Sexually distinct song cultures in a songbird metapopulation

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Abstract

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

Introduction

40 Culture is shared information or behaviour acquired through social learning from

41 conspecifics (Dawkins, 1976), involving the transmission of *memes* (units of culture) by

42 behavioural imitation. Vocal culture—the social learning of acoustic memes—has so far

43 been observed in songbirds (oscines; Passeri), some suboscines (*Procnias* spp.,

44 Cotingidae), parrots, hummingbirds, cetaceans, elephants, seals, bats, and humans (Paton

45 et al., 1981; Baptista and Schuchmann, 1990; Janik and Slater, 1997; Poole et al., 2005;

46 Sanvito et al., 2007; Catchpole and Slater, 2008; Kroodsma et al., 2013). In these taxa, the

47 vocal repertoire of a population changes as new memes are introduced through

48 immigration, copying errors, and innovation, while other memes fall out of use (Catchpole

49 and Slater, 2008). This leads to a diversification of the meme pool across the species, much

50 like the diversification of human language—resulting in dialects (Podos and Warren,

51 2007).

52 Despite the high volume of studies on male birdsong culture and dialects (Jenkins, 1978;

53 Whitehead and Rendell, 2014; Aplin, 2019), little is known about female song culture. This

54 is partly due to a northern-hemisphere-biased view of sexual selection that emphasises

55 male-male competition and female choice in driving elaborate traits in males (Darwin,

56 1871), but which does not provide a framework for understanding elaborate female traits

57 (Riebel et al., 2019). Female song (and other elaborate female traits) have been

58 overlooked as non-functional aberrations, resulting 'accidentally' from shared genetic

59 architecture with males (Darwin, 1871; Lande, 1980; see Tobias et al., 2012 for review).

60 This view has now been roundly discounted. Female song is present in 64% of surveyed

61 songbird species (Webb et al., 2016), has been recovered as the ancestral state (Odom et

62 al., 2014), can evolve independently of the male song phenotype (Price, 2015) and has

63   female-specific functions in territory and resource defence, mate attraction, mate defence,

64   and pair bonding (reviewed in Austin et al., 2021).

65   Overlooking females has impeded development of a more general theory that explains

66   song culture in both sexes. For instance, the possibility that females 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 (of just two species) have compared spatial variation of male and female

76   songs at a 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, 2018a, 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

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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 meme flow

109   between sites, and thus higher sharing of syllable types between sites than for males.

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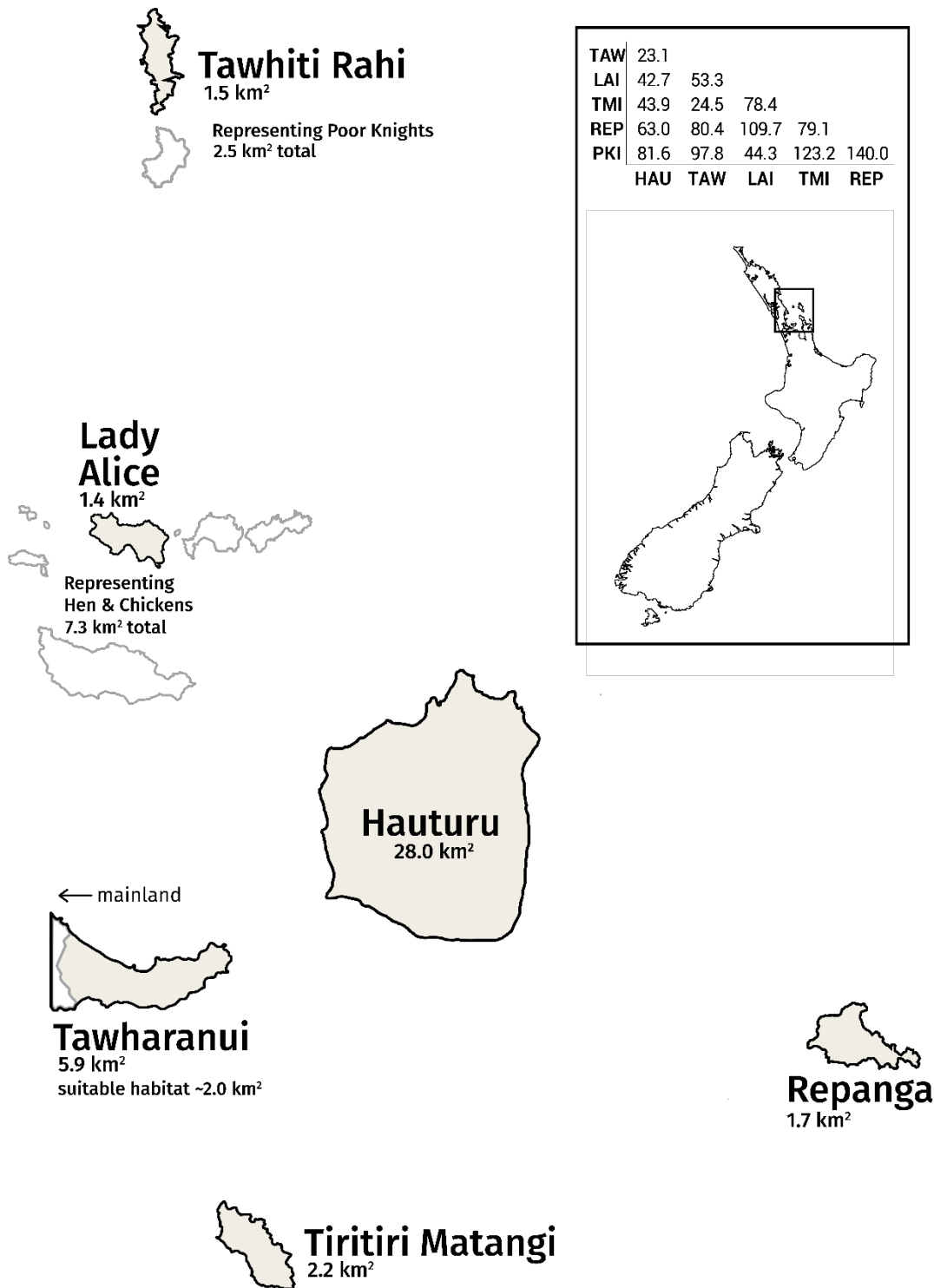
Figure 1—Simplified map of the Hauraki Gulf archipelago, home to a metapopulation of bellbirds.

Tawhiti Rahi represents the Poor Knights Islands group; likewise, Lady Alice Island represents the Hen 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 are not to scale on simplified map.

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Methods

Creating the song database

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.

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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 is from www.topomap.co.nz. In the *Sample size* column, M=male and F=female. Recording on Hauturu was restricted to an area ~3 km².

Sites	GPS Coordinates	Area (km²)	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

Segmenting songs into syllables

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

Classifying syllables

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

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

Sex differences in population-level repertoires

Male and female syllable diversity

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

Repertoire overlap of male and female population sectors

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

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

The pattern of syllable type sharing between sites

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

183   First, we conducted a Hauturu-centric analysis. The large size, geographic centrality, and

184   the long-term persistence of the Hauturu bellbird population make it likely to be a

185   substantial source of dispersing bellbirds to other sites in the Hauraki Gulf archipelago.

186   We calculated Spearman's rank correlation coefficients between *population repertoire*

187   *overlap with Hauturu* against *geographic distance from Hauturu*.

188   Next, to test for an overall isolation-by-distance pattern, we calculated Spearman's rank

189   correlation coefficients between *percentage of site–site repertoire overlap* against *site–site*

190   *geographic distance*, for all pairwise combinations of sites in the archipelago. In this case,

191   to account for non-independence of points (being pairwise combinations), we used the

192   RELATE 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).

Results

Sex differences in population repertoires

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   We found 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.

212

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*
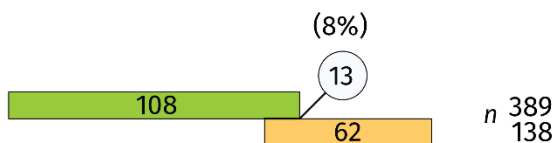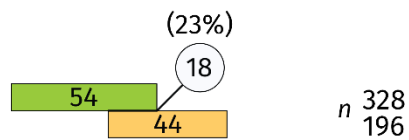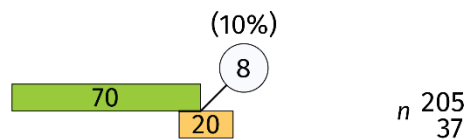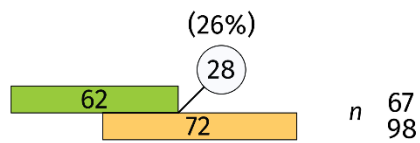
216   *S* (Colwell, 2013).

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

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Syllable types

Tawhiti Rahi
1.5 km^2

Representing
Poor Knights
2.5 km^2 total

♂ (6%) shared
6
77
33
♀
n 306
58

Lady Alice
1.4 km^2
Representing
Hen & Chickens
7.3 km^2 total

(10%)
7
48
29
n 181
126

0.4 km^2

2.6 km^2

(26%)
28
62
72
n 67
98

Hauturu
28.0 km^2

Tawharanui
5.9 km^2
Suitable habitat ~2.0 km^2

(10%)
8
70
20
n 205
37

Repanga
2.0 km^2

(23%)
18
54
44
n 328
196

Tiri 2013, 2014, 2015
2.2 km^2

(8%)
13
108
62
n 389
138

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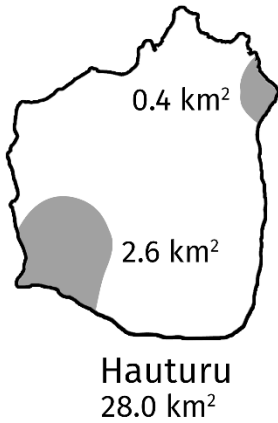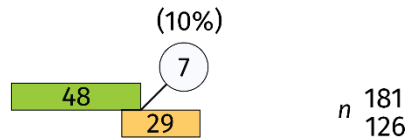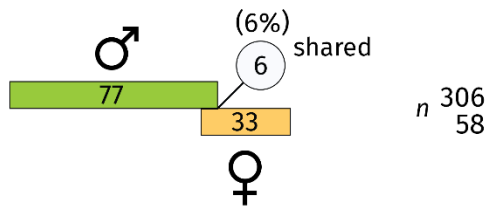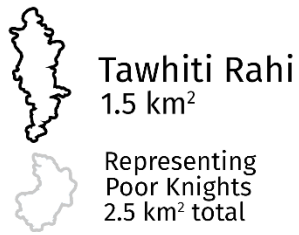
219 **Figure 2—Overlap of male and female population syllable repertoires.**

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 of shared types 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. Site outlines on the left of the figure are

229 to scale. The shaded grey area in the Hauturu outline indicates the sampled region of the island.

230

231 In the Linear Discriminant Analysis (LDA) ordination, male-only and female-only syllables

232 form two clear, partially-overlapping clusters, with shared syllables in between, when

233 data from all sites are pooled. For individual sites the configuration of the three clusters

234 varies but shows a tendency for female-only syllables to occur at lower LD1 values, male-

235 only to occur at higher LD1 values, with shared syllables in between.

236 Success of the LDA leave-one-out classifier had an overall *lift* of 1.78; that is, the LDA

237 assigned labels (male-only, female-only and shared) to syllables overall 1.78 times better

238 than random allocation of labels. Lift was 1.51 for male-only syllables, 3.99 for female-

239 only syllables, and 2.15 for shared syllables. P values for all lift tests were <0.001; i.e., in

240 all cases none of the 4999 null distributions had a lift as large as the observed lift.

241 Therefore, male-only, female-only, and shared types can be separated on the basis of

242 acoustic features.

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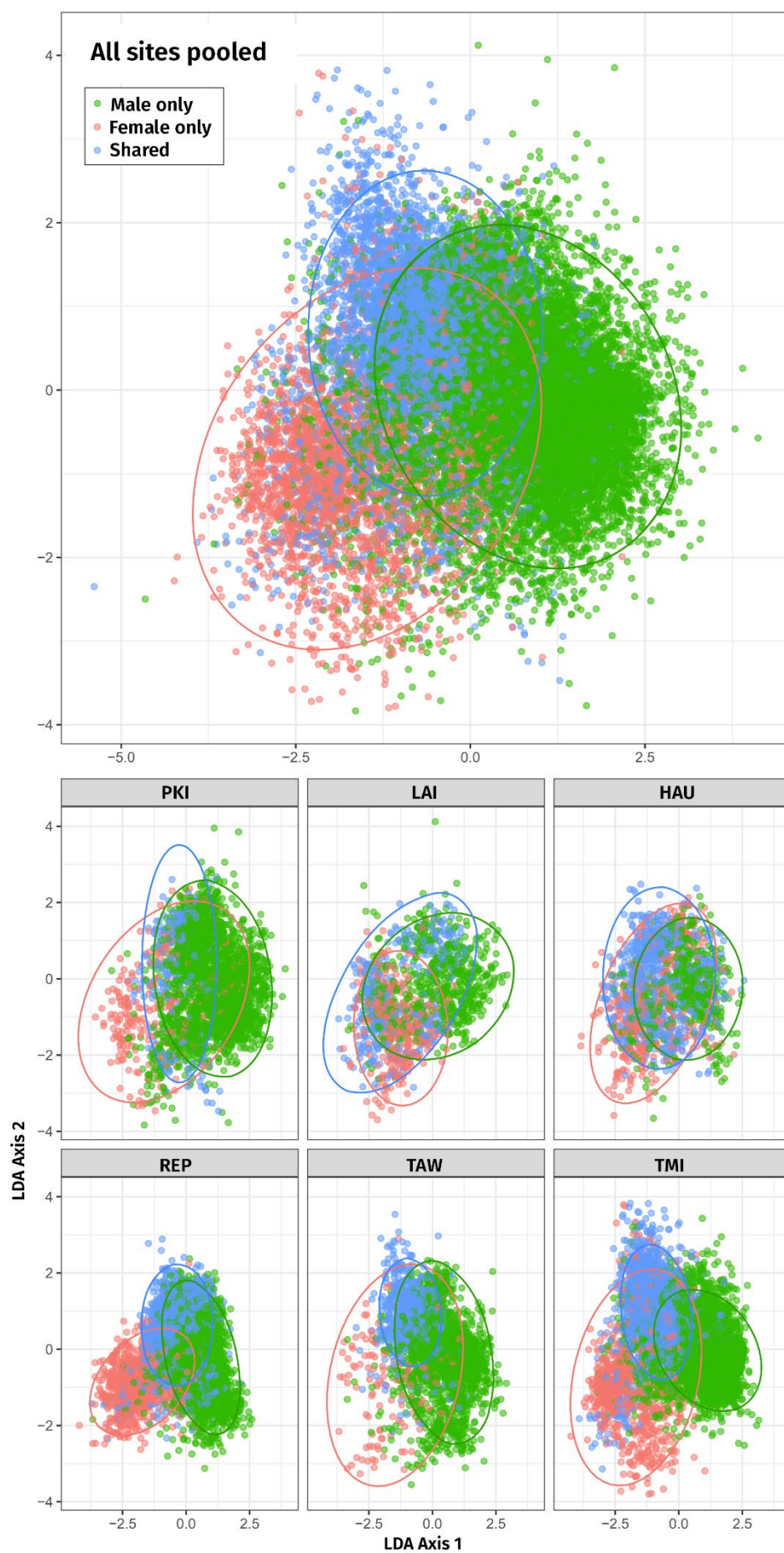
Figure 3—Two-dimensional linear discriminant analysis (LDA) of male-only, female-only, and shared syllables for all sites combined (top) and each site separately (bottom).

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

The pattern of meme sharing between sites

Site–site repertoire overlap

Matrices of site–site repertoire overlap are presented in Figure 4. The degree of site-site repertoire overlap between male populations was low, ranging 3–18% (median=6%); for females: 1–12% (median=5%). Remarkably, for both sexes, the syllable types shared between sites were almost exclusively pure-tone whistle syllables or simple stutter-like syllables. The one exception was Hauturu–Tawharanui, which additionally shared some more complex types following the recent Hauturu→Tawharanui founder event (Brunton et al., 2008). See Data S1 and Data S2.

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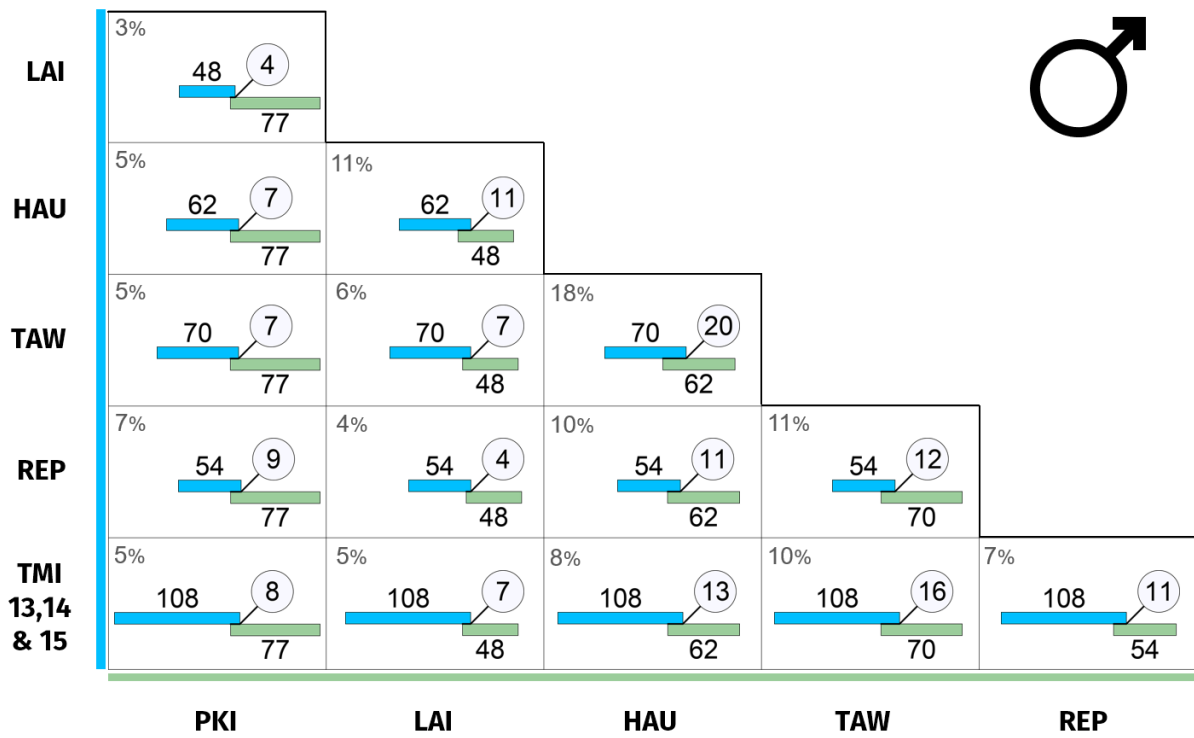
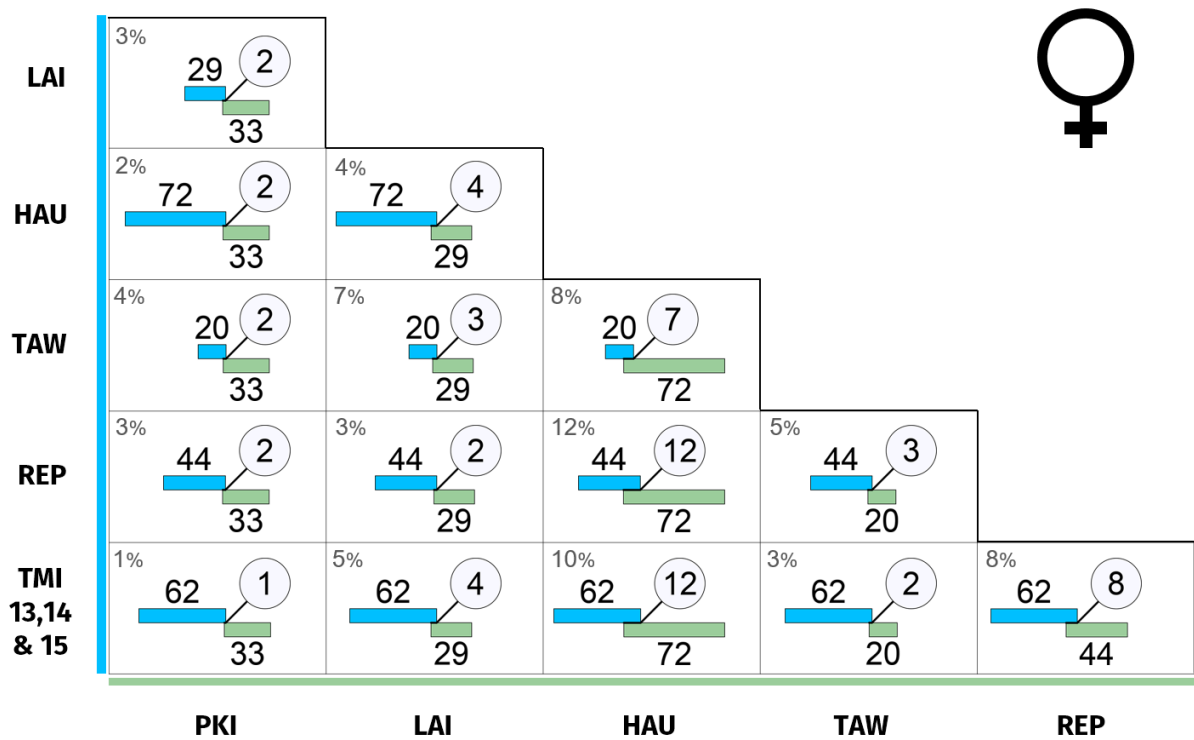271   **Figure 4—(*Top*) Male population repertoire overlap between sites. (*Bottom*) Female population**
272   **repertoire overlap between sites.**

273   Each cell indicates the recorded number of syllable types for the two sites (blue and green bars), and the

274   number of types common to both (circle). The percentage overlap is given at the top left of each cell and is

275   calculated as Jaccard similarity index: number of shared types divided by total number of types. For

276   robustness, repertoires exclude types with fewer than three occurrences within that site and sex. Bar

277   length is proportional to the number of syllable types, and overlap length is proportional to the shared

278   number of syllable types. Site abbreviations are as follows: PKI, Tawhiti Rahi (representing Poor Knights

279   Islands); LAI, Lady Alice Island (representing Hen and Chickens); HAU, Hauturu; TAW, Tawharanui; REP,

280   Repanga; TMI, Tiri.

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282 **Repertoire overlap versus distance**

283 The relationship between repertoire overlap with Hauturu versus geographic distance

284 from Hauturu is shown in Figure 5A. There was a negative correlation between sharing

285 and distance for males (r_s = -0.90, df=3, 0.03<P<0.05) but no relationship for females (r_s

286 =-0.10, df=3, P>0.10). Contrary to predictions, sites at increasing distances from Hauturu

287 did not share a progressively diminishing subset of syllable types with Hauturu, but

288 different (apparently unrelated) subsets; this was true for both males and females (Data

289 S2).

290 When considering sharing between *all* pairwise combinations of sites in the archipelago

291 (Figure 5B), we did not find evidence of an isolation-by-distance pattern, for males (ρ=

292 -0.525, P=0.064) or females (ρ=-0.525, P=0.076).

293 The recent founder event, where bellbirds from Hauturu colonised Tawharanui (Brunton

294 et al., 2008) could possibly inflate the degree of sharing between the two sites, compared

295 to other sites where both populations are well established. Therefore we tested

296 robustness of the correlations to removal of the Hauturu–Tawharanui datapoint, but

297 found little change in the slope or strength of the correlations.

298 There was no evidence of an overall difference between males and females in the degree

299 of site-site repertoire overlap; out of 15 site-site comparisons, males shared a higher

300 percentage of syllables than females in 9 cases, lower in 4 cases, and equal in two cases

301 (Sign Test P=0.17).

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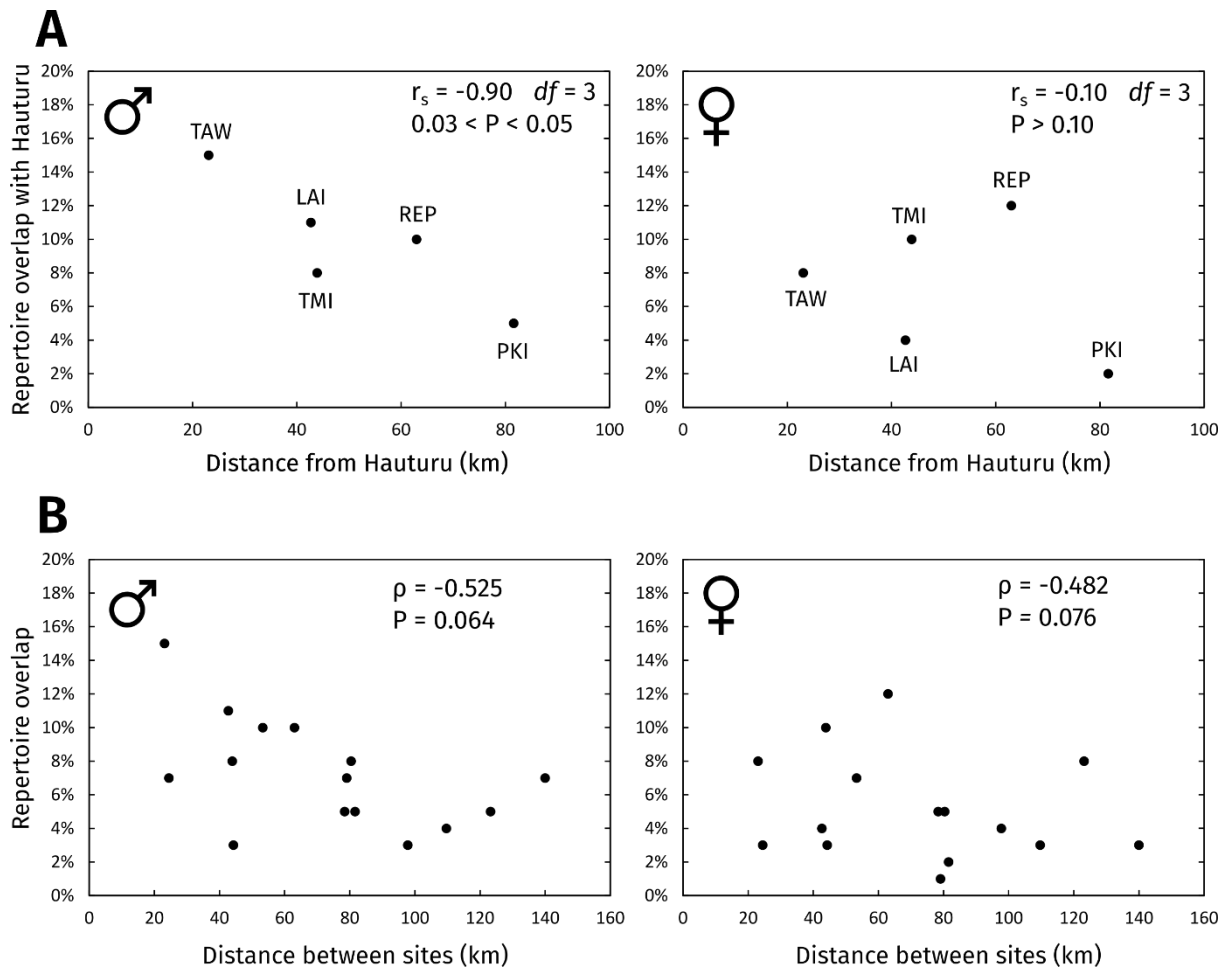
Figure 5—Repertoire overlap versus distance between sites.

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

Discussion

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318 This is one of the first comparisons of male and female song cultures across a

319 metapopulation (Mennill and Rogers, 2006; Graham et al., 2018a, 2018b, 2021). We found

320 that male and female bellbirds have comparable repertoire sizes (at a population level;

321 Table 2), and sexually distinct vocal cultures, sharing only a small percentage of syllable

322 types between sexes (6–26% within each site; Figure 2). Whether a type is male-specific,

323 female-specific, or shared between sexes can be predicted based on its acoustic properties

324 (Figure 3). Furthermore, song cultures of both sexes differ dramatically between sites—

325 demonstrating male and female song dialects (Figure 4, Data S1). Despite a large and

326 varied repertoire *within* sites, generally the only types shared *between* sites were flat-

327 contour, pure-tone whistle syllables (Article S1A) or simple stutter-like syllables.

328 Between-site sharing of these syllable types decreased with distance for males but not

329 females. These contrasting patterns of sharing across the archipelago may result from sex

330 differences in dispersal, meme mutation rates and song-learning modes.

331 Comparisons of male and female repertoire sizes typically focus on individual-level

332 repertoires. Such studies have found smaller female repertoires in some cases (e.g.,

333 rufous-and-white wrens *Thryophilus rufalbus*, Mennill and Vehrencamp, 2005; banded

334 wrens *Thryophilus pleurostictus*, Hall et al., 2015), equal-sized repertoires in other cases

335 (e.g., bay wren *Thryothorus nigricapillus*, Levin, 1996), and at least one case of larger

336 female repertoire size (stripe-headed sparrow *Peucaea r. ruficauda*, Illes, 2014). The

337 drivers of individual repertoire size are thought to differ between sexes, with males under

338 selection from male–male competition and female choice (Catchpole, 1987; Hill et al.,

339 2018), and females perhaps primarily from female–female competition for non-sexual

340 breeding resources (Tobias et al., 2012). In the present study, similar male and female

21

341   repertoire sizes may be explained by bellbird social ecology. Bellbirds are socially

342   monogamous, and both sexes are highly social and aggressive in singing interactions

343   (Roper, 2018). It is plausible, therefore, that similar intensity of competition and social

344   interaction drive the evolution of similar syllable diversity in the two sexes. However, our

345   analysis is on population-level repertoires, which are a product of both individual

346   repertoire sizes and variation between individuals. For example, equal male and female

347   population repertoire sizes could also result if male individual repertoires are larger and

348   more consistent between individuals (cultural conformity; Aplin et al., 2015), and females

349   smaller and more variable (cultural non-conformity; Riebel et al., 2015). Additional

350   focused recording of banded individuals is required to quantify these two sources of

351   diversity.

352   It is interesting that population repertoire sizes varied greatly between sites. Adaptation

353   to differing acoustic environments (Potvin and Clegg, 2015; Graham et al., 2017b) seems

354   an unlikely explanation, as all sites were coastal, with similar vegetation (though

355   soundscape was not measured). Another potential explanation is that genetic diversity

356   has driven population repertoire size. However, sites with low genetic diversity (Baillie,

357   2011) did not have correspondingly low syllable diversity, suggesting song culture is not

358   tightly constrained by genetic diversity in bellbirds (see also Graham et al., 2018). We

359   suspect that between-site differences in repertoire size are more likely driven by

360   competition level. For example, sites with higher population density may have elevated

361   competition for food, or sites with high population connectivity may experience increased

362   competitive encounters with migrants—selecting for bigger individual repertoires.

363   The discovery of sexually distinct, yet partly overlapping syllable repertoires raises

364   questions about transmission and function. Logically, all sex-specific syllable types must

365 be learnt male-to-male or female-to-female (as in rufous-and-white wrens, for example;

366 Mennill and Vehrencamp, 2005). But what of types common to both sexes? These must

367 reflect inter-sexual learning in some form, whether accidental or intentional (Evans and

368 Kleindorfer, 2016). Once learnt inter-sexually, these memes could be transmitted intra-

369 sexually and become an established part of the repertoire for that sex. Roper et al. (2018)

370 found that juvenile male and female bellbird song is spectrally similar, then diverges prior

371 to crystallisation. Perhaps both sexes of bellbird are physiologically capable of

372 overlapping in acoustic space, but other factors (e.g., learning strategies, sexual/social

373 selection) prevent it in the wild. This appears true in slate-coloured boubous *Laniarius*

374 *funebris*; male and female boubous share no syllable types in the wild, but birds hand-

375 raised under experimental conditions develop syllables of both sexes (Wickler and Seibt,

376 1988). Wild birds may choose to express sex-specific memes to help avoid being mistaken

377 for the other sex, which risks attracting same-sex rivals or repelling potential mates

378 (Logue et al., 2007). However, the benefit of *shared* syllables is unclear. Might sex-specific

379 syllables function in intra-sexual communication, and shared syllables in inter-sexual

380 communication? Sophisticated field experiments with banded individuals are needed to

381 resolve meme functions and transmission modes in bellbirds.

382 We found that male-specific and female-specific syllables do occupy two largely distinct

383 regions of acoustic space, with shared syllables occupying a cluster between in a 'sex-

384 neutral' range (Figure 3). In the ordination, the separation of male-specific and female-

385 specific memes could be due to universal morphological constraints of body size and

386 syrinx structure, as males are 20% larger than females (Heather and Robertson, 2000)

387 and have different syrinx morphologies (Roper, 2018). At the same time, the spread and

388 shape of the clusters vary widely between sites, which may reflect site-specific cultures.

389 The pattern of meme sharing between sites defied our expectations. Repertoire similarity

390 was not strongly related to geographic proximity between islands; only males showed

391 some evidence of isolation with distance from Hauturu (Figure 5). However, for both

392 sexes the percentage of syllable types shared between sites was small, and almost totally

393 limited to pure-tone whistle syllables and simple stutter-like syllables (except for

394 Hauturu–Tawharanui, which shared more types, likely due to the recent founder event

395 described in Brunton et al., 2008). The observed pattern suggests that immigrants

396 abandon most source memes after arrival, retaining only pure-tone and stutter-like types.

397 Perhaps all but these simple types incur high aggression at new sites ('colony password'

398 hypothesis; Feekes, 1977) and so are dropped in favour of the local dialect.

399 The large size and geographic centrality of the Hauturu population make it a likely source

400 of dispersing bellbirds to other sites in the archipelago. Thus, one might expect the islands

401 around Hauturu to form a chain of 'stepping stones' for bellbird dispersal, leading to

402 progressively more dissimilar repertoires away from the central source population. There

403 are many examples of such chains (Irwin et al., 2005; Parker et al., 2012; Lachlan et al.,

404 2013). In contrast, we found that for both male and female bellbirds, sites at increasing

405 distances from Hauturu did not share a progressively diminishing subset of syllable types

406 with Hauturu, but different (apparently unrelated) subsets (Data S2). Therefore, our

407 results suggest direct dispersal to each site from Hauturu, rather than serial dispersal

408 along the island chain.

409 We predicted that female-biased dispersal in bellbirds should result in higher female

410 meme flow and thus higher inter-site sharing for females than for males. Instead, we

411 found no evidence for a sexual difference in amount of sharing between sites. That females

412 do not show higher inter-site sharing suggests that other processes—such as a higher

413   turnover rate or weaker retention of source memes—counteract the greater connectivity

414   of females between sites.

415   Large-scale studies of song culture in the wild are challenging. In contrast to a laboratory

416   situation, it is difficult to amass data, the identity of individuals is not known, and there is

417   little control over the social context of singing—which limits assessment of individual-

418   level mechanisms. However, our population-level analyses reveal distinct and complex

419   female culture with different spatial patterns to male culture. This underlines the

420   inadequacy of the male-centric research paradigm and calls for comparisons of male and

421   female repertoires in many more species (Riebel et al., 2019). Sophisticated field

422   experiments are now needed to resolve the mechanisms of dispersal, selection and

423   learning modes that give rise to the pattern we have uncovered.

424

425

426   ## Author contributions

427   Dianne Brunton and Wesley Webb conceived of the study. Wesley Webb, Michelle Roper,

428   Dianne Brunton, and Aaron Harmer conducted the fieldwork with help from volunteers.

429   Wesley Webb, Yukio Fukuzawa, and Michelle Roper created the song database. Wesley

430   Webb, Yukio Fukuzawa and Matthew Pawley analysed the data, with guidance from

431   Dianne Brunton and Aaron Harmer. Wesley Webb wrote the paper with guidance from

432   the other authors.

Data availability

The interactive *Koe* database can be accessed online at koe.io.ac.nz with username *korimako* and password Bellbird_Culture. See Data S3 for a table of all acoustic units and annotations, and Data S4 for a table of all songs and their metadata. Measurements of all syllables can be accessed at 10.5281/zenodo.5072580.

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