1 Title: Assessing the similarity of song-type transitions among birds: Evidence for inter-species

2 variation

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16 **ABSTRACT**

17   In many species of songbird, individuals sing multiple song types, some of which are

18 shared with their neighbours. Individuals may also share syntactical rules that govern the

19 transitions between different song types, but few studies have attempted to study this kind of

20 sharing. Progress has been inhibited by a lack of statistical tools to compare song type transitions

21 among individuals. We present a straightforward method for comparing song transitions based

22 on Markov transition matrices. The method calculates the number of mutually-preferred song-

23 type-to-different-song-type transitions found in the song sequences of two birds, then assesses

24 whether that number is significantly greater than would be expected if the two birds ordered their

25 songs independently of one another. We applied this method to song sequences from five

26 songbird species. All pairwise comparisons among male Cassin's Vireos (*Vireo cassinii*) showed

27 significant similarity in song transitions, as did a minority of comparisons among Adelaide's

28 Warblers (*Setophaga adelaidae*), and one pair of Marsh Wrens (*Cistothorus palustris*). In

29 contrast, dyads of Rock Wrens (*Salpinctes obsoletus*) and Rufous-and-white Wrens (*Thryophilus*

30 *rufalbus*) did not share song-type transitions at levels exceeding chance. Inter-territory distance

31 was not significantly related to our measure of song transition similarity in any of our study

32 species. These results provide evidence that inter-individual similarity in song type transitions is

33 a trait that varies considerably among species. We discuss the potential drivers of similarity in

34 song transitions, but note that assessing its evolutionary breadth will require a larger sample of

35 species. The application of our method to additional species will provide a more comprehensive

36 understanding of signal use and vocal interaction in songbirds.

37 **KEYWORDS**

38 Bird song; Syntax; Adelaide's Warbler; Cassin's Vireo; Marsh Wren; Rock Wren; Rufous-and-

39 white Wren

40 **INTRODUCTION**

41   Quantitative comparison of signal repertoires can advance research in animal

42 communication (Kershenbaum et al., 2016). For example, conspecific animals living in close

43 proximity often "share" some or all of their vocal repertoires (Henry, Barbu, Lemasson, &

44 Hausberger, 2015). Research into the function of shared vocal elements has demonstrated that

45 conspecifics often deliver them preferentially during agonistic interactions (Krebs, Ashcroft, &

46 Orsdol, 1981; Todt & Naguib, 2000; Vehrencamp, 2001), that they are likely to play a role in

47 social bond formation and maintenance (Janik, 2000; Schulz, Whitehead, Gero, & Rendell,

48 2008), and that females can use them to evaluate male vocal performance (Ballentine, Hyman, &

49 Nowicki, 2004). In songbirds, vocal repertoire comparisons often begin and end at the level of

50 the song type, but similarity may extend to other dimensions of singing behaviour. Below the

51 level of the song type, birds may share parts of a song, without sharing the entire song type

52 (Anderson, Searcy, & Nowicki, 2008; Burt & Beecher, 2008). Above the level of the song type,

53 transitions between song types may be similar, in which case similarity can be considered to

54 occur at the level of the syntax governing each bird's transitions from one song type to another

55 (Ivanitskii, Marova, & Antipov, 2017).

56   Reports of similarity in song transitions date back to a study of Marsh Wrens in

57 Washington state (Verner, 1975). In western populations of this species, males sing repertoires of

58 over 100 song types, most of which are shared between neighbours. Verner (1975) made three

59 observations about the sequential ordering of songs: first, repetitions of the same song type in

60 succession were rare; second, certain transitions from one song type to another were much more

61 common (and others much less common) than expected by chance; and third, the order of song

62 types was similar among males within the population (Verner, 1975). If one individual tended to

63 transition from song type A to song type B, it was often the case that other nearby males tended

64 to do the same. A subsequent laboratory study linked this similarity in song type transitions to

65 the learning process. By tutoring two male Marsh Wrens on the same song sequence, Kroodsma

66 (1979) found that the birds learned both the acoustic structure of the song types on the tape and

67 their order of presentation. These results suggest that the patterns described by Verner (1975) in

68 the field either resulted from one bird learning the songs and transitions from his neighbour early

69 in life, or from both neighbours learning songs and transitions from a third party.

70   At least three other bird species have shown patterns similar to those Verner (1975)

71 observed among Marsh Wrens. (1) Under laboratory conditions, the song sequences produced by

72 Common Nightingales (*Luscinia megarhynchos*) were strongly influenced by the song order on

73 their tutor tapes (Todt & Hultsch, 1998). When presented with linear sequences of song, the

74 tutees appeared to divide the sequence into shorter chunks of several song types that were

75 subsequently produced together. Since these chunks were often recombined in different ways

76 during song production, the song sequences produced by the tutees were very similar, but not

77 identical, to the sequences on the tutor tapes. (2) In congeneric Thrush Nightingales (*Luscinia*

78 *luscinia*), individuals within a population delivered shared song types in similar orders (Ivanitskii

79 et al., 2017). A sequence of five song types was identified in the song sequences of all 29 males

80 whose repertoire included the five constituent song types. Shorter sequences of up to four song

81 types were also widely shared. (3) Similarly, in a population of Village Indigobirds (*Vidua*

82 *chalybeate*), transitions between song types showed little variation among individuals (Payne,

83 1979).

84   The similarity of song order was not analysed statistically in any of the aforementioned

85   studies. Statistical comparisons would be valuable because some degree of similarity in

86   transitions is to be expected by chance among birds that share song types. For example, the

87   observation that two birds transition from song type A to B may simply reflect the finite

88   repertoires from which the birds can select a successor to song type A. Moreover, the stochastic

89   nature of transitions within bird song sequences (Jin, 2013) may lead to occasional observations

90   of transitions that are peripheral to the preferred syntax of a bird. The critical consideration,

91   therefore, is not whether a particular transition occurs in the song sequences of both birds, but

92   whether a transition is preferred by both birds, and whether the set of transitions that are

93   preferred by both birds is larger than should be expected by chance given the repertoires of the

94   two birds.

95   Without an objective statistical test to formalize comparisons of song ordering among

96   birds, patterns of similarity remain anecdotal. This is not particularly troublesome in the above

97   examples, since the patterns described are sufficiently striking that there is no reason to suspect

98   they are spurious. Some species, however, might show subtler, yet still significant, levels of

99   similarity, such that patterns are difficult to detect. If so, reports of similarity of song transitions

100   in the literature may be biased towards the most extreme cases.

101   In this study, we examined inter-individual similarity in song-type-to-song-type

102   transitions. We present a statistical methodology for assessing whether two individuals show a

103   significant tendency to transition between song types in similar ways. The method quantifies

104   mutual preferences for certain song-type-to-song-type transitions, independent of rates of song

105   sharing. It can be applied to species with stochastic or deterministic transitions. Although we

106   focus on transitions between song types, our method could also be applied to assess similarity in

107   transitions at other levels of the hierarchy of song organization; for example, this method could

108   be used to examine shared transitions between syllables within a song (Briefer, Aubin, Lehongre,

109   & Rybak, 2008). The method could also be used to examine signal type transitions in animals

110   other than birds that possess signal repertoires. Here we apply this method to song sequences of

111   five songbird species (Cassin's Vireo, *Vireo cassinii*; Adelaide's Warbler, *Setophaga adelaidae*;

112   Rock Wren, *Salpinctes obsoletus*; Rufous-and-white Wren, *Thryophilus rufalbus*; Marsh Wren,

113   *Cistothorus palustris*) to examine interspecific variation in song-type transition patterns. We also

114   investigate whether inter-territory distance explains variation in this metric.

115   **METHODS**

116   *Song Sequence Datasets*

117   We used song recording datasets from four species: Adelaide's Warbler (*Setophaga*

118   *adelaidae*), Rock Wren (*Salpinctes obsoletus*), Rufous-and-white Wren (*Thryophilus rufalbus*),

119   and Cassin's Vireo (*Vireo cassinii*). For each of these species, the song sequences were

120   annotated according to a population-level song-type classification key (a separate key for each

121   species) so that individual repertoires could be enumerated and rates of song sharing could be

122   assessed. Spectrogram images are provided in Figs S1-S4 to clarify what is meant by shared and

123   unshared song types in each species. We calculated several summary statistics for each species,

124   including the average number of songs recorded from each individual of each species, the song

125   repertoire size of each bird, and the average number of shared songs between males in each

126   population. In addition to these four datasets, we analysed published transition networks for two

127   Marsh Wrens (*Cistothorus palustris*) that appear as figures 11 and 12 in Verner (1975). Although

128   the availability of only two individuals precludes broader conclusions about this species, Marsh

129 Wrens were included as a means of comparing our quantitative approach with a historical,

130 qualitative description of two birds with highly similar song-type transitions.

131   *Adelaide's Warbler*

132   We recorded nine colour-banded male Adelaide's warblers at the Cabo Rojo National

133 Wildlife Refuge, Puerto Rico (17.98º N, 67.17º W) between March and June, 2012. Males were

134 recorded for four days each. Observations began 30 minutes before sunrise and continued until

135 three hours after sunrise. Recordings were collected with a portable solid-state recorder (Marantz

136 PMD661) and a directional microphone (Sennheiser ME67). Songs were classified to song type

137 according to their appearance on sound spectrograms in Syrinx PC v2.6f Sound Analysis

138 Software (Fig S1; J. Burt, Seattle, WA, U.S.A). Trained observers labelled song-types separately

139 for each male. Later, two people independently chose "holotypes" to define a population-level

140 classification key, and classified song types across individuals. They did this separately at first,

141 then discussed disagreements to come to a final decision. Finally, one person (DML) compared

142 every song recording to the holotypes, corrected scoring errors, and reclassified (lumped) similar

143 types, resulting in an annotated dataset of 9499 songs. To estimate the repeatability of this final

144 step, a second observer independently classified 22-23 randomly selected songs from each of

145 nine males (total = 200 songs) using the population-level classification key. In total, 174 of 200

146 (87%) scores matched. For further details on this dataset, see Schraft, Medina, McClure, Pereira,

147 & Logue (2017).

148   *Rock Wren*

149   We recorded 12 male rock wrens in Larimer County, Colorado (40.47 - 40.96º N, 105.15

150 – 105.36º W) during May, June, and July of 2012 and 2013. Most study subjects were not

151 banded, but could be easily relocated because members of this species show strong territory

152   fidelity (Warning & Benedict, 2015) and individual song patterning. At least 900 songs per

153   individual were recorded over the course of one to three recording sessions on different days. All

154   recordings were of unprovoked, natural broadcast singing of territorial males. Recordings were

155   collected with a portable solid-state recorder (Marantz PMD 671) and a directional microphone

156   (Sennheiser MKH-60). Songs for all individuals were classified to song type by one observer

157   (LB) after visualizing recordings in Raven Pro Sound Analysis Software (Fig S2; Cornell

158   Laboratory of Ornithology, NY, U.S.A.). To assess the repeatability of the classification of songs

159   to song type, a second observer classified a subset of ten songs from each of ten individuals

160   using a population-level classification key. The two observers agreed on the classification of 88

161   out of 100 songs (88%). For more information about this data set, see Benedict & Warning

162   (2017).

163   *Rufous-and-white Wren*

164   We recorded 41 colour-banded male rufous-and-white wrens in Sector Santa Rosa of the

165   Area de Conservación Guanacaste, Costa Rica (10.85º N, 85.6º W) between April and July of

166   2003 through 2014. Songs were recorded from spontaneously singing birds using a portable

167   solid-state recorder (Marantz PMD660 or PMD670) and a directional microphone (Sennheiser

168   MKH70 or ME67). Songs were visualized and classified to song type based on their spectro-

169   temporal properties according to a population-level classification key using Syrinx PC Sound

170   Analysis Software (J. Burt, Seattle, WA, U.S.A). To assess the reliability of classification of

171   songs to song types, two observers independently classified a sample of 200 songs (20 songs

172   from each of 10 different males, selected randomly) using the population-level classification key.

173   The two observers agreed on the classification of 193 out of 200 songs (96.5%). Additional

174   details about this dataset are provided in Harris, Wilson, Graham, & Mennill (2016).

175   *Cassin's Vireo*

176   We recorded eleven colour-banded Cassin's vireos in May and June, 2014 at a site on

177   private land in Amador County, California, USA (38.49º N, 120.63 º W). Recordings were made

178   opportunistically by one observer, by approaching the known territory of a male and recording

179   song output until the bird moved out of the range of the microphone, stopped singing for a long

180   period of time, or engaged in a close boundary dispute that made recording difficult. Songs were

181   recorded using a portable solid-state recorder (Marantz PMD-661) and a directional microphone

182   (Sennheiser MKH20-P48) with a Telinga parabolic reflector. Prior work on this species has

183   referred to songs and song types as phrases and phrase types, respectively (Hedley, 2016b), but

184   we use the former terms in this paper for consistency with the other species. Songs were

185   annotated to song type by one observer (RH) by visually inspecting a spectrogram (Fig S4) in the

186   linguistics software Praat (Boersma & Weenink, 2014). Spectrogram inspection has been shown

187   to give nearly identical results to automated methods of song type classification in this species

188   (Hedley, 2016b), and also shows over 99% repeatability from one human observer to the next

189   (Hedley, Denton, & Weiss, 2017).

190   **Terminology and Motivation for Statistical Approach**

191   We define the term *preferred transition*, as a transition from one song type to another that

192   occurs at statistically inflated rates relative to the overall rate of occurrence of the two

193   constituent song types. Apart from preferred transitions, a dataset from a bird will typically

194   include some transitions that are observed rarely, and others that are not observed at all, but

195   which are possible given the bird's repertoire of song types. We combined rare and unobserved

196   transitions under the category of *non-preferred transitions*, justified by the fact that rare

197   transitions could result when a bird is interrupted, commits an error while producing a preferred

198   transition, or alters its song in response to external conditions. In other words, while preferred

199   transitions show evidence of being intentionally delivered, rare transitions may result from

200   mistakes that are likely to accumulate as recording proceeds. The binary classification of

201   transitions as preferred or non-preferred is sure to obfuscate some of the variation within each of

202   these categories, but has the benefit of simplifying subsequent analyses.

203   We define *mutually-preferred transition* as a transition that is preferred by two or more

204   birds. Our analysis assesses whether the number of mutually-preferred transitions in the song

205   sequences of two birds is higher than expected, given the rate of song sharing and number of

206   preferred transitions of the two birds. Pairs of birds whose mutually-preferred transitions

207   significantly exceed chance levels are considered to have similar song transitions.

208   Two birds who exhibit many shared song types may have many mutually-preferred

209   transitions (Fig 1a) or few mutually-preferred transitions (Fig 1b). The null expectation is a low

210   number of mutually-preferred transitions if the sequencing tendencies of the two birds were

211   developed independently of one another. Birds sharing few song types can still show evidence of

212   higher than expected mutually-preferred transitions (Fig 1c), but individuals that do not share

213   any song types cannot exhibit mutually-preferred transitions.

214
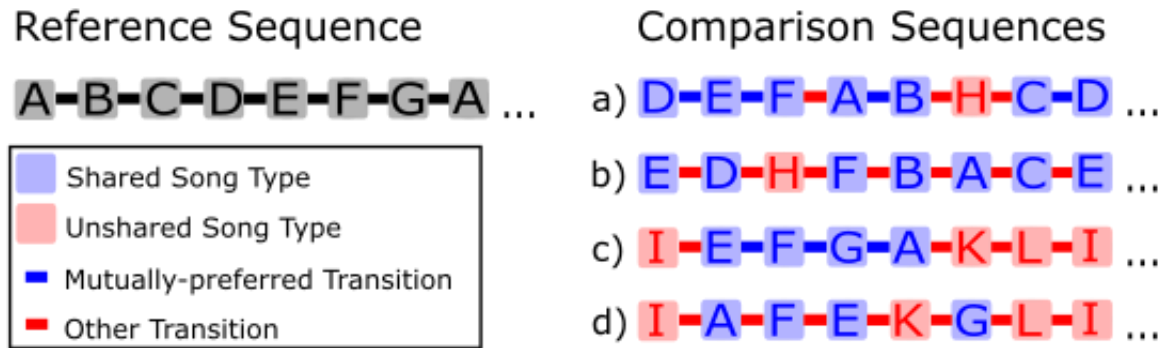
Figure 1: Simplified examples of four birds (a-d) that vary in the number of song types and mutually-preferred transitions in common with a reference sequence (grey boxes). For simplicity, these hypothetical birds sing with a completely deterministic syntax, cycling linearly through their repertoire of seven song types, so every transition is a "preferred transition" (see text). The last song type in each sequence is the same as the first to signify singing in a cyclical pattern. The number of shared song types and mutually-preferred transitions can vary independently. Bird a shares six song types (blue boxes) and four mutually-preferred transitions (blue lines) with the reference bird. Bird b shares six song types and zero mutually-preferred transitions. Bird c shares four song types and three mutually-preferred transitions. Bird d shares four song types and zero mutually-preferred transitions.

Statistical Methods

Our method has four steps: 1) construction of transition matrices from the song sequences of the two focal birds and removal of song-type repetitions along the diagonal of the matrix; 2) analysis of each transition matrix to identify preferred transitions; 3) identification of shared song types and filtering of transition matrices to include only transitions between shared song types; and 4) counting mutually-preferred transitions and comparing the observed number

232   against a null expectation to test for a significant association between the transition matrices.

233   These steps are explained in more detail below and are illustrated in Figure 2.
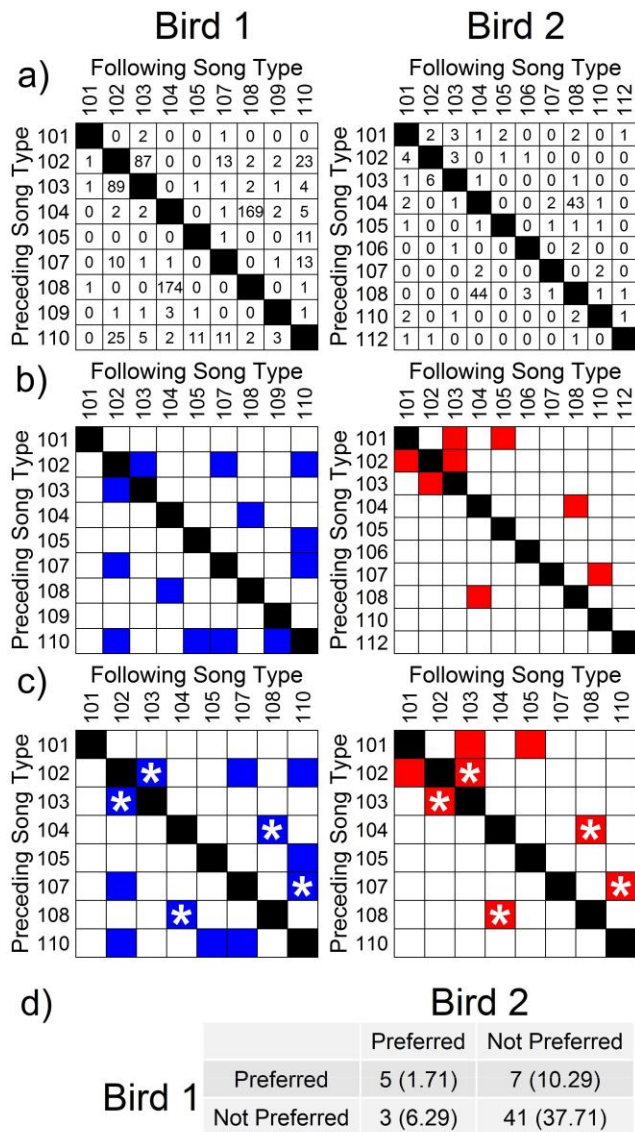
234

235   **Figure 2**: An illustration of our method for comparing song transitions, using two

236   Rufous-and-White Wrens as an example. a) First, a transition matrix is constructed from each

237   bird's song sequences (left and right matrices). Cells contain the number of transitions from the

238   preceding song type to the following song type. Self-transitions along the diagonal are ignored.

239   b) Each transition is determined to be preferred or not. It is not the absolute number of times that

240   a transition is observed that determines whether or not it is preferred, but rather the number of

241   times that a transition is observed relative to the number of times each of the two song types in

242   the transition was sung within the dataset as a whole. Blue and red cells show the preferred

243   transitions for the two birds, and white cells show non-preferred transitions. c) Matrices are

244   filtered to include only transitions between shared song types, such that the resulting matrices are

245   the same size and have the same row and column song types (in this case the unshared song

246   types 109 and 112 are removed). Mutually-preferred transitions can then be identified (white

247   stars) as transitions that are preferred by both birds, and this value can be compared against a null

248   expectation. In this example, the two birds had five mutually-preferred transitions in common:

249   102-to-103, 103-to-102, 104-to-108, 108-to-104, and 107-to-110. d) A contingency table is

250   produced summarizing the preferred and non-preferred transitions of each bird. Observed values

251   are given with expected values in parentheses. The five mutually-preferred transitions among

252   these two birds are more than the 1.71 that were expected by chance. A one-tailed Fisher's Exact

253   test showed a p-value of 0.008 for this comparison. This p-value, however, did not meet the

254   threshold for significance once multiple comparisons among all Rufous-and-white Wrens

255   included in the study were accounted for.

256

257   The details of constructing a transition (or Markov) matrix, as required for step 1, were

258   described by Chatfield & Lemon (1970). Briefly, for a bird with repertoire size C, the transition

259   matrix contains C rows and C columns corresponding to each of the song types in the bird's

260   repertoire. A cell in row i and column j is filled with a count of the number of times the bird

261   transitioned from song type i to song type j in the recording sample (Fig 2a). Diagonals in the

262   matrix represent self-transitions, where a bird repeated the same song type consecutively, but it is

263   often desirable to investigate transitions between types independent of repetitions (Hailman,

264   Ficken & Ficken, 1985). We opted to exclude entries along the diagonal because the tendency to

265   repeat song types appears primarily to be a species-level trait with less variation among

266   individuals of a species than between species. This has led to the common designation of species

267   as singing with either eventual variety or immediate variety based on the frequency of repetitions

268   in their song sequences (Kroodsma & Verner, 1978). Moreover, a syntactic "rule" designating a

269   repetition is qualitatively different from one designating a transition between two song types.

270   Repetitions could be underpinned by a rule like *repeat(x)*, regardless of what *x* is. Transitions, in

271   contrast, require association of different song types (e.g. transition from *x* to *y*). Efforts to model

272   birdsong syntax have frequently shown that repetitions are not well described by the same

273   processes that govern between-type transitions (Hedley, 2016a; Jin & Kozhevnikov, 2011;

274   Kershenbaum, Bowles, Freeberg, Jin, & Lameira, 2014), suggesting that these two types of rules

275   may be encoded differently within the avian brain. Therefore, we excluded repetitions in our

276   primary analyses, but note that only slight modifications to our method are needed to include

277   repetitions. Analyses with repetitions included are presented in Supplementary Text 2.

278   In step two, we examined each cell in the transition matrix to assess whether the

279   transition occurred at statistically inflated rates given the number of occurrences of the two

280   constituent song types. To do this, we used a cell-by-cell Fisher's Exact Test. This test collapses

281   the *C*x*C* transition matrix to a 2x2 contingency table for each cell [*i,j*] where the margins

282   represent the count in row *i* and not in row *i* on one margin, and the count in column *j* and not in

283   column *j* on the other. A one-tailed Fisher's Exact Test then tests whether the count in the cell

284   [*i,j*] exceeds that expected given the overall rate of occurrence of the constituent song types *i* and

285   *j*. Cells with significantly inflated counts at a significance level of $p < 0.05$ were subsequently

286   assigned a value of 1, and cells with counts that were not significantly inflated were assigned a

287   value of 0 (Fig 2b). This can be thought of as a thresholding step to eliminate rare transitions,

288   where the threshold tends to be lower for transitions between rare song types than for transitions

289   between common song types. This differs from thresholding based on transition probabilities,

290   because transition probabilities consider the overall rate of occurrence of the preceding song type

291   alone, while our approach considers the rates of occurrence of both the preceding and following

292   song types.

293   In step three, we identified song types shared between the two birds. Rows and columns

294   associated with shared song types were isolated from the matrix and arranged in an identical

295   order in the matrices of the two birds. If the number of shared song types was *M*, this step

296   resulted in two *M*x*M* transition matrices with the same column- and row-names, but which

297   differed in terms of which cells contained ones and zeroes (Fig 2c). Each cell in these matrices

298   can be thought of as a potential mutually-preferred transition, given the repertoire of the two

299   birds.

300   In step four, we assessed whether the distributions of the preferred transitions of each

301   bird were independent of one another. To do this, a 2x2 contingency table was produced, where

302   the margins represented the transitions preferred and not preferred by bird 1, and those preferred

303   and not preferred by bird 2 (Fig 2d). Another one-tailed Fisher's Exact Test conducted on this

304   table assessed whether the number of mutually-preferred transitions exceeded the expected

305   number. To measure the magnitude of this association, we also divided the observed number of

306   mutually-preferred transitions by the expected number, where the expected number was

307   calculated using the formula $E[i, j] = \frac{(Row\ i\ total) * (Column\ j\ total)}{Grand\ total}$ (Whitlock & Schluter, 2015).

308   The rationale for this step is that, given the known repertoires of each bird and their number of

309   shared song types M, there are $M(M-1)$ possible transitions between shared song types (i.e. $M(M-

310   1)$ is the grand total). If both birds select their preferred transitions independently from this set of

311   possibilities, the number of mutually-preferred transitions is expected to be the product of the

312   proportion of possible transitions that are preferred for each bird, multiplied by the grand total of

313   possible transitions. Significant deviations from this expected value imply a lack of

314   independence in the selection of preferred transitions of the two birds.

315

316   *Data Analysis*

317   We tested for significance at three levels: between dyads, at the species level, and

318   between species. At the dyad level, we calculated the number of mutually-preferred transitions

319   between each possible dyad in the population, as well as the effect size (observed number of

320   mutually-preferred transitions divided by expected, as above) and the p-value comparing the

321   number of mutually-preferred transitions to the expected value for those two birds. To account

322   for the large number of comparisons made within each species, we controlled the false-discovery

323   rate using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995). In this method, p-

324   values are sorted from smallest to largest and assigned an index k from 1 to m, where m is the

325   number of hypotheses tested. All null hypotheses with p-values less than or equal to the largest k

326   that satisfies $p_k \leq \frac{k}{m}\alpha$ are rejected. We used $\alpha = 0.05$. To compare whether the species as a

327   whole showed a significant effect, we compared the effect sizes of all dyads for that species

328   against a null expected value of 1 using a one-tailed Wilcoxon signed-rank test. To make

329   comparisons among species, we compared the effect size values among the five species using a

330   Mann-Whitney U test.

331   We used GPS points from the birds' breeding territories to assess whether effect size was

332   explained by the distance between the territories of two birds. To do this, we constructed two

333   matrices for each species with rows and columns corresponding to the individuals of that species.

334   The entry in cell [*i,j*] of one matrix contained the effect sizes (observed/expected) for the

335   comparison between bird *i* and bird *j*. Cell [*i,j*] in the other matrix contained the distance between

336   the territories of the two birds, in meters. We compared these two matrices using a Mantel test.

337   The Mantel test randomly permuted the rows and columns of one matrix 10 000 times to assess

338   whether the relationship between inter-territory distance and effect size was significantly greater

339   than expected by chance. All analyses were conducted in R, version 3.3.1 (R Core Team, 2016).

340   Data and code are available on Figshare (https://figshare.com/s/d065cd8fe7f4642b4b4f). The R

341   code reads in a set of transition matrices for a species, and conducts comparisons at the dyad

342   level, calculating the effect sizes and p-values for all possible dyadic comparisons.

343   **RESULTS**

344   All five species exhibited large repertoires and high rates of song sharing (Table 1),

345   allowing us to proceed with our comparisons of song-type transitions in the five species. At the

346   dyad level, some species showed significant similarity in transitions, but others did not. The

347   results are summarized in Table 2 and visualized in Figure 3. No comparisons were significant in

348   Rufous-and-white Wrens or Rock Wrens when the Benjamini-Hochberg procedure was used to

349   account for multiple comparisons. In Adelaide's Warblers an intermediate pattern was apparent,

350   where 6% (2/36) of comparisons were significant. Cassin's Vireos showed strong evidence of

351   mutually-preferred transitions in each of 55 pairwise comparisons. Effect sizes in this species

352   ranged from 5.1 to 12.5, indicating that individuals shared mutually-preferred transitions at

353 several times the level expected by chance. The two Marsh Wren individuals showed the highest

354 similarity of all, with an effect size 34.6 times the level expected by chance (p<0.0001).

355 Inspection of Figure 3 shows that some comparisons had high effect sizes but non-

356 significant p-values. This can be attributed to comparisons that had very low expected numbers

357 of mutually-preferred transitions. For instance, a comparison with an expected value of 0.1 and

358 an observed value of 1 would not reach statistical significance, while one with an expected value

359 of 1 and an observed value of 10 would, even though the effect size in both cases is 10.

360 Accordingly, both the p-values and effect sizes are important for proper interpretation of any

361 dyadic comparisons.

362 **Table 1**: Summary characteristics of the songs of the five species analysed.

| Species	Individuals (N)	Songs Per Individual (mean ± SD)	Repertoire Size (mean ± SD)	No. Shared Song Types (mean ± SD)*
Adelaide's Warbler	9	1035 ± 201	29 ± 4	14.6 ± 6.1
Cassin's Vireo	11	3461 ± 2018	51.4 ± 4.4	25.6 ± 4.4
Rock Wren	12	1535 ± 403	76.6 ± 17.6	31.8 ± 8.1
Rufous-and-white Wren	41	3651 ± 2447	8.1 ± 1.2	6.7 ± 1.2
Marsh Wren	2	450 ± 13	110 ± 0	100

363 * Calculated for all pairwise comparisons among individuals within a species.

364

365 At the species level, Cassin's Vireos showed systematically greater than expected

366 numbers of mutually-preferred transitions (W=1540, p<0.001). Rock Wrens showed

367 significantly greater than expected numbers of mutually-preferred transitions as well at the

368 species level (W=1367, p=0.047). However, the effect was slight (median effect size in Rock

369   Wren was 1.25 times chance levels, compared to 8.38 times chance levels in Cassin's Vireos),

370   and not reinforced by statistical significance in any of the pairwise comparisons. Adelaide's

371   Warblers and Rufous-and-white Wrens showed no such effect at the species level (Adelaide's

372   Warbler: Median: 1.04 times chance levels, W=385, p=0.25; Rufous-and-white Wren: Median:

373   1.00 times chance levels, W=153 610, p=0.97). Small sample sizes precluded species-level

374   analysis of Marsh Wren data.

375   Effect sizes differed significantly between the five species tested (Kruskal-Wallis test,

376    $\chi^2(4)=164$, p<0.001). Post-hoc Mann-Whitney U tests with a Bonferroni adjustment showed that

377   Cassin's Vireos differed significantly from Adelaide's Warbler (U=48, p<0.001), Rock Wren

378   (U=3630, p<0.001), and Rufous-and-white Wren (U=44463, p<0.001). The latter three species

379   did not differ from one another (Adelaide's Warbler vs Rock Wren: U=1182, p=1; Adelaide's

380   Warbler vs Rufous-and-white Wren: U=15482, p=1; Rock Wren vs Rufous-and-white Wren:

381   U=24054, p=1). Post hoc analyses of Marsh Wren observations were not conducted, since only

382   one data point was available for that species.

383
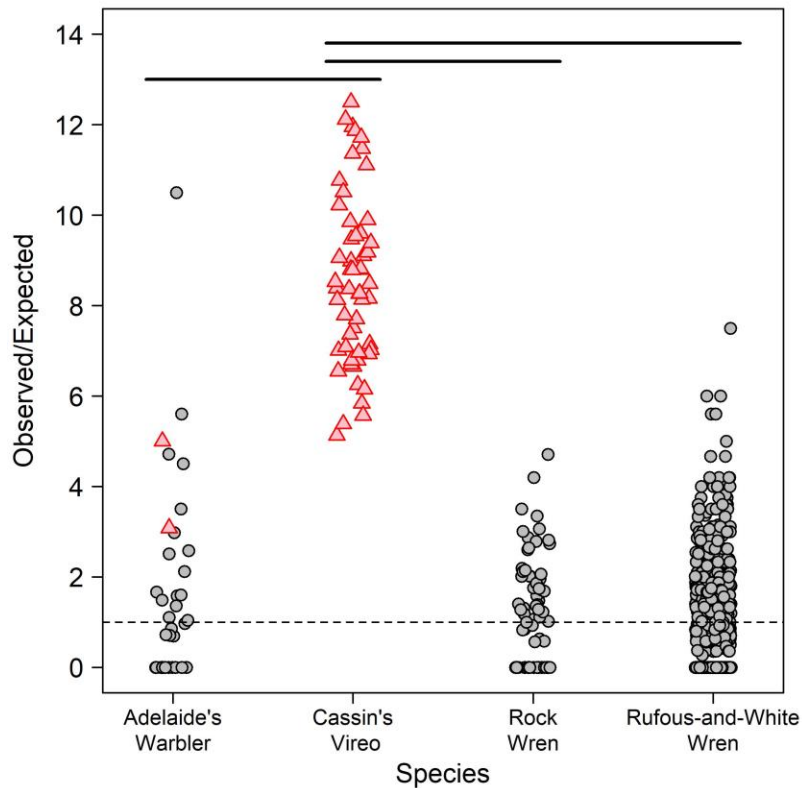
Figure 3: Summary of pairwise comparisons of song-type transitions among four species. Pairwise comparisons that were deemed significant with the Benjamini-Hochberg procedure are displayed as red triangles, while non-significant comparisons are shown with grey circles. Significant differences between species, as determined by post-hoc Mann-Whitney U tests, are indicated with black bars above the points. The horizontal dotted line indicates an observed/expected value of one, the expected similarity if the song transitions of two birds were independently arranged. Higher observed/expected values indicate higher levels of similarity. The single comparison between the two Marsh Wren individuals is not shown, but had an observed/expected value of 34.6.

Table 2: Summary of pairwise comparisons of song transitions among individuals within each of the five species examined here.

Species	Individuals (N)	Inter-individual Distance (m, mean ± SD)	Comparisons (N(N-1)/2)	Significant comparisons (Benjamini-Hochberg procedure)	Effect size (mean ± SD of Obs/Exp)
Adelaide's Warbler	9	225± 153	36	2	1.73 ± 2.23
Cassin's Vireo	11	255 ± 106	55	55	8.54 ± 1.87
Rock Wren	12	17553 ± 14954	66	0	1.30 ± 1.18
Rufous-and-white Wren	41	1745 ± 1209	820	0	1.10 ± 1.09
Marsh Wren	2	1600	1	1	34.6

396

397   Mantel tests revealed no significant relationship between inter-territory distance and

398 effect size within any of the species (Adelaide's Warbler: p=0.46; Rock Wren: p=0.50; Rufous-

399 and-white Wren: p=0.09; Cassin's Vireo: p=0.40). A Mantel test could not be conducted for

400 Marsh Wrens since this species was represented by just two birds.

401 **DISCUSSION**

402   *Comparisons of Similarity of Song Order*

403   We developed a method for comparing the similarity of transitions between shared song

404 types of two birds. The method assesses the number of mutually-preferred transitions in

405   sequences of song from two individuals and compares this number to an expected value. We

406   used this technique to show higher-than-expected numbers of mutually-preferred transitions for

407   all pairwise comparisons in a population of Cassin's Vireo and for a small minority of pairwise

408   comparisons in a population of Adelaide's Warblers. In addition, we confirmed the high levels of

409   similarity in the order of song delivery among Marsh Wrens that were described, but not

410   statistically analysed, by Verner (1975). We did not find higher-than-expected numbers of

411   mutually-preferred transitions in the songs of Rufous-and-white Wrens or most Adelaide's

412   Warblers. Rock Wrens showed slightly inflated levels of mutually preferred transitions overall,

413   but no pairwise comparisons reached the threshold of significance.

414   One implication of these results is that interspecific variation in the similarity of song-

415   type transitions can begin to be evaluated on a larger scale with the method presented here.

416   Evidence of similarity in the delivery order of vocalizations has been described previously in a

417   few species of birds and mammals (Ivanitskii et al., 2017; Kershenbaum, Ilany, Blaustein, &

418   Geffen, 2012; Payne, 1979; Verner, 1975). Cassin's Vireo is one such species, where similarity

419   in song order had been described but not analysed in depth (Hedley et al., 2017). The results of

420   this study are therefore in line with previous descriptions for that species, but provide a level of

421   quantification that has been previously lacking. The negative results from Rufous-and-white

422   Wrens in our study are also important, as no study had shown the absence of a pattern in any

423   species before now, which raised the question of whether this pattern was widespread or

424   phylogenetically restricted. These negative results, along with the variation between species in

425   this study (Fig 3), imply that similarity in song transitions is not ubiquitous, but instead varies

426   considerably among species.

427   The negative results from Adelaide's Warblers and Rock Wrens are more difficult to

428   interpret. In Adelaide's Warbler, some pairwise comparisons were significant, while average

429   effect sizes across birds were not significantly different from chance expectations. In Rock

430   Wrens, in contrast, no pairwise comparisons were significant, but the aggregate effect sizes were

431   slightly greater than chance, albeit with marginal significance in a one-tailed test. More research

432   would be worthwhile in these species to clarify how these results can best be interpreted.

433   Regardless, it seems clear that average effect sizes in these species are not much different from

434   chance expectations, and are significantly lower than those of Cassin's Vireo.

435   Although our results demonstrate variation across species in the similarity of song type

436   transitions, the nature of this variation remains poorly known. Is similarity in this trait between

437   neighbouring birds common, or restricted to a few species? Addressing whether the species

438   examined in this study are representative of all songbirds will require a much larger sample.

439   Descriptive studies of song are common in the literature, and often include assessments of song

440   sharing as a matter of course (Benedict, Rose, & Warning, 2013; Borror, 1987; Molles &

441   Vehrencamp, 1999; Morton, 1987; Sosa-López & Mennill, 2014). We propose that assessments

442   of similarity of song-type transitions can be included in such studies as well, which in time will

443   reveal whether the patterns identified here are common or rare.

444   Our method for comparing song-type transitions should be applicable to any sequence

445   data involving transitions between distinct behavioural states. For instance, courtship displays,

446   such as the diving displays of hummingbirds (Stiles, 1982) or the dancing displays of manakins

447   (Lukianchuk & Doucet, 2014) often involve transitions between discrete components, and the

448   composition of these sequences differs among species (Clark, Feo, & Escalante, 2011).

449   Transition matrices have also been frequently applied to the study of agonistic interactions (e.g.

450   Chen, Lee, Bowens, Huber, & Kravitz, 2002; Ismayilova et al., 2013), so our method could find

451   utility for comparing sequences of aggressive behaviours of any animal species in those contexts.

452   A further application of this method within the field of birdsong research would be to

453   compare the duetting behaviours of different pairs of birds. In some songbird species, song duets

454   are governed by stimulus-response rules called duet codes (Logue, 2006), in which the stimulus

455   is a song type from the repertoire of one member of the pair, and the appropriate response is a

456   different song type from the duetting partner's repertoire. A minor alteration to our method –

457   where transition matrices are made to represent the stimulus-response transitions recorded from a

458   pair of birds rather than the song-type transitions of a single bird – would allow an assessment of

459   whether duet codes are shared between pairs beyond the level expected by chance. In a similar

460   vein, rather than looking at differences between species, as we have done here (Fig 3), this

461   method could also be applied to investigate difference in singing behaviour between sexes of the

462   same species, a topic which has been understudied in birds (Riebel, Hall, & Langmore, 2005).

463   Other approaches have been proposed for the task of comparing sequences and transition

464   matrices (Vishwanathan, Schraudolph, Kondor, & Borgwardt, 2010), but our method has the

465   advantage of offering a straightforward statistical comparison of song transitions that is suitable

466   for a broad range of species and contexts. Ivanitskii et al. (2017) used an N-gram-based approach

467   by scanning their sequences for chunks of up to five consecutive songs that were shared between

468   individuals. Our approach can also be thought of as an N-gram-based approach, if rather than

469   mutually-preferred transitions being viewed as "transitions" that are mutually preferred, they are

470   viewed as "bigrams" that are shared among birds. Where our approach differs from that of

471   Ivanitskii et al. (2017) is by providing a significance test to estimate the number of shared

472   transitions that should be expected by chance.

473   Wu, Thompson, Bertram, & Johnson (2008) used Kullbeck-Liebler divergence between

474   transition probability distributions to examine changes in the singing behaviour of captive Zebra

475   Finches (*Taeniopygia guttata*) following surgery. Their metric of syntactic similarity was

476   intended for cases where the repertoire remains constant but transition probabilities may change,

477   as in a longitudinal study of a single individual. While their approach is useful for such contexts,

478   our method appears more generally suitable to situations where repertoires and transition

479   probabilities both differ between individuals, which is typical of many bird species.

480   Kershenbaum & Garland (2015) compared several methods for quantifying the similarity

481   of sequences of vocalizations, and advocated the use of edit distance as a suitable metric of

482   similarity. Edit distance compares two sequences against an upper bound of perfect similarity

483   (i.e. an edit distance of zero). A shortcoming of edit distance and other distance metrics, at least

484   for the goals of this paper, is that dissimilarity (i.e. non-zero edit distance) is effectively

485   unbounded and could emerge from differences in repertoire, syntax, or sequence length. With

486   three potential drivers of dissimilarity, it is not obvious what level of dissimilarity should be

487   expected by chance between two birds, since their vocal outputs would likely differ in all three

488   characteristics. Our proposed method, in contrast, controls for differences in repertoires and

489   sequence length, and compares the similarity of transition matrices against a null expectation.

490   This is not to say that our approach is superior to Kershenbaum & Garland's (2015) edit distance

491   method, but only that they are fundamentally different. One scenario where edit distance would

492   be more appropriate is for examining whether the song output of a single bird changes under

493   different social contexts, seasonally, or from one year to the next. Our proposed method is

494   specifically suited to the task of comparing the song-type transitions of two individuals. The

495   decision of which method to use should be made with a specific research question in mind.

496   ***Proximate Causes of Song Order Similarity***

497   The tendency for individual Cassin's Vireos, Marsh Wrens and some Adelaide Warblers

498 to employ similar song-type-to-song-type transitions implies that the development of these

499 transitions may be controlled by factors common to multiple individuals within a population.

500 One factor that may underlie shared behavioural patterns is a genetic underpinning to the

501 behaviour. Genes might encode, for example, a rule such as "B follows A" to underlie the

502 sequence AB. Eastern Phoebe song appears to be innately encoded in this way, as birds raised

503 without auditory feedback develop normal song sequences in this species (Kroodsma & Konishi,

504 1991). The species typically alternates its two song types (ABAB...), suggesting that this simple

505 sequencing rule, in addition to the acoustic structure of the song, is genetically determined.

506   While such a mechanism would seem reasonable for species that do not learn their songs,

507 it is less plausible for the species investigated here, which are all Oscine songbirds. Oscines are

508 notable for the tendency of many species to develop elaborate songs through the process of

509 social learning (Beecher & Brenowitz, 2005; Nottebohm, 1972). During the song learning

510 process, exposure to song types is a crucial precondition for the development of a normal and

511 high quality adult song, and is essential for the development of shared song types. It seems

512 unlikely that a sequencing rule such as "B follows A" could be genetically encoded, when the

513 acoustic structures of A and B are learned. Thus, although syntax, in the broad sense, may be

514 influenced by genes, we don't find it likely that transitions from one specific song type to

515 another are genetically encoded within our study species.

516   A second possibility is that different birds converge on similar transitions because of

517 physiological constraints prohibiting the production of certain transitions. Although the influence

518 of physiological performance constraints on syntax is worthy of further consideration, we do not

519   find it a likely explanation for our results. Demonstrated performance constraints in other species

520   occur within song types, rather than between them, and impact silent intervals that are only a

521   fraction of a second in duration (Geberzahn & Aubin, 2014; Podos, 1997; Podos et al., 2016). In

522   all species that showed significant similarity in song order in our analyses, songs are spaced out

523   by 1 s or more of silence, which is probably more than sufficient for the vocal apparatus to

524   reconfigure itself such that any song type might follow any other.

525   A final explanation for our results, and one that we find most likely, is that exposure to

526   similar song sequences during the process of song learning may lead individuals in a population

527   to deliver them in similar orders as adults. Laboratory experiments on Marsh Wrens (Kroodsma,

528   1979) and Common Nightingales (Todt & Hultsch, 1998) support this interpretation, since

529   individuals adopted the sequencing patterns presented in a tutor tape. Song learning is much

530   more challenging to document in the field, however, typically requiring inference based on

531   observational rather than experimental evidence. Our re-analysis of the available Marsh Wren

532   song sequence data from Verner (1975) confirmed a high similarity of song delivery order

533   between nearby birds in that species, suggesting that the laboratory results can generalize to field

534   conditions. It seems likely that similarity of song sequences in nearby individuals is driven by

535   song learning in that species. It is tempting to generalize this learning ability to other species of

536   wrens, given the close phylogenetic relationships, but our results suggest that Rock Wrens and

537   Rufous-and-white Wrens do not learn to share song type transitions in the same way that Marsh

538   Wrens do. The three species of wrens use distinct song ordering strategies, suggesting variability

539   in song sequence learning even within members of the same family.

540   Nothing is known about if and how tutoring shapes song development in Adelaide's

541   Warbler and Cassin's Vireo, which limits our ability to assess the role of learning in driving the

542   patterns shown in our results. One expectation of this hypothesis is that the similarity of song

543   order between tutor and tutee should be greater than between non-tutor and tutee. This should

544   give rise to pronounced declines in song order similarity as a function of geographic separation,

545   provided tutors and tutees remain in close geographic proximity. Previous studies have

546   documented this phenomenon, known as "syntactic dialects", in birds (Balaban, 1988) and

547   mammals (Kershenbaum et al., 2012). In those studies, the order of delivery of vocal elements,

548   but not necessarily the vocal elements themselves, changed with increasing geographic distance.

549   We did not find evidence of this in our dataset, where all species lacked a clear relationship

550   between our measure of song order similarity and the geographic distance separating their

551   territories. This does not, however, rule out song learning as a driver of similarity in song order,

552   since many songbirds learn songs prior to post-fledging dispersal (Hultsch & Todt, 2004). If that

553   is the case, dispersal may mask the pattern over short distances, but declines in similarity may

554   still be apparent over larger distances. Our data were too geographically restricted to examine

555   this, but an opportunity exists for future studies to examine this over a larger area or to track

556   dispersal from hatching, to shed light on the mechanisms underlying these patterns.

557   ***Potential Roles for Similarity of Song Order in Vocal Interactions***

558   The markedly different patterns in the similarity of song-type transitions between the four

559   species examined here raise the question: why do some species show similarity in song

560   transitions, while others do not? One possibility is that the ordering of songs might be important

561   during counter-singing in some species. Kroodsma (1979) showed that the song choices of two

562   captive male Marsh Wrens were influenced by one another. Both individuals were tutored on the

563   same song sequence and adopted similar song-type-to-song-type transitions as adults. During

564   vocal interactions, the socially dominant bird consistently took a leading position in delivery of

565 this shared sequence, and the subordinate bird consistently followed, engaging in a form of song

566 matching akin to what has been described in several other species (Akçay, Tom, Campbell, &

567 Beecher, 2013; Beecher, Campbell, Burt, Hill, & Nordby, 2000).

568   Cassin's Vireos showed a similar behaviour in response to playback; birds responded to

569 playback of one of the song types in their repertoire by singing the song type that normally

570 follows it in their own song sequences (Hedley et al., 2017). As with the Marsh Wrens, this

571 sometimes resulted in the responding bird taking a leading role in a song exchange, causing the

572 singer to pre-empt an upcoming playback song type. Some authors have proposed that leaders

573 and followers in vocal interactions reap asymmetrical benefits from eavesdroppers (Bartsch,

574 Wenchel, Kaiser, & Kipper, 2014). If so, the tendency to deliver songs in similar orders as other

575 birds in the population may allow a bird to take a leadership role in the delivery of a shared

576 sequence, even without any prior familiarity with the other bird's singing tendencies. Our results

577 from Cassin's Vireos in this study suggest that they could interact with any other bird in the

578 population in this way, since pairwise measures of song order similarity were high among all

579 eleven individuals included in this study. Some Adelaide's warblers may do the same, but many

580 would not, and no rock wrens or rufous-and-white-wrens would accrue this potential benefit

581 within counter-singing exchanges.

582   Another possible reason that nearby individuals might show similarity in song transitions

583 is to facilitate individual identifications or to signal group membership. Briefer et al. (2008)

584 demonstrated that Skylark songs contained shared sequences (referred to as phrases) that varied

585 from one group to the next. Playback experiments revealed that birds responded less aggressively

586 to sequences containing phrases typical of their group, regardless of the identity of the singer,

587 and more aggressively to sequences whose order had been altered (Briefer, Rybak, & Aubin,

588   2013). This implies that the order of syllables, rather than the acoustic structure of the constituent

589   vocal units, was the basis upon which discrimination occurred. Contrary to this hypothesis,

590   Cassin's Vireos did not respond differently to playback of song sequences arranged according to

591   population norms and those deviating from population norms (Hedley et al., 2017), suggesting

592   that the order of song does not convey information pertaining to group identity.

593   Alternatively, the patterns observed here might emerge as a by-product of song learning

594   without any functional consequences later on. Todt & Hultsch (1998) proposed that birds

595   memorize large repertoires by subdividing the tutor songs into chunks of several song types

596   during learning, and they showed that these chunks re-emerge in similar orders during song

597   production. Perhaps, if this is extended to the population level, it could lead to all individuals

598   transitioning between song types in similar ways, even if the order of song delivery has no

599   relevance in communication. We find this possibility unlikely, given the apparent role for similar

600   song delivery order in counter-singing interactions in Cassin's Vireos (Hedley et al., 2017) and

601   Marsh Wrens (Kroodsma, 1979; Verner, 1975). Moreover, despite possessing large repertoires of

602   over 70 song types, Rock Wrens showed little evidence of similarity in song-type transitions,

603   suggesting that at least in some species, constraints on memorizing large repertoires are not the

604   sole determinant of this pattern.

605   In conclusion, the technique we presented to quantify the similarity of song transition

606   matrices revealed marked variation among five species of songbirds. Cassin's Vireos and Marsh

607   Wrens showed clear tendencies to transition between shared song types in similar ways, as did a

608   few dyads of Adelaide's Warblers. Dyads of Rock Wrens and Rufous-and-White Wrens showed

609   no such tendency. These results highlight an under-explored axis of behavioural variation among

610   songbird species. Although we have proposed various hypotheses regarding the proximate and

611 ultimate causes of this variation, few conclusions can be firmly drawn without further study. The

612 method we have presented can be applied to a broad array of behavioural sequence data, to

613 illuminate the consequences of similarity in song-type transitions in animal communication.

614

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