

1 **Title:** Sex role similarity and sexual selection predict male and female song elaboration and
2 dimorphism in fairy-wrens

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44
45 **Keywords:** Fairy-wren, female song, dimorphism, elaboration, sex roles, sexual selection

46
47 **Running head:** Male and female fairy-wren song dimorphism

48 **Abstract**

49 Historically, bird song complexity was thought to evolve primarily through sexual selection on
50 males, yet in many species both sexes sing. Previous research suggests competition for mates and
51 resources during short, synchronous breeding seasons leads to more elaborate male songs at high
52 latitudes. In contrast, we expect male-female song dimorphism and elaboration to be more
53 similar at lower latitudes because longer breeding seasons and year-round territoriality yield
54 similar social selection pressures in both sexes. However, studies seldom take both selective
55 pressures and sexes into account. We examined song elaboration and sexual dimorphism in 15
56 populations of nine fairy-wren species (Maluridae), a Southern Hemisphere clade with female
57 song. We compared song elaboration and sexual song dimorphism to latitude and life history
58 variables tied to sexual and social selection pressures and sex roles. Our results suggest that song
59 elaboration evolved in part due to sexual competition in males: male song variability was more
60 positively correlated with temperate breeding and greater breeding synchrony than female song.
61 We also found strong evidence that sex-role similarity contributed to male-female song
62 similarity: male and female songs were shorter and more similar when parental care was more
63 equal and when male survival was high. Contrary to Northern Hemisphere latitudinal patterns,
64 songs were less dimorphic at higher, temperate latitudes. These results suggest that selection on
65 song can be sex-specific, with male song elaboration favored in contexts coincident with sexual
66 selection. However, selection pressures associated with sex-role similarity also appear to
67 constrain sex specific song evolution and song dimorphism.

68

69 Elaborate traits, including conspicuous colors, complex vocalizations, and vigorous
70 displays are often thought of as a product of sexual selection acting on males (Andersson 1994).
71 However, females also display elaborate traits, and recent research shows that these can be
72 similarly adaptive and not exclusively sexually selected (Langmore 1998; Amundsen 2000;
73 Odom et al. 2014; Dale et al. 2015). These findings suggest a more complex selective landscape
74 responsible for trait elaboration, especially sexual dimorphism (Rosvall 2011; Tobias et al. 2012;
75 Price 2015). Sexual selection theory makes straightforward predictions that traits should be more
76 elaborate when competition for matings is high (Andersson 1994; Tobias et al. 2012). This
77 theory is less applicable to females, as access to mates is seldom what affects variance in female
78 reproductive success (Emlen and Oring 1977; West-Eberhard 1983, but see Langmore et al.
79 1996). Instead, evidence suggests that elaborate female traits often function in female-female
80 competition to gain access to resources (for themselves or their offspring), and less often
81 exclusively to obtain mates (Rosvall 2011; Tobias et al. 2012). Thus, social selection in the form
82 of intra-sexual competition for resources other than mates may have played a particularly large
83 role in the evolution of elaborate female traits (Clutton-Brock 2009; Rosvall 2011; Tobias et al.
84 2012).

85 Similarly, sexual dimorphism is thought to evolve primarily through strong sexual
86 selection for elaboration in males (Catchpole 1982; Andersson 1994). However, dimorphism
87 may arise from a number of selective pressures, including initial selection for elaborate
88 monomorphism in both sexes, followed by selection away from elaboration in females (Hofmann
89 et al. 2008; Odom et al. 2014; Dale et al. 2015). Along these lines, recent research shows that
90 elaborate female traits can be selected against by nest predation risk or other reproductive costs
91 associated with those traits (Soler and Moreno 2012; Kleindorfer et al. 2016; but see Cain et al.
92 2019). In such instances, multiple selective pressures acting in concert on both males and
93 females could also influence overall patterns of sexual dimorphism (Wiens 2001; Hofmann et al.
94 2008; Johnson et al. 2013; Dale et al. 2015). In other instances, male and female elaborate traits
95 can be selected for by similar selective pressures, but the strength or direction of selection may
96 differ between the sexes (Soler and Moreno 2012; Dale et al. 2015). Therefore, to understand
97 how dimorphism evolves, it is important to consider the selective pressures that promote
98 similarity, as well as differences, in both males and females (Price 2015).

99 Bird songs offer an excellent system to investigate the range of selective pressures that
100 have shaped variation in male and female elaboration and dimorphism. Northern temperate male
101 bird song is thought to be sexually selected, but other forms of selection have attracted less
102 attention (Catchpole & Slater, 2008). The recent realization that female bird song is globally
103 widespread and ancestral suggests that diverse selective pressures are likely to act on females, as
104 well as males, to produce the range of variation in male and female song seen today (Odom et al.
105 2014; Riebel et al. 2019).

106 One pattern commonly associated with sexual selection on male song is increased song
107 complexity at higher, more temperate latitudes (Read & Weary, 1992; Catchpole & Slater, 2008;
108 Najar & Benedict, 2019). It is hypothesized that increased complexity at higher latitudes occurs
109 because of increased sexual selection on migrating males to establish territories quickly and
110 attract females during short, synchronous temperate breeding seasons (Catchpole, 1982; Slater &
111 Mann, 2004). However, support for this pattern is mixed. About half of the studies on this topic
112 find no support for this or even the opposite pattern (reviewed in Najar and Benedict 2019).
113 Variation in these findings could be due to which song metrics are compared within each of these
114 studies (Benedict and Najar 2019), or to different evolutionary pressures acting on different

115 aspects of song structure and morphology (e.g., sexual selective pressures vs morphological
116 constraints; Cardoso and Hu 2011; Derryberry et al. 2012; Greig et al. 2013). Additionally,
117 virtually all of these studies have focused on northern temperate or Palearctic species. However,
118 latitudinal patterns of avian life history may differ in the equatorial regions and Southern
119 Hemisphere from those observed in the Northern Hemisphere (Robinson 1949; Martin 1996).
120 Lastly, to decipher overall patterns of bird song complexity, sex-specific differences in selective
121 pressures should be considered. This means that we need to consider the selective pressures
122 responsible for divergent sex roles, as well as selective pressures that might be actively selecting
123 for or maintaining similar sex roles (Price 2015; Riebel et al. 2019).

124 In contrast to the expected patterns of increased song complexity in high, temperate
125 latitudes, at low, tropical latitudes avian life-histories associated with more sedentary lifestyles
126 seem to select for more similar sex roles. At lower tropical latitudes, pairs often defend a
127 territory year-round, are longer lived, and may breed for extended parts of the year (Stutchbury
128 and Morton 2001; Martin 2015; Tobias et al. 2016). Longer lifespans coupled with year-round
129 territoriality and partnerships probably result in fewer vacant territories and potential partners,
130 and thus higher levels of competition for breeding opportunities (Slater and Mann 2004). In
131 addition, nest predation rates are higher in the tropics when controlling for nesting period, so,
132 along with longer breeding seasons, this may necessitate greater bi-parental care (Freeman et al.
133 2019). Altogether, these life history patterns appear to select for suites of traits, including
134 socially monogamous, long-term pair bonds, and similarity in sex roles in many non-migratory
135 songbirds (Slater and Mann 2004). Indeed, several studies find correlations between the presence
136 of female song or male-female duets and year-round territoriality, monogamy, long-term pair
137 bonds, and tropical or sedentary life-histories (Benedict 2008; Price 2009; Logue and Hall 2014;
138 Tobias et al. 2016). Therefore, the selective pressures that mediate sex role similarity in tropical
139 regions may also influence the evolution of ornamental traits in both females and males,
140 selecting for more similar behaviors and similar levels of trait elaboration (Slater and Mann
141 2004). With fewer migratory species in the Southern Hemisphere, we may expect to find life
142 history patterns there that are more similar to those seen in the tropics (Samaš et al. 2013; Lloyd
143 et al. 2014). Therefore, the Southern Hemisphere offers a good system to investigate whether
144 song complexity increases with latitude or if the expected relationships between song structure
145 and life history persist in the absence of latitudinal life history gradients. In general,
146 biogeographic patterns of song and life history in the Southern Hemisphere are a much needed
147 area of study (Martin 1996; Xiao et al. 2017).

148 In order to investigate these biogeographical patterns and the potential selective pressures
149 that may have shaped male and female variation in song, we compared a suite of life history
150 traits with elaboration and dimorphism of male and female song within and among nine fairy-
151 wren species belonging to the Maluridae, a well-studied clade with extensive breeding, social
152 organization, and life history data (Brouwer et al. 2017). We addressed three main questions: (1)
153 how similar are male and female songs within and among species, (2) which life history traits are
154 associated with elaboration in male and female song, and (3) which life history traits are
155 associated with dimorphism between male and female song? To evaluate possible selective
156 pressures associated with song elaboration and dimorphism, we compared a number of
157 reproductive and social variables to song structure, including extra-pair paternity, brood size,
158 breeding synchrony, proportion of provisioning by males, adult male survival, group size,
159 breeding density, and latitude.

160 If male and female song elaboration has been sexually selected, then we expect song
161 elaboration in each sex to increase with aspects of fairy-wren breeding behavior that are
162 associated with competition for mates, such as extra-pair mating, brood size, and breeding
163 synchrony. Extra-pair paternity is likely to reflect male variability in reproductive success
164 (Macedo et al. 2008; Brouwer and Griffith 2019). Similarly, breeding synchrony may represent
165 increased competition for social and extra-pair mates at the start of the breeding season, whereas
166 brood size may reflect variation in female reproductive investment (Stutchbury & Morton, 2001;
167 Catchpole & Slater, 2008). Conversely, if male and female song structure has been socially
168 selected or has been shaped more exclusively by intra-sexual social competition, then we expect
169 elaboration in each sex, and dimorphism, to increase with aspects of social structure, such as
170 group size or breeding density per population. Lastly, if song elaboration and dimorphism are
171 influenced by selective pressures associated with sex role similarity, then we expect male and
172 female songs to be most similar in conditions in which male and female roles are similar (e.g.,
173 high rates of bi-parental care, pair-breeding (rather than cooperative breeding) and potentially at
174 low, tropical latitudes). Moreover, male songs may be comparatively more elaborate when sex
175 roles are more divergent (e.g., low rates of paternal care and in temperate regions). These
176 hypotheses are not mutually exclusive, but rather may work together to shape overall patterns of
177 female and male variation in song.

178

179 **Methods**

180 In order to examine factors influencing sex differences in song, we obtained recordings
181 and life history data for 15 populations of nine species of fairy-wrens, resulting in data for the
182 following species and populations in Australia and Papua New Guinea: lovely (*Malurus*
183 *amabilis*; Cairns, QLD, 16.9186° S, 145.7781° E), purple-backed (*M. assimilis*; Brookfield
184 Conservation Park, SA, 34.3615° S, 139.4862° E (*M. a. assimilis*) & Kakadu (*M. a. dulcis*), NT
185 13.43 ° S, 132.42 ° E), purple-crowned (*M. coronatus*; Mornington, WA, 17.5289° S, 126.1034°
186 E), red-backed (*M. melanocephalus*; Herberton, QLD, 17.3833° S, 145.3833° E, & Lake
187 Samsonvale, QLD, 27.2613° S, 152.9000° E), red-winged (*M. elegans*; Smith Brook, WA,
188 34.3658° S, 116.2072° E), splendid (*M. splendens*; Brookfield Conservation Park, SA, 34.3615°
189 S, 139.4862° E), superb (*M. cyaneus*; Australian National Botanic Gardens, ACT, 35.2789° S,
190 149.1089° E, Campbell Park, ACT, 35.2822° S, 149.1722° E, Cleland, SA, 34.9701° S,
191 138.6941° E, Kangaroo Island, SA 35.7752° S, 137.2142° E, Lara, VIC, 38.00° S, 144.41 ° E),
192 variegated (*M. lamberti*; Lake Samsonvale, QLD, 27.2613° S, 152.9000° E), and white-
193 shouldered (*M. alboscapulatus lorentzi*; Obo, Western Province, New Guinea, -7.6056°,
194 141.3064°).

195

196 *Study species*

197 Fairy-wren species share many aspects of their natural history (all species are
198 insectivorous, sedentary, socially monogamous), but populations and species differ in important
199 aspects of their ecology, including levels of extra-pair paternity, breeding season length, and
200 cooperative breeding (with different proportions of individuals delaying dispersal to help raise
201 young). These behaviors have been well studied across populations of several fairy-wren species
202 and were recently collated into a single dataset including reproductive rates, breeding densities,
203 parental care, and survival (Brouwer et al. 2017). Fairy-wrens are also a good study system for
204 this investigation because both males and females regularly sing (Rowley and Russell 1997;
205 Evans and Kleindorfer 2016; Mahr et al. 2016). Male and female songs have been well-studied

206 in certain species, providing evidence that male and female songs play a role in territory defense
207 and same-sex competition (Cooney and Cockburn 1995; Dalziell and Cockburn 2008; Hall and
208 Peters 2008; Dowling and Webster 2013; Kleindorfer et al. 2013; Cain and Langmore 2015;
209 Colombelli-Négrel 2016), and female song is related to annual reproductive success and habitat
210 quality (Cain et al. 2015; Cain and Langmore 2016). Male fairy-wrens of many species give two
211 song types: type I and type II songs (Langmore and Mulder 1992); females largely only give type
212 I songs (Langmore and Mulder 1992; Rowley and Russell 1997; but see Greig and Pruett-Jones
213 2008). Type I songs are produced throughout the day and appear to be used in territory defense,
214 whereas male type II songs are delivered either in the dawn chorus or immediately following a
215 loud sound, such as the call of a predatory bird (Langmore and Mulder 1992; Dalziell and
216 Cockburn 2008; Greig and Pruett-Jones 2010; Greig and Webster 2014). Comparative studies
217 across fairy-wrens suggest that male type I song structure is shaped by sexual selection, as well
218 as other selective pressures (Greig et al. 2013). In the current study, we compare the structure of
219 male and female type I songs.

220

221 *Field recordings*

222 Most recordings for this study were collected by K. Cain in 2015 and 2016 (Austral
223 summer) with recordings for specific, additional populations contributed by individual
224 researchers or research groups studying those populations. All recordings were collected from
225 banded populations of birds and most recordings were collected from free-roaming birds during
226 natural singing bouts or following experimental playback trials. The stimuli varied depending on
227 the research focus within the population the recordings came from, most being natural songs of
228 male and/or female conspecifics. Recordings of lovely fairy-wrens were supplemented with
229 recordings of wild birds temporarily caged during experimental trials because these recordings
230 were higher quality than the natural recordings available for this species (Leitão et al. 2019a).
231 Supplementary Table S1 contains a full list of sample sizes for males and females at each
232 recording location, including details about dates, recording equipment, and playback stimuli
233 used.

234

235 *Life history data*

236 Life history data were compiled primarily from Brouwer et al. (2017). Where we had
237 recordings for additional populations, we extended the life history dataset. This included adding
238 the following populations to the dataset using existing breeding season data: Campbell Park,
239 Kakadu, Kangaroo Island, Cleland, and Cairns (Colombelli-Négrel et al. 2009; Leitão et al.
240 2019b). We also added additional years of data to the original Brouwer dataset for Western
241 Province, New Guinea (Enbody et al. 2019). Variables used from Brouwer et al. (2017) included
242 population-specific estimates of: proportion of extra-pair offspring, brood size, breeding
243 synchrony, group size, density of breeding males in the population, average proportion of
244 provisioning nest visits made by the dominant male in pairs without helpers, latitude of the field
245 site, and mean annual adult male survival (an estimate of male survival that may reflect variation
246 in both male and species survival rates per population). See Brouwer et al. (2017) for details on
247 how each variable was calculated. We evaluated possible correlations among these variables. We
248 identified collinearity among explanatory variables ($r > 0.7$; Dormann et al. 2013) using a
249 Pearson product-moment correlation test and excluded collinear variables. Correlations among
250 most explanatory variables were well below a correlation coefficient of 0.50 (see supplementary
251 Table S2).

252

253 *Phylogenetic tree*

254 For our phylogenetically controlled mixed models, we used overall topology from the
255 most recent species tree for the fairy-wrens (Lee et al. 2012). This well-resolved tree is based on
256 18 molecular markers, including exons, introns, and mitochondrial DNA. We used Mesquite
257 v3.6 to manually place purple-backed fairy-wren (*M. assimilis*), a recent species split from the
258 variegated fairy-wren (*M. lamberti*), as sister to the lovely fairy-wren (*M. amabilis*). This
259 position for the added branch is justified by multiple findings that purple-backed fairy-wrens are
260 sister to lovely fairy-wrens (Driskell et al. 2011; McLean et al. 2012). We then calibrated this
261 uncalibrated version of the Lee et al. (2012) tree. We used the *chronos* function in the *ape*
262 package in R (Paradis et al. 2004; R Core Team 2015) to assign nodes in common with a recent,
263 well-resolved supermatrix phylogeny for the Meliphagides by Marki et al. (2017) as hard values.
264 From these values, we estimated branch lengths and values for nodes not shared in both trees.

265

266 *Song analysis*

267 All songs were recorded in uncompressed WAV format and all recordings were
268 standardized to a sample rate of 44.1 kHz and a bit depth of 16 prior to measuring. We used
269 Raven Sound Analysis Software v1.5 (Bioacoustics Research Program 2017) to select and
270 extract measurements for the fundamental frequency for each element in each song, excluding
271 additional harmonics as much as possible. We defined an element as a single, continuous trace
272 on a spectrogram, separated from other elements by a visible break in time. For spectrographic
273 analysis we used a 512-point window length with a 90% window overlap and a Hann window
274 function for a time resolution of 1.161 ms and a frequency resolution of 86.1 Hz.

275 From these selections, we extracted acoustic parameters used to create both element-level
276 and song-level acoustic spaces. The element-level acoustic space was used to estimate element
277 diversity, which was used in subsequent song-level analyses. Here we describe the acoustic
278 parameters extracted to create the acoustic spaces. See the *Statistical analysis* section for
279 explanations of how the acoustic spaces were created.

280 *Element-level acoustic parameters* – For the element-level acoustic space, for every
281 element in all songs we extracted robust (energy-based) measurements of time and frequency
282 from Raven v1.5 (Bioacoustics Research Program 2017). We then transferred all selections to R
283 using the *Raven* package (Araya-Salas 2017) and extracted additional acoustic parameters using
284 the *R warbleR* package (Araya-Salas and Smith-Vidaurre 2017). Prior to random forest analysis
285 (see below), we removed highly correlated acoustic variables ($r \geq |0.95|$), resulting in the
286 following sets of parameters extracted from each program and used in subsequent analysis:
287 Raven – duration 90%, interquartile range duration, center time, frequency 5%, frequency 25%,
288 frequency 75%, 90% bandwidth, interquartile bandwidth, peak frequency, maximum of peak
289 frequency contour, range of the peak frequency contour, slope of peak frequency contour,
290 number of inflections in peak frequency contour; *warbleR* – mean frequency, standard deviation
291 of frequency, median frequency, skewness, time entropy, entropy, spectral flatness, modulation
292 index, and dominant frequency slope. For a few instances of the slope of peak frequency contour
293 metric, elements were too short to correctly calculate a value. We filled these missing
294 measurements with zero. This is a fair representation as these elements were too short to show
295 any significant frequency modulation. Robust measurements of frequency and time were
296 calculated in Raven from the cumulative amplitude of the spectrum or envelope, as applicable

297 (Charif et al. 2003). See Table S3 and Raven or warbleR manuals for detailed definitions of each
298 parameter (Charif et al. 2003; Araya-Salas and Smith-Vidaurre 2017).

299 *Song-level acoustic parameters* – The following seven acoustic parameters were
300 extracted from the elements composing each song and used in subsequent statistical analyses:
301 song duration (difference between the start and end times of the song), frequency 5% and 95%,
302 frequency range (range between top and bottom frequency among all elements), element number
303 (the total number of elements per song), element rate (element number divided by song
304 duration), and element diversity (a 95% minimum convex polygon area calculated from an
305 element-level acoustic space, see *Estimation of element diversity* section). Frequency 5% and
306 95% were not used in analyses involving elaboration since higher or lower frequencies on their
307 own are not considered more or less elaborate, but these parameters were used in all other
308 analyses. Therefore, we assessed song elaboration based on higher values for any acoustic
309 variables or combination of variables that typically vary directionally and for which larger
310 quantities are considered ‘more elaborate’ (e.g., song duration, element diversity, element
311 number, or element rate). We assessed the extent of dimorphism based on male-female
312 differences in any acoustic feature or combination of features. In this way, we also evaluated
313 dimorphism in acoustic variability (the difference in magnitude of variation between male and
314 female songs in acoustic feature space).

315

316 *Statistical analysis*

317 We evaluated variation in male and female song structure across fairy-wrens by
318 comparing correct classification of male and female songs in acoustic space using random forest
319 models (described below). In line with our goals, we then used phylogenetically informed mixed
320 models to assess statistically: (1) species and sex differences in song, (2) correlations between
321 song elaboration in both sexes and the life history variables, and (3) correlations between sexual
322 dimorphism in song and the life history variables. Multiple steps were involved in creation of
323 acoustic spaces and the variables used in each analysis differed slightly. We primarily used a
324 combination of supervised and unsupervised random forest techniques to plot and differentiate
325 among male and female songs in acoustic space. Random forest is a machine learning approach
326 for classification and regression that is based on constructing and evaluating a large number of
327 decision trees. Supervised random forest uses labeled data to assess the correct assignment of
328 data to a particular category. In unsupervised random forest the data are unlabeled and
329 classification or exploring patterns within the data is often the goal (Ramasubramanian & Singh,
330 2016). The steps, metrics, and analyses used in each analysis are explained below.

331 *(1) Species and sex differences in song* – To evaluate species and sex differences in song,
332 we used supervised random forests to assess correct classification of male and female songs. We
333 then used Bayesian phylogenetic mixed models to assess statistically which song variables
334 contributed to sex differences in each species.

335 We calculated correct classification of male and female songs on a species-by-species
336 basis within a song-level acoustic space. For this analysis, we calculated separate acoustic spaces
337 for each species in order to have the highest resolution to test discrimination between male and
338 female songs. We used all seven song-level acoustic parameters in each species’ acoustic space.
339 To create the acoustic spaces, we conducted a supervised random forest analysis in the R
340 package ranger (Wright and Ziegler 2017) with the following parameters: 10000 trees, minimal
341 node size of 1, Gini impurity index as split rule and 3 randomly sampled variables at each split.
342 We used the out-of-bag error as an indicator of classification accuracy for each species. Out-of-

343 bag error is measured as the classification of each sample with a model that was trained without
344 that particular sample. Phylogenetic comparisons for all analyses are described below.

345 *(2) Song elaboration* – To evaluate whether song elaboration is correlated with any of the
346 life history variables, we created a reduced set of elaboration variables to examine the life history
347 variables in phylogenetically controlled mixed models. The reduced set of song elaboration
348 variables was created using principal component analysis (PCA). PCA was conducted using the
349 princomp function in R (R Core Team 2015) on the correlation matrix with the following song-
350 level acoustic parameters: song duration, frequency range, element number, element rate, and
351 element diversity. Frequency 5% and 95% related parameters were not used in this analysis, as
352 there are not distinct predictions about how these frequency metrics represent song elaboration.
353 We extracted PC scores for the first three principal components to be used in phylogenetic
354 comparative analyses.

355 *(3) Song dimorphism* – To evaluate whether song dimorphism is correlated with any of
356 the life history variables, we created a reduced set of song dimorphism variables to examine the
357 life history variables in phylogenetically informed mixed models. We computed three metrics
358 representing male-female song dimorphism based on male-female differences in a song-level
359 acoustic space that contained all species: 1. male-female acoustic area overlap, 2. male-female
360 acoustic area distance, and 3. male-female acoustic area size difference. The song-level acoustic
361 space was created from unsupervised random forests in the R package randomForest (Liaw and
362 Wiener 2002) using all song-level acoustic parameters as input variables and using the following
363 function parameter settings: 10000 trees, minimal node size of 1, Gini impurity index as split
364 rule, 3 randomly sampled variables at each split and out-of-bag proximity. The resulting
365 proximity matrix was transformed into a set of two vectors by Kruskal's Non-metric
366 Multidimensional Scaling using the function isoMDS in the R package MASS (Venables and
367 Ripley 2002). We then computed 95% minimum convex polygon areas for each sex within each
368 population to represent acoustic area.

369 We used these acoustic areas to calculate the three male-female song dimorphism
370 metrics. Male-female acoustic area overlap was calculated by population as the area overlap of
371 male and female 95% minimum convex polygons, taken as a proportion of the entire acoustic
372 area for each population. Male-female acoustic area distance was calculated as the distance
373 between the centroids of the male and female acoustic areas. Centroids were calculated as the
374 average values for each dimension of the acoustic space and the distance between centroids was
375 calculated using the dist function in R. Dimensions of the acoustic space (i.e. MDS vectors) were
376 z-transformed to make male-female centroid distances comparable across populations and
377 species. Male-female acoustic area size difference was calculated as the absolute value of the
378 difference between male and female acoustic areas, proportional to the total acoustic area of the
379 population. This value represents the size difference between male and female songs in acoustic
380 space, or rather, differences in male-female song variability. To control for sample size
381 differences between the sexes when computing each dimorphism metric, we selected a random
382 subset of the data equal to the sample size of the sex with fewer samples. We did this over 100
383 iterations and then averaged the resulting dimorphism values.

384 *Estimation of element diversity* – We calculated element diversity for each song as the
385 95% minimum convex polygon area surrounding that song's elements in an element-level
386 acoustic space, using the function mcp in the adehabitatHR R package (Calenge 2015).
387 Therefore, each area serves as an estimate of the variability or diversity of elements for a given
388 song among all other song elements in the acoustic space. The resulting element diversity values

389 were used in the above song-level analyses. For comparisons across all species, we created the
390 element-level acoustic space by inputting all element-level acoustic parameters for every element
391 for all songs of all species into an unsupervised random forest using the randomForest package
392 in R (Liaw and Wiener 2002). Similarly, we created species-specific element diversity scores for
393 our evaluation of correct classification of males and females to their respective sex, which was
394 evaluated by species. For creation of both sets of element diversity scores, the random forest was
395 run with the following specifications: 10000 trees, minimal node size of 1, Gini impurity index
396 as split rule, 5 randomly sampled variables at each split and out-of-bag proximity. This produced
397 a proximity matrix, which we transformed into a set of five vectors using classic
398 multidimensional scaling (MDS). Multidimensional scaling was performed using the cmdscale
399 function in the stats R package. We used the first two MDS vectors to create a 2-D acoustic
400 space containing all elements of all songs. We then extracted 95% minimum convex polygon
401 areas defined by the elements for each song using the function mcp in the adehabitatHR R
402 package (Calenge 2015). Therefore, each area quantitatively represented element diversity for
403 each song in subsequent analyses.

404 *Phylogenetic mixed models* – We constructed Bayesian phylogenetically controlled
405 mixed models with MCMCglmm in R (Hadfield 2010) to evaluate the extent of male and female
406 song differences statistically and to evaluate whether life history variables correlate to song
407 elaboration or dimorphism among fairy-wren populations. For models investigating sex
408 differences in song, we ran separate models for each song-level acoustic parameter as the
409 response variable. Each model controlled for phylogeny, contained sex, species, and their
410 interaction as fixed effects, and individual ID and population nested within species as random
411 intercepts to account for non-independence of songs from the same bird and population.

412 We also ran separate univariate models for each life history trait; as each trait had
413 different instances of missing values and the life history variables were averaged per population
414 (this approach prevented model overfitting). We ran six sets of models: one for each of the three
415 PC elaboration scores and one for each of three dimorphism metrics as response variables. Each
416 life history variable was included as a fixed effect in each univariate model, and to evaluate
417 potential sex differences in response to life history, for models of song elaboration, we also
418 included sex and its interaction with each life history trait as fixed effects. Individual ID, species,
419 and population nested within species were included as random intercepts. These analyses
420 allowed us to assess if song elaboration and dimorphism were correlated to any life-history traits
421 across all 15 fairy-wren populations.

422 For all models we used a non-informative, parameter-extended prior to improve mixing
423 with R-structure $V=1$, $\nu=0.002$ and G-structure $V=1$, $\nu=1$, $\alpha.\mu=0$, and $\alpha.V=25^2$.
424 Models of male-female song differences were run with 1,750,000 iterations, a burn-in of 300,
425 and thinning of 15. Life history models for elaboration were run with 300,000 iterations, a burn-
426 in of 300 and thinning of 30. Life history models for dimorphism were run with 500,000
427 iterations, a burn-in of 500 and thinning of 30. We examined all results to ensure stationarity had
428 been reached and that there was no autocorrelation. We used Bayesian p-values, a value
429 analogous to traditional p-values, with a cutoff of less than or equal to 0.05 to evaluate which
430 variables contributed substantially to variation in each model.

431 In addition, we also performed model selection procedures for multivariate comparative
432 analyses of elaboration and dimorphism compared to life history traits using the function dredge
433 in the R package MuMIn (Bartoń and Kamil 2019). We used the same priors, burn-in, thinning,
434 and number of iterations as for the univariate analyses. To compensate for explanatory variables

435 with missing data, we scaled all explanatory variables and set the missing values to zero, ie. the
436 mean (Nakagawa and Freckleton 2011). Selection of the best model was determined based on
437 DIC. If top models differed by less than 2 DIC values, then we chose the model with the fewest
438 parameters. The appropriateness of using DIC for model selection is debated (Spiegelhalter et al.
439 2014). Therefore, we used the model selection results mainly to evaluate consistency with the
440 univariate analyses. In the main text, we present the univariate analysis results and emphasize
441 findings that were supported by both sets of analyses. We provide the model selection results and
442 discuss those findings as supplementary material (Table S4).

443

444 *Phylogenetic signal*

445 To directly evaluate the extent to which phylogenetic relationships explain expression of
446 these vocal parameters, we computed phylogenetic signal for each of the component variables
447 that went into the song-level acoustic space. We calculated Blomberg's K using the phylosig
448 function in the phytools R package (Blomberg et al. 2003; Revell 2012).

449

450 **Results**

451 *Sex and species differences*

452 Overall, male and female fairy-wren songs were structurally similar within each species,
453 occupying similar regions in acoustic space (Figures 1 & 2). The capacity to reliably classify
454 songs to the correct sex ranged from low in some fairy-wren species (e.g., superb 61.5%,
455 splendid 62.2%, and red-winged and variegated 62.5%) to moderately high in others (e.g.,
456 purple-backed 73.4%, purple-crowned 78.7%, and red-backed 83.1%; Table 1). In some species,
457 such as white-shouldered fairy-wrens, overall classification of songs to the correct sex was
458 considerably higher for one sex than for the other (90% correct classification for females vs 25%
459 for males; Table 1), suggesting that songs for one sex were more variable than the other (i.e., the
460 songs of one sex fell entirely within the acoustic space of the other, but in only a subset of the
461 other sex's acoustic space; Figure 2). Overall, fairy-wren songs could be readily classified to
462 their respective species with a moderately high correct classification of 73.19% (Figure S1 &
463 S2).

464 The variables that contributed to male-female differences in song varied by species
465 (supplementary materials: Figure S3; Table S5 & S6). For example, random forest variable
466 importance rankings indicated that high frequency and element rate contributed most to male and
467 female differences in purple-crowned fairy-wrens, whereas song duration, high frequency, and
468 element number contributed most to male-female differences in red-backed fairy-wrens (Figure
469 S3; Table S5). More specifically, phylogenetically controlled mixed models of sex differences by
470 species indicated that different variables contributed significantly to male and female differences
471 in song in each fairy-wren species (Figure S3, Tables S4 & S5). The direction and magnitude of
472 differences between the sexes varied across species (Tables S4 & S5). For example, male red-
473 backed fairy-wrens had significantly higher element diversity than females, whereas male white-
474 shouldered fairy-wrens had a significantly lower frequency range than females.

475

476 *Song elaboration*

477 We quantified song elaboration via principal component analysis in three components:
478 song length (PC1), element rate (PC2), and song variability (PC3; Table 2 shows loadings for all
479 contributing acoustic variables). Relationships between song elaboration and life history traits

480 were sex-specific in multiple cases, suggesting that male and female songs have evolved
481 differently in response to certain life history traits (Figures 3 & 4; Table 3 & S6). For example,
482 male song length (PC1) had a stronger negative association with male survival and male
483 provisioning rates than did female song length (sex*male provisioning: $p = 0.009$; sex*male
484 survival: $p = 0.003$). The association between male provisioning rate and song length (PC1) was
485 not recovered by the model selection results (Table S4) likely due to the correlation between
486 male survival and provisioning ($r = 0.7$; Table S3). Overall, female song length was more
487 consistent across life history variables than male song length (Figure 3; Table 3). Specifically, on
488 average male songs were longer than female songs in populations with low male survival and
489 less male provisioning, whereas male and female songs were of similar lengths and shorter
490 overall in populations in which males are long-lived and in populations in which males provision
491 offspring at higher rates (Figure 3). There was also a non-significant interaction between song
492 length and sex, in which males tended to have longer songs than females at tropical latitudes, but
493 shorter, similar length songs at temperate latitudes ($p = 0.063$; Table 3). In general, fairy-wrens
494 tended to sing longer songs (PC1) at low latitudes ($p = 0.075$).

495 Element rate (PC2) and song variability (PC3) also exhibited sex-specific patterns, with
496 male songs showing stronger, positive relationships to variables tied to mate competition,
497 whereas female songs were more consistent across variation in life history traits (Table 3).
498 Specifically, element rate (PC2) exhibited an interaction between sex and breeding synchrony
499 such that female songs were slower paced than male songs in less synchronously breeding
500 populations, whereas male and female element rates were similar in more synchronously
501 breeding populations (sex*breeding synchrony $p = 0.024$; Figure 4a). As for song variability
502 (PC3), male song variability had a stronger positive association than female song variability with
503 breeding synchrony ($p = 0.080$) and latitude ($p = 0.019$). Interestingly, female songs were more
504 variable than male songs in populations with high breeding synchrony and at high latitudes
505 ($p < 0.027$, Table 3). Conversely, male songs were more variable than female songs in more
506 synchronously breeding populations and songs of both sexes were more similarly variable at
507 higher latitudes (Figure 4b&c). Both males and females tended to sing faster paced songs (PC2)
508 at low latitudes ($p = 0.076$), and their songs tended to be more variable (PC3) in more
509 synchronously breeding populations ($p = 0.072$), especially in males (*sex, $p = 0.008$; Figure 3;
510 Table 3).

511

512

513 *Song dimorphism*

514 Male and female song similarity was correlated with variables linked to sex role
515 convergence, consistent with the differences between the sexes in elaboration found above. Male
516 and female songs were most similar, measured as both overlap and distance in acoustic space, in
517 populations with high male survival ($p = 0.022$ & $p = 0.025$, respectively; Figure 5; Table 4).
518 There was also a non-significant trend for male and female songs to be more similar when the
519 proportion of provisioning by males was higher, (i.e., when male and female provisioning was
520 more equal; $p = 0.082$). Interestingly, fairy-wrens also exhibited patterns contrary to any
521 hypotheses that we considered: male and female songs were similarly variable (had similarly
522 sized acoustic areas) at temperate latitudes, whereas sexual dimorphism in song variability was
523 higher at more tropical latitudes ($p = 0.036$; Figure 5; Table 4), consistent with the song
524 elaboration findings above (c.f. Figure 4c). In addition, model selection results recovered
525 positive correlations between male-female overlap in acoustic space and extra-pair paternity

526 rates ($p = 0.030$; higher EPP rates in species with more monomorphic songs) and male-female
527 differences in song variability and breeding synchrony ($p = 0.039$; marginally higher breeding
528 synchrony in species with similar male-female song variability; Table S4).

529

530 *Phylogenetic signal*

531 Song duration and element number had high phylogenetic signal ($K = 1.35$ and 1.42 ,
532 respectively), indicating that these song features are most similar among closely related species
533 and could be constrained by shared ancestry. Element diversity ($K = 0.80$), frequency range ($K =$
534 0.87), and element rate ($K = 0.91$) had intermediate phylogenetic signal, indicating that these
535 traits are more similar in closely related species and phylogeny could play some role in shaping
536 these traits, but that they also evolve somewhat independently of phylogeny. For the high and
537 low frequency variables, however, phylogenetic signal was lower than expected under Brownian
538 motion (K appreciably less than one: frequency 5%, $K = 0.69$; frequency 95%, $K = 0.58$),
539 suggesting that these aspects of song have not been constrained by phylogenetic relationships.

540

541 **Discussion**

542 Male and female fairy-wren songs were generally structurally similar, but sexual song
543 dimorphism was greater in some fairy-wren species than in others. The song parameters that
544 differed between males and females varied widely across species. Song elaboration was weakly
545 related to life history variables overall, but showed some sex-specific relationships, suggesting
546 that different selective pressures have shaped some aspects of song elaboration in each sex.
547 Trends were consistent with stronger sexual selection having acted on males than on females in
548 some populations, but selection for similar sex roles in other populations. In contrast, sexual
549 song dimorphism was strongly associated with divergence in sex-roles: in species with life-
550 histories involving similar sex-roles, males and females also had more similar songs. Finally,
551 some aspects of song structure showed strong phylogenetic signal, whereas others differed even
552 between closely related species, suggesting there could be evolutionary constraints on female
553 and male fairy-wren songs. We conclude that song elaboration and sexual song dimorphism
554 across fairy-wrens has been shaped by diverse selective pressures, including sexual selection and
555 especially selection favoring sex-role similarity. Lastly, we did not detect a positive correlation
556 between song complexity and latitude, as has been observed in the Northern Hemisphere. Thus,
557 in Southern Hemisphere species, selective pressures associated with tropical-temperate gradients
558 may be weaker or absent.

559

560 *Song elaboration*

561 Our results suggest that song elaboration in fairy-wrens has been shaped at least in part
562 by sexual selection acting more strongly on male song than on female song in certain situations.
563 Male song variability increased more strongly with breeding synchrony and latitude than did
564 female song variability (Figure 4b&c). Interestingly, females had slower-paced songs than males
565 in populations with low breeding synchrony (Figure 4c) and shorter songs than males in short-
566 lived species and when males provisioned less (Figure 3). However, female songs were more
567 variable than male songs in populations with low breeding synchrony (Figure 4b). The stronger
568 correlation of male song elaboration with factors germane to mating opportunities supports the
569 idea that song elaboration has been sexually selected in males, but not females. This finding is
570 consistent with Greig et al.'s (2013) finding that several aspects of male fairy-wren type 1 song
571 were correlated with testes mass, also indicating that male song structure is sexually selected in

572 fairy-wrens. Nevertheless, we did not find any relationship between male or female song
573 elaboration and extra-pair paternity rates, as a potential predictor of sexual selection. This is
574 consistent with meta-analyses and other comparative studies of song which also did not find
575 correlations between song elaboration and extra-pair paternity (Garamszegi and Moller 2004,
576 Soma and Garamszegi 2010). To our knowledge no studies have looked for similar patterns in
577 female song. Field studies should follow up on our findings to determine whether these are
578 aspects of male and/or female song that fairy-wrens attend to, and whether variation in these
579 traits are associated with differential mating success in males or reproductive success in females.
580 In addition, such studies should gather metrics of reproductive success that are applicable to
581 females (e.g., fecundity or fledgling success), as EPP is probably not as meaningful a metric of
582 reproductive success in females as in males.

583 Sexual selection on male and female fairy-wren songs appeared relatively weak, based on
584 the slopes of associations between song complexity and life history traits, especially compared
585 to observed associations with dimorphism. Therefore, our results are potentially even more
586 consistent with song elaboration in fairy-wrens being associated with selective pressures that
587 have favored sex-role similarity, and possibly selection for consistently variable songs in
588 females. For example, song duration showed a stronger correlation with lower provisioning and
589 reduced survival in males than in females. However, male and female songs were both shorter
590 and more similar overall when male and female provisioning was more equal and male survival
591 was high (Figure 3). These patterns are consistent with divergent selective pressures or different
592 strengths of selective pressures having resulted in shorter, monomorphic songs in some
593 populations and longer, dimorphic songs in other populations (Catchpole 1982; Najar and
594 Benedict 2019). Conversely, natural selection against elaborate female songs could have
595 constrained female song length in populations where females provide most of the provisioning.
596 While our results do not provide direct evidence for this, nest predation has been tied to high
597 song rates in the nest in female superb fairy-wrens (Kleindorfer et al. 2016) and would be
598 consistent with the patterns we found (but see Cain et al. 2015, Cain & Langmore 2016).
599 Moreover, female songs have similar variability among species than male songs, and female
600 songs are actually more variable than male songs in populations with lower breeding synchrony
601 (Figure 4). This suggests that there could have been selection to maintain high variability of
602 female songs within fairy-wrens. In superb fairy-wrens, the songs of young males and females
603 share similar element diversity with their parents (Evans and Kleindorfer 2016). If element
604 diversity helps dispersing females establish a territory, then it is possible that only females with
605 more diverse element repertoires are able to acquire territories, consistent with the pattern we
606 observe. Past research has focused largely on directional selection toward male song diversity
607 and elaboration. Recent research suggests, however, that bird song is likely under balancing
608 selection for intermediate sized song repertoires (Snyder and Creanza 2019). This pattern is
609 consistent with bird song evolution being shaped by a suite of selection pressures acting both for
610 and against elaborate song in both sexes under different evolutionary scenarios.

611 Sex differences in song elaboration may also reflect different intensities of sexual
612 selection acting on male and female song. Specifically, intra-sexual selection may have been
613 important in both sexes, whereas inter-sexual selection may have been more important in males.
614 Female song elaboration followed similar patterns to those observed in males, although female
615 songs varied less across life history traits. This could be due in part to correlated evolution of
616 female song structure with male song structure, coupled with relaxation of selection on female
617 song traits (Lande 1980). However, fairy-wren natural history better supports the idea that song

618 is sexually selected in males, but is an important tool for intra-sexual competition for non-mate
619 resources in females (Cooney and Cockburn 1995). Female fairy-wren song is used for territory
620 defense, and the consequences of losing, or failing to gain, a territory may be more dire for
621 females than males (Cooney and Cockburn 1995; Cain and Langmore 2015; Colombelli-Négrel
622 2016; Enbody et al. 2018; Leitao 2019). Moreover, females that sing and exhibit greater
623 aggression to simulated intrusions also have higher reproductive success, though the relationship
624 varies according to habitat quality (Cain et al. 2015, Cain & Langmore 2016). Therefore, female
625 song is functional with known reproductive benefits. Song structure in female fairy-wrens may
626 thus be a balance between the use of song to enhance offspring quality and win competitive
627 interactions versus the costs associated with certain aspects of female song (Cain and Rosvall
628 2014; Kleindorfer et al. 2016).

629

630 *Sex differences & song dimorphism*

631 Our results also provide strong evidence that fairy-wren song structure has been shaped
632 by selective pressures favoring sex-role similarity. Male and female songs were shorter and more
633 similar when males and females provision more equally and when male survival is high (in
634 longer-lived species; Figure 3). Therefore, patterns of song dimorphism are likely not just a by-
635 product of strong, directional selection on males, but rather a balance between sexual selection,
636 natural selection, and active maintenance of sex-role similarity in certain populations. This may
637 represent two sides of the same coin, but to understand selective pressures responsible for sexual
638 dimorphism specifically (as opposed simply to trait elaboration), we need to independently
639 investigate selective pressures that act on both males and females (Price 2015). This is
640 particularly true if we want to elucidate the selective pressures responsible for sexual
641 dimorphism from a mutually ornamented ancestor. In this case, we need to consider not only the
642 selective pressures responsible for elaboration, but also maintenance of song in both sexes. Our
643 findings provide evidence that selection has favored both dimorphism and sexual
644 monomorphism in song under different circumstances.

645 Sex-specific song may also be selected for by factors other than those related to sexual
646 selection and sex-role similarity. Interestingly, three species known to regularly duet, the purple-
647 crowned, red-backed, and white-shouldered fairy-wrens (Rowley and Russell 1997), also had
648 some of the most sexually dimorphic songs. This is consistent with some other major lineages of
649 duetting species, which often have sex-specific song (e.g., Cisticolidae: Thorpe et al. 1972;
650 Malaconotidae: Grafe and Bitz 2004; Van Den Heuvel et al. 2013; Troglodytidae: Logue et al.
651 2007; Mann et al. 2009). This suggests that duetting species may have experienced additional
652 selective pressures for sex-specific song structure. In the Neotropical wrens (Troglodytes), a
653 family well-known for their highly coordinated duets, distinct male and female song structure
654 has been hypothesized to allow rapid sex or identity signaling when both sexes defend territories
655 cooperatively (Hall 2004; Logue et al. 2007). Therefore, sexual selection and sex-role
656 similarities might not be the only selective pressures that have resulted in the dimorphic songs
657 observed between female and male fairy-wrens. Frameworks to explain sexual dimorphism in
658 song structure should take these additional functions and selective pressures of sex-specific song
659 into account, as they may be important in cases where tropical or sedentary species display
660 sexually dimorphic signals (for example, Grafe and Bitz 2004; Mays et al. 2006; Logue et al.
661 2007; Rivera-Cáceres et al. 2018).

662 The acoustic parameters driving male and female fairy-wren song dimorphism differed
663 across species. Based on random forest variable importance scores, frequency parameters (low

664 frequency, high frequency, or frequency bandwidth) contributed to classification of males and
665 females in most species, which is not unexpected given the sexes typically differ slightly in body
666 size. However, depending on the species, element diversity, song duration, and element rate also
667 contributed considerably to sex differences (Figure S3). Therefore, the features of songs that
668 capture male-female dimorphism appear to be very species-specific, possibly as a result of
669 character displacement or the role different features play in mate recognition (Grant 1972; Price
670 2007; Queller and Strassmann 2018). As a group, fairy-wren songs are fairly similar across
671 species, so the fact that different variables contribute to sex differences in this clade suggests that
672 the features that explain song dimorphism are probably quite variable across all species,
673 especially in more distantly related taxa. Therefore, it may be important to measure a wide range
674 of features when trying to assess sexual dimorphism in song (Benedict and Najar 2019).

675

676 *Latitude, song & the Southern Hemisphere*

677 Hypotheses based on Northern Hemisphere species predict that song elaboration will be
678 greatest in higher latitudes (Catchpole 1982; Read and Weary 1992; Najar and Benedict 2019).
679 However, instead we found that male songs tended to be shorter and male and female songs were
680 more similar and less variable at higher (temperate) latitudes. Nevertheless, both male and
681 female songs were shorter and more similar when males provide more care and when male
682 survival is higher (i.e., in long-lived species). These results together support the hypothesis that
683 song similarity and complexity are tied to selection for sex-role similarity, rather than latitude,
684 per se. While this finding is not mutually exclusive from sexual selection driving elaboration on
685 male song, it provides empirical evidence for a framework by which variation in male and
686 female songs are actively maintained, and helps us understand the range of evolutionary
687 mechanisms dictating broad geographic patterns of bird song. Importantly, this pattern adds to
688 other recent findings that observed/predicted relationships between latitude and complexity are
689 not always empirically supported, particularly when applying those based on Northern
690 Hemisphere species to southern species (Najar and Benedict 2019).

691 Nevertheless, we did find support for the hypothesis that both selection for similar sex-
692 roles and sexual selection pressures have shaped fairy-wren song structure. Therefore, we found
693 support for the evolutionary mechanisms for which latitude is expected to be a proxy (trade-offs
694 in sexual versus natural selection), though in the absence of clear geographic patterns. We
695 suggest that this is because the relationship between song complexity and latitude may reflect
696 Northern Hemisphere life history patterns, which may not apply or be as pronounced in the
697 Southern Hemisphere. Many northern temperate songbirds are migratory (latitudinal or
698 altitudinal) and are only seasonally territorial. In contrast to north temperate climate patterns,
699 winter temperatures in Australia are often more moderate and many species, including fairy-
700 wrens, remain on their territories year-round (Rowley and Russell 1997; Del Hoyo et al. 2010).
701 In addition, fairy-wrens are socially monogamous, cooperative breeders with considerable
702 variation in their reproductive strategies, a combination that is uncommon in north temperate
703 regions (Cockburn 2003; Jetz and Rubenstein 2011; Feeney et al. 2013). Therefore, for a variety
704 of reasons, Southern Hemisphere species, and specifically fairy-wrens, may contradict expected
705 latitudinal life history patterns associated with north temperate latitudes (see Table S2 for low
706 correlations between latitude and survival, male provisioning rates, and breeding synchrony). For
707 these reasons, our study system offers a unique opportunity to tease apart underlying selective
708 pressures dictating global patterns of bird song elaboration and dimorphism, irrespective of

709 climate and latitude. We expect that our findings broadly reflect the underlying balance of
710 selective pressures expected to shape male and female bird song evolution generally.

711
712

713 **Conclusions**

714 Understanding the selective forces that have shaped trait elaboration and sex differences
715 across species is a key issue for evolutionary biologists and requires detailed data on life-
716 histories and trait variation. Drawing on such data, we provide evidence that similar forces have
717 shaped female and male song elaboration in a well-studied Southern Hemisphere clade, and that
718 these forces are to some extent decoupled from the latitudinal patterns predicted from Northern
719 Hemisphere studies. Further, we find evidence for sex differences in the elaboration of song that
720 are consistent with sexual selection theory, with males in some instances having more elaborate
721 songs than females. Yet our results are also consistent with social selection for consistently
722 elaborate songs in females and possibly natural selection for shorter female songs in some
723 species. Moreover, selective pressures that favor more similar sex-roles also appear to have
724 shaped song structure in both sexes, providing evidence that complex songs in fairy-wrens are
725 not driven primarily by inter-sexual selection. Instead, our findings indicate that song structure
726 may be an interplay of both sexual selection on males and selective pressures that mediate sex-
727 role similarity, and that song dimorphism results from the balance between these two
728 evolutionary forces.

729

730 **Acknowledgements**

731 We acknowledge the Traditional Owners of country throughout Australia and their
732 continuing connection to land, culture, and community. We pay our respects to the Elders past
733 and present. We thank the following entities for access to land, permits, and permissions: staff at
734 the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary, Parks Victoria's
735 Serendip Sanctuary; W. Dimond for coordinating the Campbell Park study site; H. Osmond for
736 coordinating access to the Australian National Botanic Gardens; landowners, local, and
737 provincial governments of Milne Bay and Western Province; Cairns airport and city council; and
738 Western Australian Department of Biodiversity Conservation and Attractions (DBCA); South
739 Australia Department for Environment and Water and Friends of Parks for access of and support
740 at Brookfield Conservation Park; Department for Environment and Water, South Australia; The
741 Gagudju people, Traditional Owners and Custodians of Kakadu National Park. The Australian
742 Bird and Bat Banding Scheme gave permission for colour-banding. Funding was provided by: a
743 Cornell Lab of Ornithology Rose Postdoctoral Fellowship and a U.S. National Science
744 Foundation (NSF) Postdoctoral Research Fellowship in Biology to KJO (grant no. 1612861),
745 NSF grant number 1354133 to JK, NSF grant number 1701781 to JK and EDE, National
746 Geographic Society Young Explorers Grant to EDE, Nature Foundation of South Australia
747 Grand Start Grant and Holsworth Wildlife Research Endowment awarded to CE, Australian
748 Research Council DECRA to LB (DE130100174), Australian Research Council Discovery Grant
749 DP110101966 to RAM and NEL (DP150101652), Australia & Pacific Science Foundation to
750 RAM and MLH (APSF1406), and Birdlife Australia grant to AVL. Research was conducted
751 under the following permits: animal ethics 1212668.2, 1513677.1 and scientific research
752 WISP13237913 and RK865 to RAM, MLH, and KEC.

753

754

755 **Data accessibility**

756 Code and data for these analyses are available at dryad.org DOI: XXXX (data will be
757 uploaded upon acceptance). Select songs measured for the acoustic analysis have been made
758 available at macaulaylibrary.org.

759

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Table 1. Correct classification of fairy-wren songs to sex, based on random forest classification, including total percent correct for both sexes together and the percent correct for each sex.

Species	Total % correct	Female % correct	Male % correct
Superb	61.5%	68.2%	53.5%
Splendid	62.2%	66.0%	57.5%
Red-winged	62.5%	57.9%	66.7%
Variegated	62.5%	66.7%	57.7%
Lovely	63.3%	64.4%	62.2%
White-shouldered	67.4%	90.0%	25.0%
Purple-backed	73.4%	67.3%	77.8%
Purple-crowned	78.7%	74.3%	82.5%
Red-backed	83.1%	82.1%	84.1%

Table 2. Principle component analysis (A) eigenvalues and the proportion and cumulative variance of each component, and (B) component loadings for each acoustic variable. Bold values indicate loadings for variables that contribute > 0.5 to each PC.

(A) Eigenvalues and variance:

	PC1 - Song length	PC2 - Element rate	PC3 - Song variability
Standard deviation	1.4385	1.1441	0.9654
Proportion of Variance	0.4139	0.2618	0.1864
Cumulative Proportion	0.4139	0.6757	0.8620

(B) Loadings:

	PC1	PC2	PC3
Duration	0.538	-0.416	0.415
Element number	0.623	0.202	0.352
Element rate	0.133	0.823	-
Frequency range	0.344	-0.270	-0.689
Element diversity	0.432	0.188	-0.478

Table 3. Phylogenetic mixed model results for song complexity compared to life-history traits across nine fairy-wren species, highlighting model results that were significant for life-history parameters according to Bayesian p-values (*** p < 0.001, ** p < 0.01, * p < 0.05, . p < 0.1). See Table S6 for a full set of model results. Values in bold are results that are supported by both univariate model and best model results. Note that PC3 loadings are negative, so more negative values for PC3 reflect more variable songs.

Response variable	Predictor variable	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	Bayesian p-value	
PC1 (Song length)	Male feeding rates	-3.39	-8.29	1.80	4754	0.189	
	Sex: male	1.47	0.68	2.29	9990	< 0.001	***
	Male feeding rates - Sex: male	-2.65	-4.58	-0.64	9990	0.009	**
	Male survival	-0.77	-4.51	2.85	6109	0.681	
	Sex: male	2.10	1.09	3.16	9456	< 0.001	***
	Male survival - Sex: male	-2.34	-3.86	-0.87	9584	0.003	**
	Latitude	-0.03	-0.07	0.00	9990	0.075	.
	Sex: male	1.00	0.42	1.61	9990	0.001	***
	Latitude - Sex: male	-0.02	-0.04	0.00	9281	0.063	.
PC2 (Element rate)	Breeding synchrony	3.43	-7.78	16.45	1022	0.684	
	Sex: male	0.60	0.26	0.94	9990	0.001	***
	Breeding synchrony - Sex: male	-2.46	-4.54	-0.28	9990	0.024	*
	Latitude	-0.05	-0.11	0.00	2098	0.076	.
	Sex: male	0.16	-0.17	0.51	9990	0.353	
	Latitude - Sex: male	0.00	-0.01	0.01	9990	0.837	
PC3 (Song variability)	Breeding synchrony	-4.25	-9.34	0.56	7909	0.072	.
	Sex: male	0.51	0.15	0.91	9990	0.010	*
	Breeding synchrony - Sex: male	-3.17	-5.60	-0.90	9990	0.008	*
	Latitude	0.00	-0.03	0.03	4836	0.720	
	Sex: male	0.43	0.04	0.81	9990	0.027	*
	Latitude - Sex: male	-0.02	-0.03	0.00	9990	0.019	*

977

978

Table 4. Phylogenetic mixed model results for song dimorphism compared to life-history traits across nine fairy-wren species. *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, $p \leq 0.1$ according to Bayesian p-values. Values in bold are results that are supported by both univariate model and best model results (See Table S4 for more details).

Response variable	Predictor variable	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	Bayesian p-value
Male-female overlap in acoustic area	Percent extra-pair paternity	0.39	-0.12	0.87	16650	0.093 .
	Brood size	-0.14	-0.37	0.06	16650	0.167
	Group size	0.00	-0.17	0.17	16650	1.000
	Percent male subordinates	0.30	-0.47	1.08	16650	0.410
	Provisioning by male	0.82	-0.54	2.18	16650	0.210
	Male survival	0.65	0.16	1.19	16154	0.022 *
	Breeding synchrony	0.02	-1.88	2.17	16650	0.954
	Latitude	0.00	-0.01	0.01	17718	0.801
	Breeding male density	2.75	-4.43	10.21	16650	0.420
Male-female distance in acoustic area	Percent extra-pair paternity	-0.79	-2.84	1.23	17685	0.403
	Brood size	0.29	-0.45	1.03	17695	0.410
	Group size	-0.04	-0.55	0.45	14849	0.890
	Percent male subordinates	-0.44	-2.45	1.63	16650	0.650
	Provisioning by male	-2.79	-6.03	0.40	16650	0.082 .
	Male survival	-1.89	-3.52	-0.29	16650	0.025 *
	Breeding synchrony	-1.27	-7.90	3.68	11874	0.820
	Latitude	-0.01	-0.04	0.03	16650	0.725
	Breeding male density	-9.09	-27.94	8.83	16650	0.271
Male-female acoustic area size difference	Percent extra-pair paternity	-1.09	-2.70	0.48	16049	0.157
	Brood size	0.03	-0.50	0.55	17832	0.920
	Group size	-0.12	-0.40	0.17	17312	0.350
	Percent male subordinates	0.33	-1.15	1.92	16650	0.680
	Provisioning by male	0.41	-1.88	2.59	15907	0.710
	Male survival	-0.50	-2.06	0.98	15966	0.490
	Breeding synchrony	0.78	-2.96	4.49	16650	0.650
	Latitude	-0.03	-0.05	0.00	15528	0.036 *
	Breeding male density	-1.28	-15.97	12.47	16870	0.850

981 **Figure captions**

982

983 **Figure 1.** Spectrograms showing male and female songs for nine species of fairy-wrens. Overall,
984 male and female songs are similar to each other, while overall song structure differs among the
985 nine species. Artwork by Allison E. Johnson.

986

987 **Figure 2.** Overlap of male and female songs in acoustic space is similar overall for nine species
988 of fairy-wren. Male and female songs of certain species (e.g., purple-crowned, red-backed,
989 variegated) show some dimorphism based on separation in acoustic space, however, in other
990 species (e.g., lovely, superb) male and female songs are nearly identical. Axes represent the first
991 and second multidimensional scaling (MDS) vectors (D1 and D2).

992

993 **Figure 3.** Song length (PC1) compared to (A) proportion of provisioning by the dominant male
994 (compared to the dominant female) and (B) male survival and across 15 fairy-wren populations.
995 Male songs (blue) were significantly longer than female songs (red) in populations with low
996 male provisioning rates and survival, whereas male and female songs were shorter and similar
997 lengths in populations in which males are long-lived and provide more equal provisioning
998 compared to females. Each point represents a single song. Trendlines are based on univariate
999 model output.

1000

1001 **Figure 4.** Element rate (PC2) compared to (A) breeding synchrony and song variability (PC3)
1002 compared to (B) breeding synchrony and (C) latitude. For PC2, female songs (red) were slower
1003 paced than male songs (blue) in less synchronously breeding populations, but similarly paced to
1004 male songs in more synchronously breeding populations. For PC3, male song variability (blue)
1005 was more positively correlated than female song (red) to these life-history traits (Table 3). Note
1006 that element diversity and frequency range load negatively on PC3 such that more negative
1007 values represent more variable songs (Table 2). We flipped the axes on graphs of PC3 so that the
1008 relationships with life-history traits and increasing elaboration can be more readily visualized.
1009 Each point represents a single song. Trendlines are based on univariate model output.

1010

1011 **Figure 5.** Sexual song dimorphism compared to life-history traits for 15 populations of fairy-
1012 wrens. Male and female (A) acoustic areas overlapped most and (B) were closest together in
1013 populations with high male survival. Male and female (C) acoustic areas were similarly variable
1014 at high latitudes. Each point represents song dimorphism for a single species. Trendlines are
1015 based on univariate model output.

1016

1017 **Figure S1.** A two-dimensional acoustic space illustrating how songs group for the nine fairy-
1018 wren species from 15 populations. The feature space was created by plotting the first two
1019 multidimensional scaling (MDS) coordinates (D1 and D2).

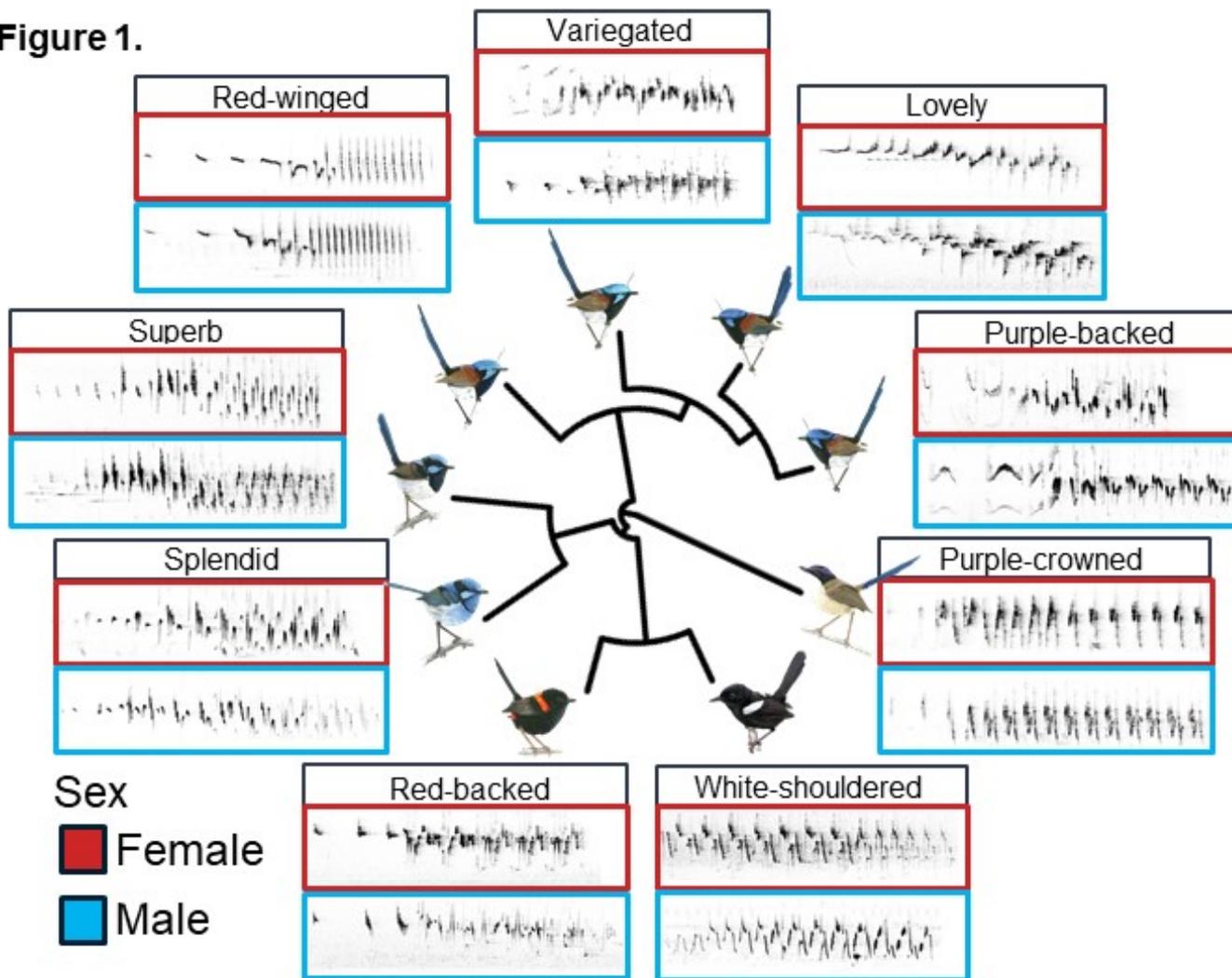
1020

1021 **Figure S2.** Correct classification for all nine fairy-wren species within the study compared to
1022 each other species.

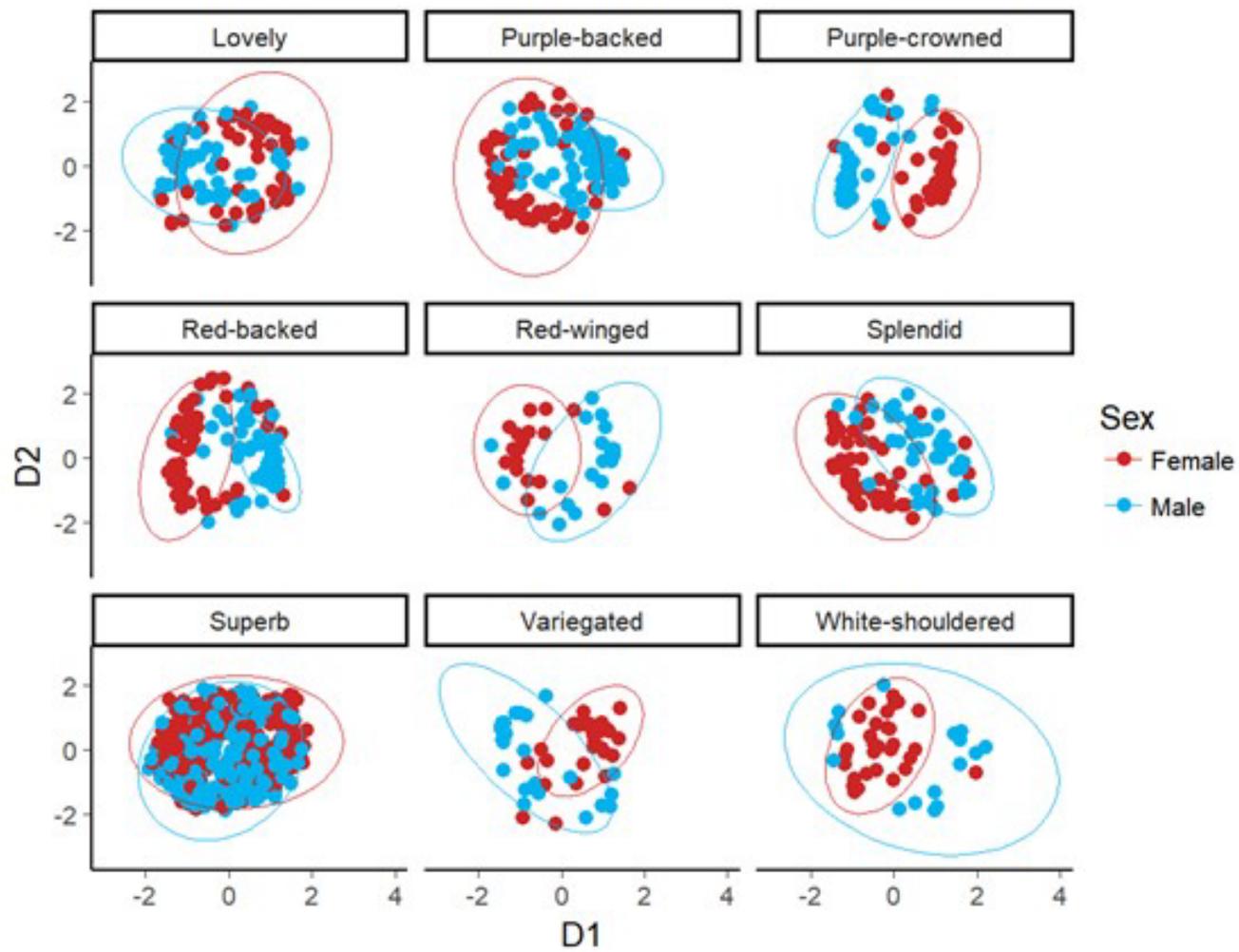
1023

1024 **Figure S3.** Variable importance scores indicating the contribution of each song-level parameter
1025 to correct classification of males and females to each species acoustic space. Scores were
1026 calculated from supervised random forest analysis conducted separately for each species.

Figure 1.



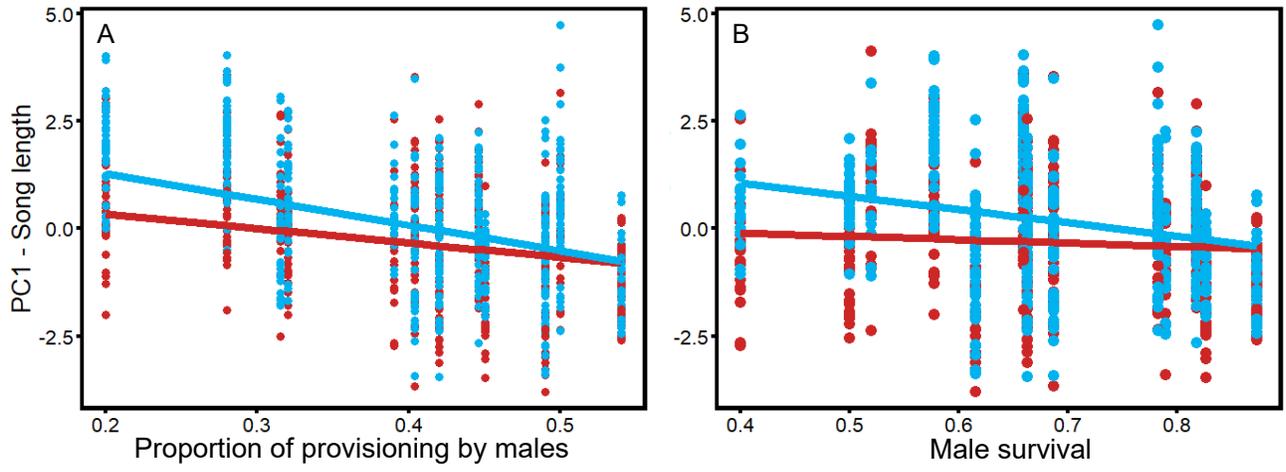
1032 Figure 2.



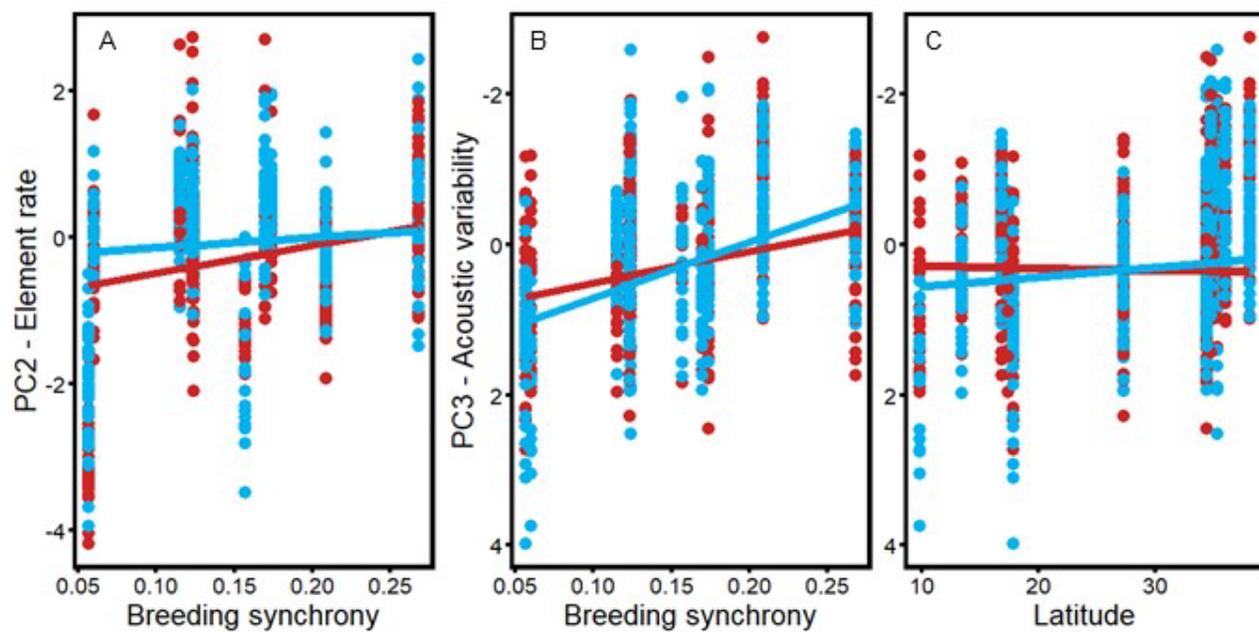
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Figure 3.

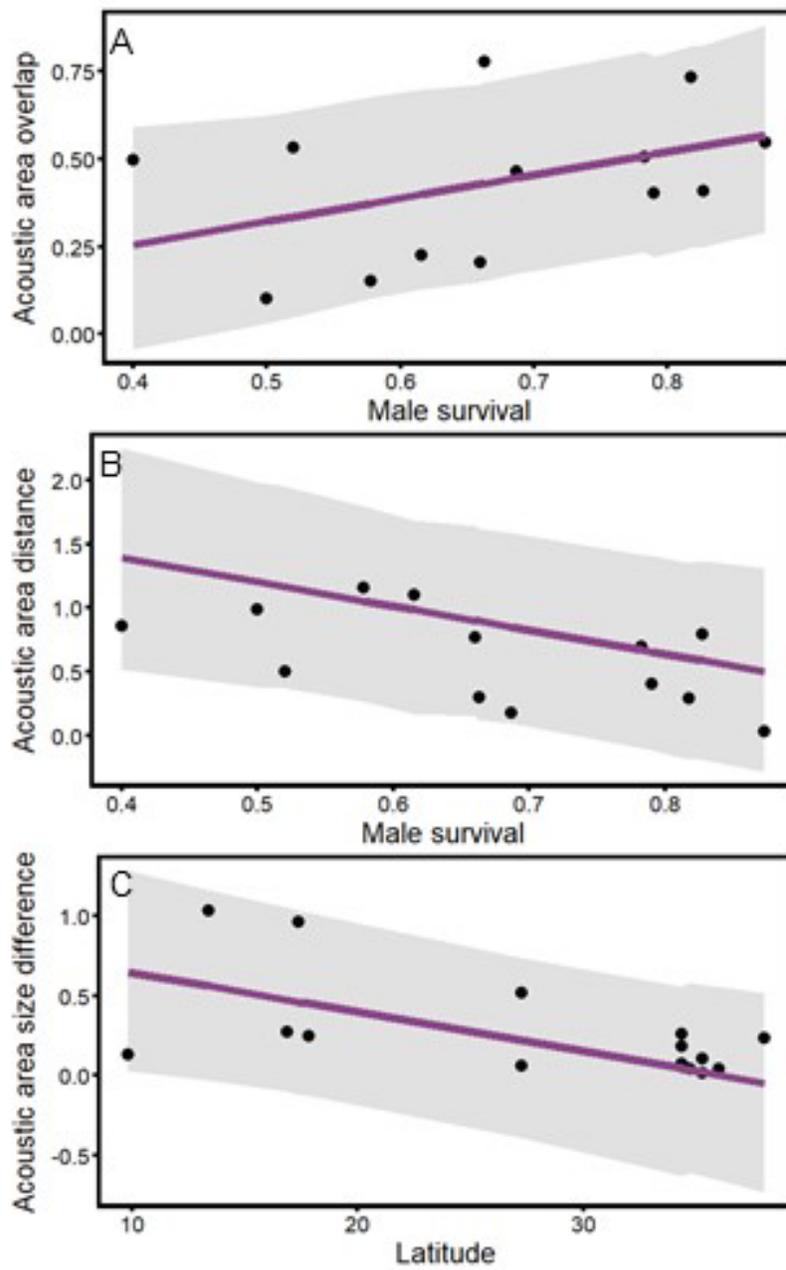


1038 Figure 4.



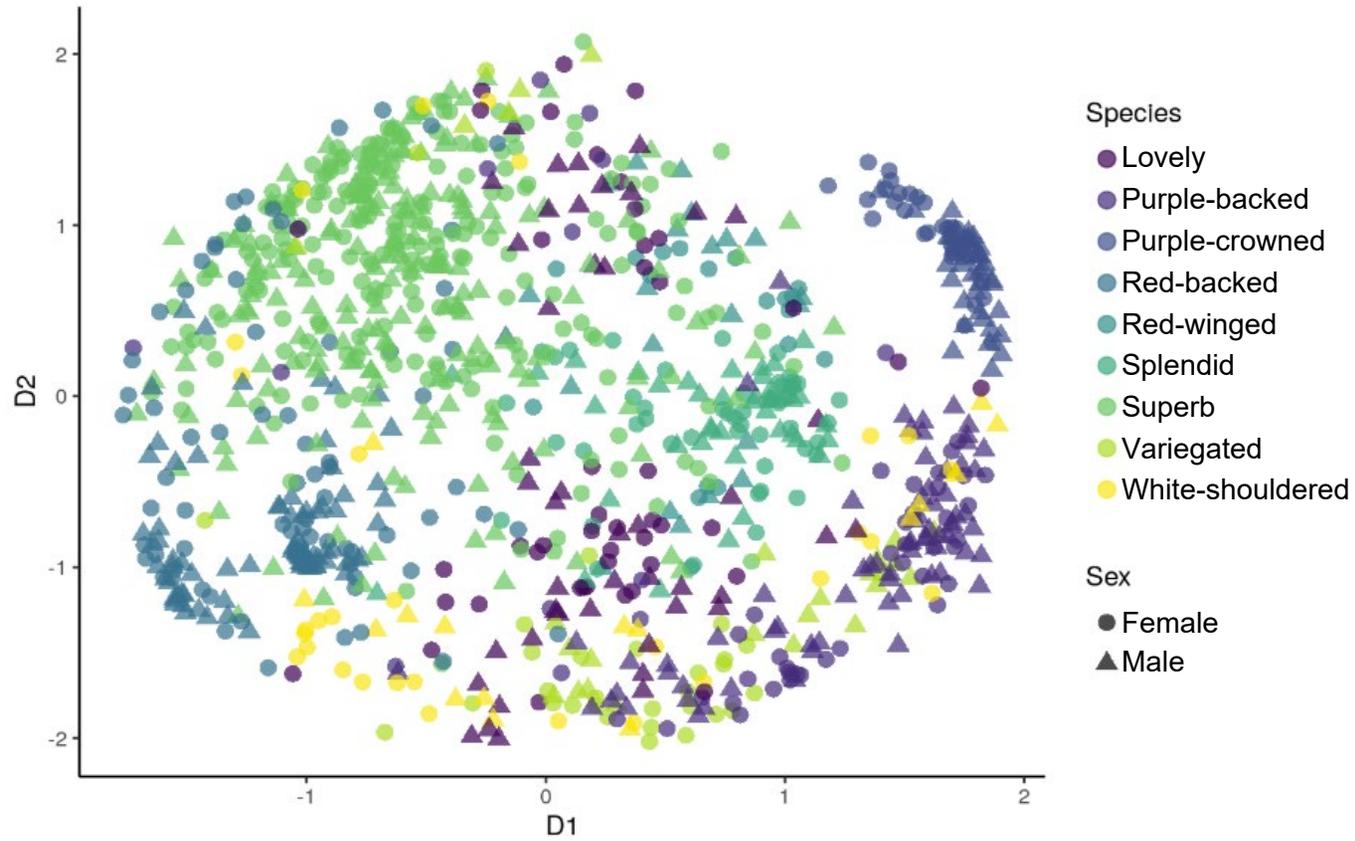
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1041 Figure 5.

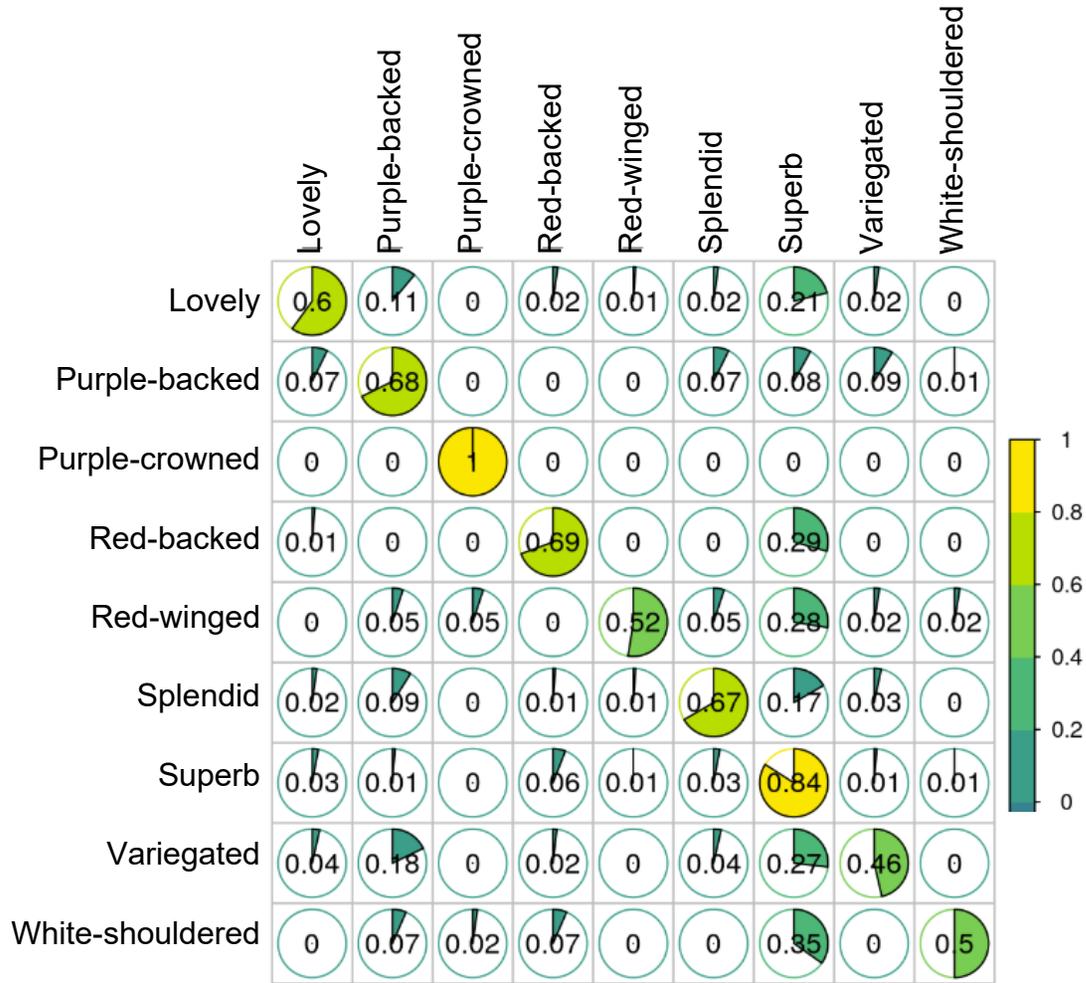


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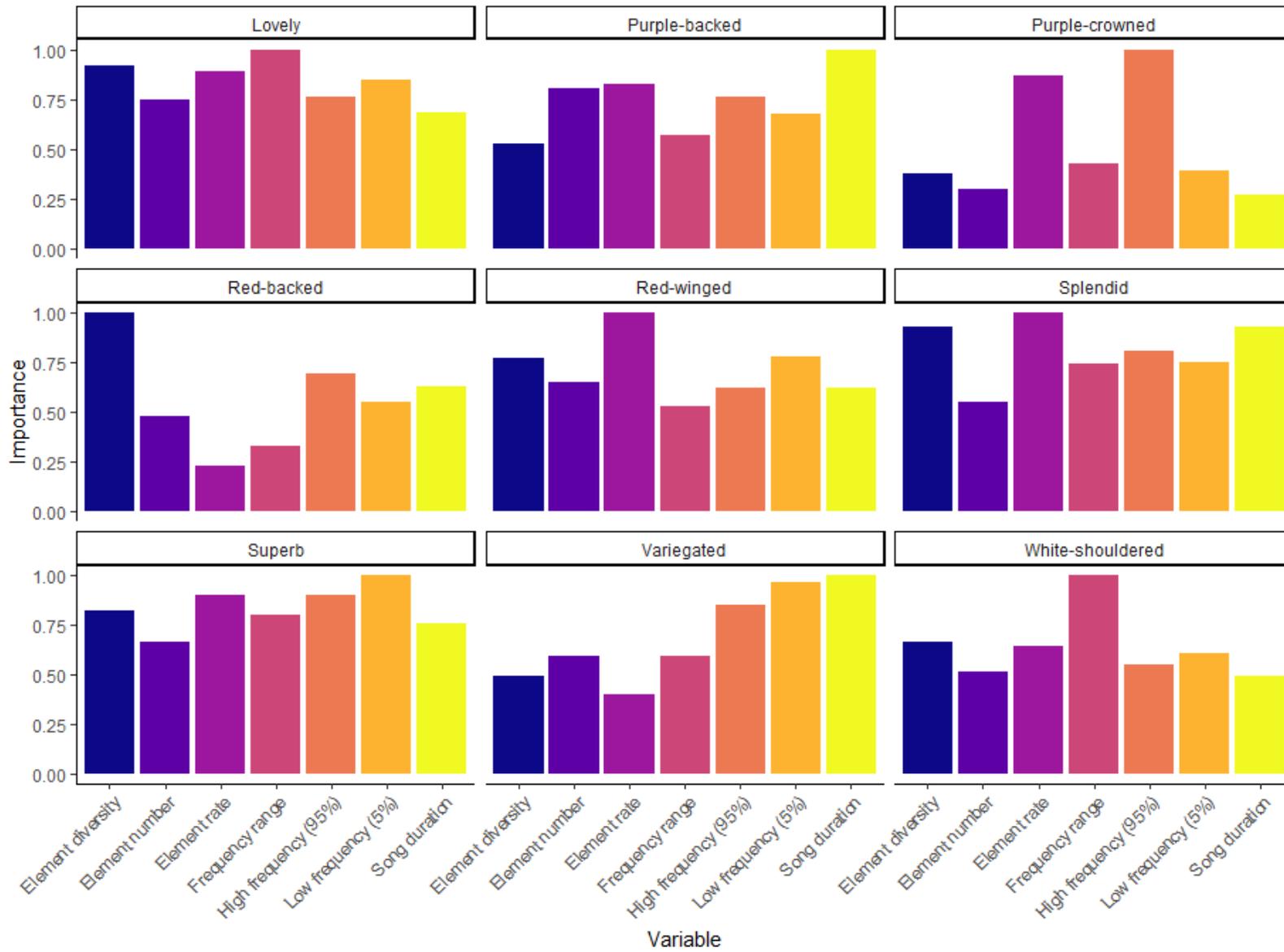
1043 Figure S1.
1044
1045



1046 Figure S2.
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 1048



1049 Figure S3.



1050