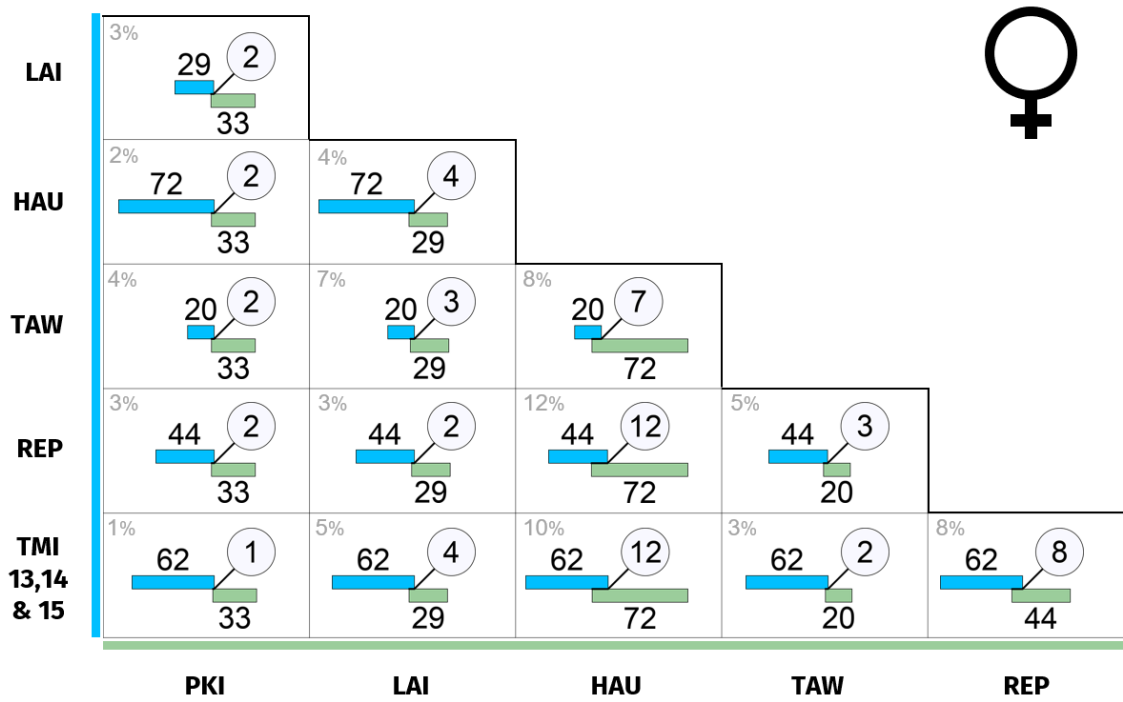
256 Matrices of site–site repertoire overlap are presented in Figure 4. The degree of site-site  
257 repertoire overlap between male populations was low, ranging 3–18% (median=6%); for  
258 females: 1–12% (median=5%). Remarkably, for both sexes, the syllable types shared  
259 between sites were almost exclusively pure-tone whistle syllables or simple stutter-like  
260 syllables. The one exception was Hauturu–Tawharanui, which additionally shared some  
261 more complex types following the recent Hauturu→Tawharanui founder event (Brunton  
262 et al., 2008). See Data S2.

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269 **Figure 4—(Top) Male population repertoire overlap between sites. (Bottom) Female population**  
270 **repertoire overlap between sites.**

271 Each cell indicates the recorded number of syllable types for the two sites (blue and green bars), and the  
272 number of types common to both (circle). The percentage overlap is given at the top left of each cell and is  
273 calculated as Jaccard similarity index:  $\text{Number of types shared} / (\text{number of types at Site A} + \text{number of}$   
274  $\text{types at Site B} - \text{number of types shared})$ . For robustness, repertoires exclude types with fewer than three  
275 occurrences within that site and sex. Bar length is proportional to the number of syllable types, and  
276 overlap length is proportional to the shared number of syllable types. Site abbreviations are as follows:  
277 PKI, Tawhiti Rahi (representing Poor Knights Islands); LAI, Lady Alice Island (representing Hen and  
278 Chickens); HAU, Hauturu; TAW, Tawharanui; REP, Repanga; TMI, Tiri.

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280 **Repertoire overlap versus distance**

281 Repertoire overlap with Hauturu versus geographic distance from Hauturu is shown in  
282 Figure 5A. There was a negative correlation between sharing and distance for males ( $r_s = -$   
283  $0.90$ ,  $df=3$ ,  $0.03 < p < 0.05$ ) but no relationship for females ( $r_s = -0.10$ ,  $df=3$ ,  $p > 0.10$ ). Contrary  
284 to predictions, sites at increasing distances from Hauturu did not share a progressively  
285 diminishing subset of syllable types with Hauturu, but different (apparently unrelated)  
286 subsets; this was true for both males and females (Data S2).

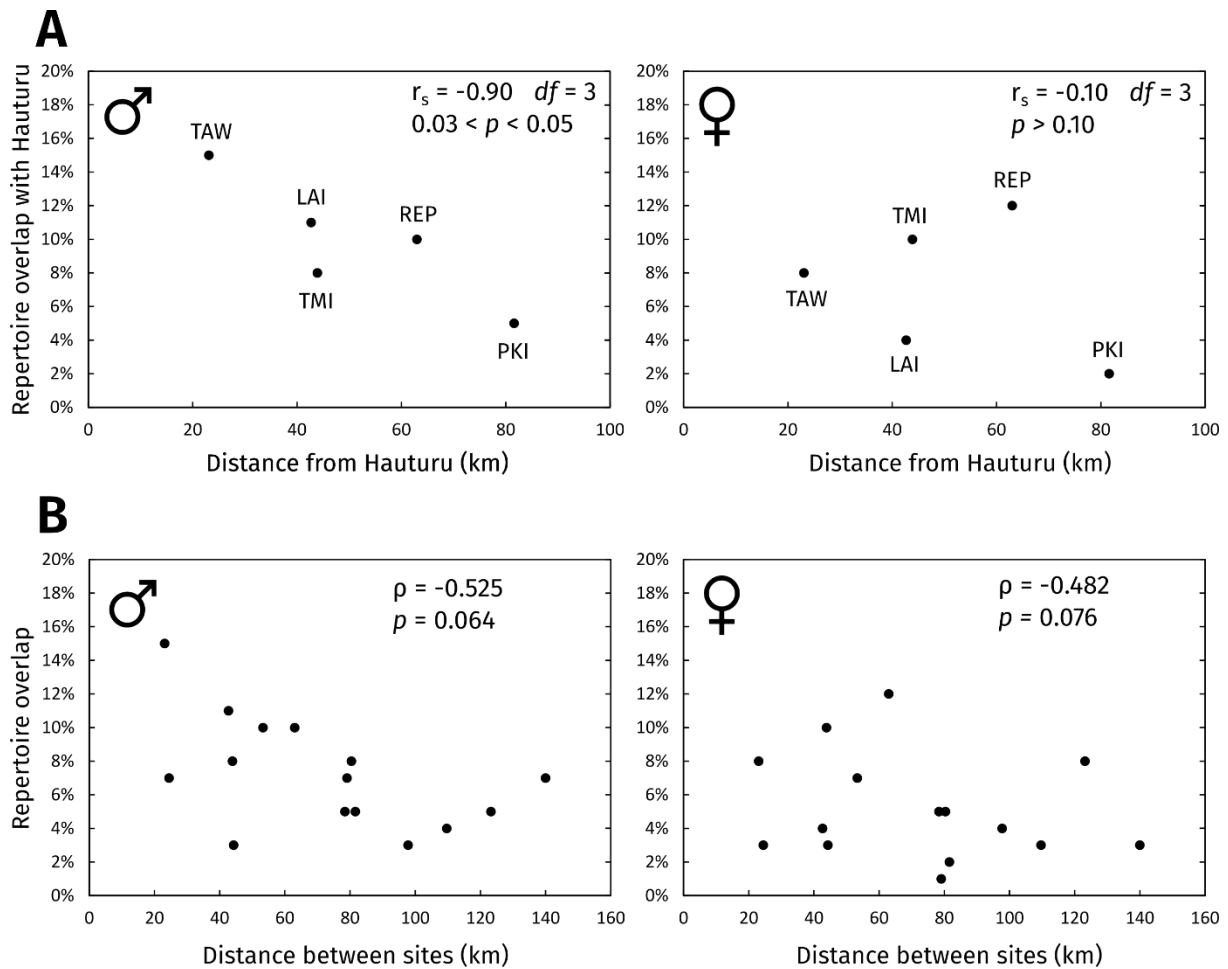
287 When considering sharing between *all* pairwise combinations of sites in the archipelago  
288 (Figure 5B), we did not find evidence of an isolation-by-distance pattern, for males ( $\rho = -$   
289  $0.525$ ,  $p = 0.064$ ) and females ( $\rho = -0.525$ ,  $p = 0.076$ ).

290 The recent founder event, where bellbirds from Hauturu colonised Tawharanui (Brunton  
291 et al., 2008) could possibly inflate the degree of sharing between the two sites, compared  
292 to other sites where both populations are long-established. Therefore we tested  
293 robustness of the correlations to removal of the Hauturu–Tawharanui datapoint, but  
294 found little change in the slope or strength of the correlations.

295 There was no evidence of an overall difference between males and females in the degree  
296 of site-site repertoire overlap; out of 15 site-site comparisons, males shared a higher  
297 percentage of syllables than females in 9 cases, lower in 4 cases, and equal in two cases  
298 (Sign Test  $p = 0.17$ ).

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303 **Figure 5—Repertoire overlap versus distance between sites.**

304 **(A)** Repertoire overlap with Hauturu versus distance from Hauturu. Overlaps were calculated on  
305 repertoire lists of types with 3+ occurrences within each site-and-sex group. Site abbreviations: TAW,  
306 Tawharanui; LAI, Lady Alice Island (representing Hen and Chickens); TMI, Tiri (2013, 2014, 2015); REP,  
307 Repanga; PKI, Tawhiti Rahi (representing Poor Knights Islands). **(B)** Site-site repertoire overlap versus  
308 site-site geographic distance, for all pairs of sites. Spearman rank correlations were calculated using the  
309 RELATE routine in *PRIMER* (version 7) with 9999 permutations, accounting for the non-independence of  
310 points.

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## 314 **Discussion**

315 This is one of the first comparisons of male and female song cultures over space (Mennill  
316 and Rogers, 2006; Graham et al., 2018a, 2018b, 2021). We found that male and female  
317 bellbirds have comparable repertoire sizes (at a population level; Table 2), and sexually  
318 distinct vocal cultures, sharing only a small percentage of syllable types between sexes  
319 (6–26% within each site; Figure 2). Whether a type is male-specific, female-specific, or  
320 shared between sexes can be predicted based on its acoustic properties (Figure 3).  
321 Furthermore, song cultures of both sexes differ dramatically between sites—  
322 demonstrating male and female song dialects (Figure 4, Data S1). Despite a large and  
323 varied repertoire *within* sites, generally the only types shared *between* sites were flat-  
324 contour, pure-tone whistle syllables (Article S1A) or simple stutter-like syllables.  
325 Between-site sharing of these syllable types decreased with distance for males but not  
326 females. These contrasting patterns of sharing across the archipelago may result from sex  
327 differences in dispersal, meme mutation rates and song-learning modes.

328 Comparisons of male and female repertoire sizes typically focus on individual-level  
329 repertoires. Such studies have found smaller female repertoires in some cases (e.g.  
330 rufous-and-white wrens *Thryophilus rufalbus*, Mennill and Vehrencamp, 2005; banded  
331 wrens *Thryophilus pleurostictus*, Hall et al., 2015), equal-sized repertoires in other cases  
332 (e.g. bay wren *Thryothorus nigricapillus*, Levin, 1996), and at least one case of larger  
333 female repertoire size (stripe-headed sparrow *Peucaea r. ruficauda*, Illes, 2014). The  
334 drivers of individual repertoire size are thought to differ between sexes, with males under  
335 selection from male–male competition and female choice (Catchpole, 1987; Hill et al.,  
336 2018), and females primarily from female–female competition for non-sexual breeding  
337 resources (Tobias et al., 2012). In the present study, similar male and female repertoire

338 sizes could be explained by bellbird social ecology. Bellbirds are socially monogamous  
339 (Roper, 2018), and both sexes are highly social and aggressive in singing interactions. It  
340 is plausible, therefore, that similar intensity of competition and social interaction drive  
341 the evolution of similar syllable diversity in the two sexes. However, our analysis is on  
342 population-level repertoires, which are a product of both individual repertoire sizes and  
343 variation between individuals. For example, equal male and female population repertoire  
344 sizes could also result if male individual repertoires are larger and more consistent  
345 between individuals (cultural conformity; Aplin et al., 2015), and females smaller and  
346 more variable (cultural non-conformity; Riebel et al., 2015). Additional focused recording  
347 of banded individuals is required to quantify these two sources of diversity.

348 It is interesting that population repertoire sizes varied greatly between sites. Adaptation  
349 to differing acoustic environments (Potvin and Clegg, 2015; Graham et al., 2017b) seems  
350 an unlikely explanation, as all sites were coastal, with similar vegetation structure  
351 (though soundscape was not measured). Another potential explanation is that genetic  
352 diversity has driven population repertoire size. However, sites with low genetic diversity  
353 (Baillie, 2011) did not have correspondingly low syllable diversity, suggesting song  
354 culture is not tightly constrained by genetic diversity in bellbirds (see also Graham et al.,  
355 2018). We suspect that between-site differences in repertoire size are more likely driven  
356 by competition level. For example, sites with higher population density may have elevated  
357 competition for food, or sites with high population connectivity may experience increased  
358 competitive encounters with migrants—selecting for bigger individual repertoires.

359 The discovery of sexually distinct, yet partly overlapping syllable repertoires raises  
360 questions about transmission and function. Logically, all sex-specific syllables types must  
361 be learnt male-to-male or female-to-female (as in rufous-and-white wrens, for example;

362 Mennill and Vehrencamp, 2005). But what of types common to both sexes? These must  
363 reflect inter-sexual learning in some form, whether accidental or intentional (Evans and  
364 Kleindorfer, 2016). Once learnt inter-sexually, these memes could be transmitted intra-  
365 sexually and become an established part of the repertoire for that sex. Roper et al. (2018)  
366 found that juvenile male and female bellbird song is spectrally similar, then diverges prior  
367 to crystallisation. Perhaps both sexes of bellbird are physiologically capable of  
368 overlapping in acoustic space, but other factors (e.g. learning strategies, sexual/social  
369 selection) prevent it in the wild. This appears true in slate-coloured boubous *Laniarius*  
370 *funnebris*; male and female boubous share no syllable types in the wild, but birds hand-  
371 raised under experimental conditions develop syllables of both sexes (Wickler and Seibt,  
372 1988). Wild birds may choose to express sex-specific memes to help avoid being mistaken  
373 for the other sex, which risks attracting same-sex rivals or repelling potential mates  
374 (Logue et al., 2007). However, the benefit of *shared* syllables is unclear. Might sex-specific  
375 syllables function in intra-sexual communication, and shared syllables in inter-sexual  
376 communication? Sophisticated field experiments with banded individuals are needed to  
377 resolve meme functions and transmission modes in bellbirds.

378 We found that male-specific and female-specific syllables do occupy two largely distinct  
379 regions of acoustic space, with shared syllables occupying a cluster between in a 'sex-  
380 neutral' range (Figure 3). In the ordination, the consistent separation of male-specific and  
381 female-specific memes could be due to universal morphological constraints of body size  
382 and syrinx structure, as males are 20% larger than females (Heather and Robertson,  
383 2000) and have different syrinx morphologies (Roper, 2018). At the same time, the spread  
384 and shape of the clusters vary widely between sites, which may reflect site-specific  
385 cultures.



386 The pattern of meme sharing between sites defied our expectations. Repertoire similarity  
387 was not strongly related to geographic proximity between islands; only males showed  
388 some evidence of isolation with distance from Hauturu (Figure 5). However, for both  
389 sexes the percentage of syllable types shared between sites was small, and almost totally  
390 limited to pure-tone whistle syllables and simple stutter-like syllables (except for  
391 Hauturu–Tawharanui, which shared more types, likely due to the recent founder event  
392 described in Brunton et al., 2008). The observed pattern suggests that immigrants  
393 abandon most source memes after arrival, retaining only simple pure-tone and stutter-  
394 like types. Perhaps all but these simple types incur high aggression at new sites (‘colony  
395 password’ hypothesis; Feekes, 1977) and so are dropped in favour of the local dialect.

396 The large size and geographic centrality of the Hauturu population make it a likely source  
397 of dispersing bellbirds to other sites in the archipelago. Thus, one might expect the islands  
398 around Hauturu to form a chain of ‘stepping stones’ for bellbird dispersal, leading to  
399 progressively more dissimilar repertoires away from the central source population. There  
400 are many examples of such chains (Irwin et al., 2005; Parker et al., 2012; Lachlan et al.,  
401 2013). In contrast, we found that for both male and female bellbirds, sites at increasing  
402 distances from Hauturu did not share a progressively diminishing subset of syllable types  
403 with Hauturu, but different (apparently unrelated) subsets (Data S2). Therefore, our  
404 results suggest direct dispersal to each site from Hauturu, rather than serial dispersal  
405 along the island chain.

406 We predicted that female-biased dispersal in bellbirds should result in higher female  
407 meme flow and thus higher inter-site sharing for females than for males. Instead, we  
408 found no evidence for a sexual difference in amount of sharing between sites. That females  
409 do not show higher inter-site sharing suggests that other processes—such as a higher

410 turnover rate or weaker retention of source memes— counteract the greater connectivity  
411 of female memes between sites.

412 Large-scale studies of song culture in the wild are challenging. In contrast to a laboratory  
413 situation, it is difficult to amass data, the identity of individuals is not known, and there is  
414 little control over the social context of singing—which limits assessment of individual-  
415 level mechanisms. However, our population-level analyses reveal distinct and complex  
416 female culture with different spatial patterns to male culture. This underlines the  
417 inadequacy of the male-centric research paradigm and calls for comparisons of male and  
418 female repertoires in many more species (Riebel et al., 2019). Sophisticated field  
419 experiments are now needed to resolve the mechanisms of dispersal, selection and  
420 learning modes that give rise to the pattern we have uncovered.

421

422

## 423 **Author contributions**

424 Dianne Brunton and Wesley Webb conceived of the study. Wesley Webb, Michelle Roper,  
425 Dianne Brunton, and Aaron Harmer conducted the fieldwork with help from volunteers.  
426 Wesley Webb, Yukio Fukuzawa, and Michelle Roper created the song database. Wesley  
427 Webb, Yukio Fukuzawa and Matthew Pawley analysed the data, with guidance from  
428 Dianne Brunton and Aaron Harmer. Wesley Webb wrote the paper with guidance from  
429 the other authors.

## 430 **Data availability**

431 The interactive *Koe* database can be accessed online at [koe.io.ac.nz](http://koe.io.ac.nz) with username  
432 *korimako* and password Bellbird\_Culture. See Data S3 for a table of all acoustic units and  
433 annotations, and Data S4 for a table of all songs and their metadata. Measurements of all  
434 syllables can be accessed at [10.5281/zenodo.5072580](https://zenodo.org/record/5072580).

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440

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