

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

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15

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 (17.98° N, 67.17° 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 - 40.96° N, 105.15
150 - 105.36° 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 (10.85° N, 85.6° 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 (38.49° N, 120.63 ° 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***

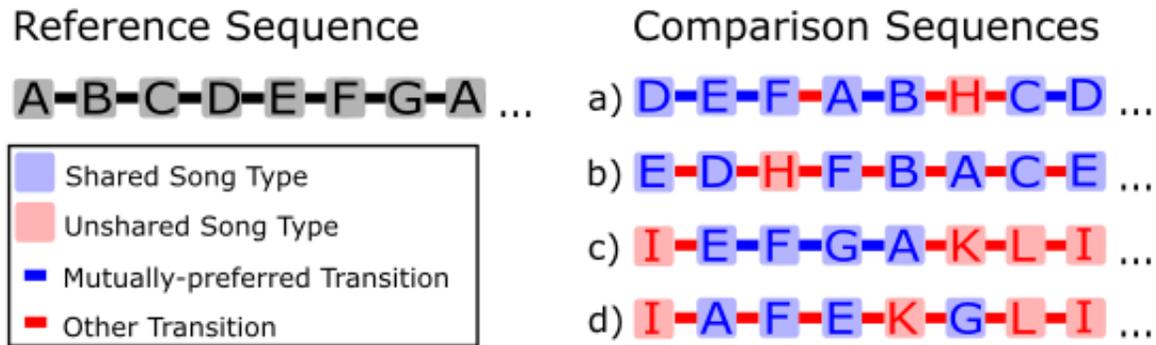
191 We define the term *preferred transition*, as a transition from one song type to another that
192 occurs at statistically inflated rates relative to the overall rate of occurrence of the two
193 constituent song types. Apart from preferred transitions, a dataset from a bird will typically
194 include 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



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

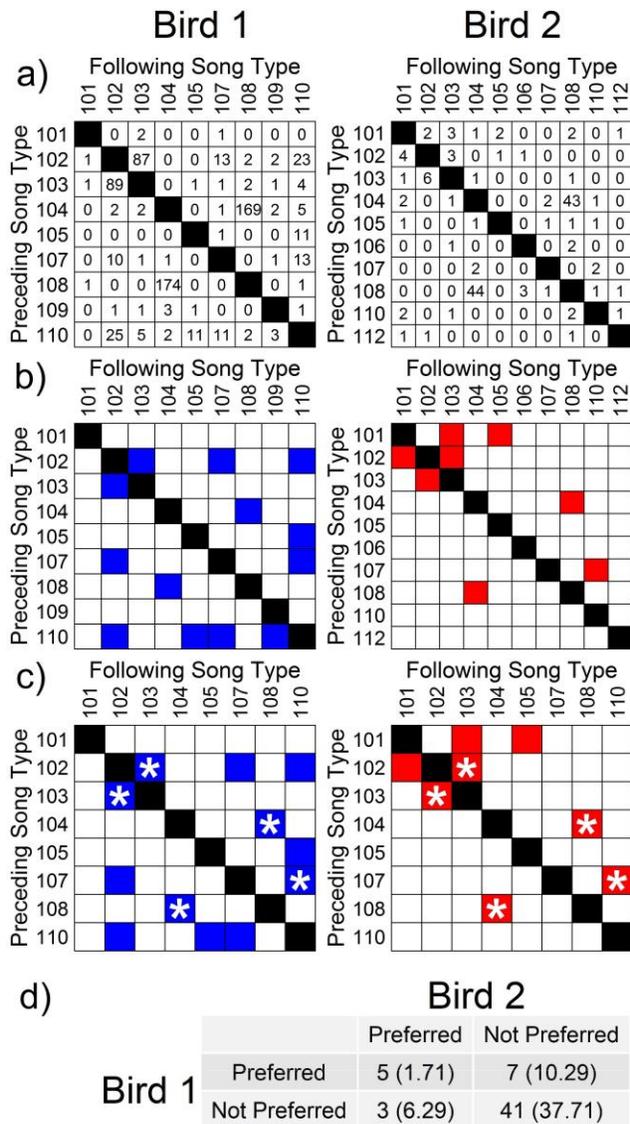
225

226 ***Statistical Methods***

227 Our method has four steps: 1) construction of transition matrices from the song sequences
 228 of the two focal birds and removal of song-type repetitions along the diagonal of the matrix; 2)
 229 analysis of each transition matrix to identify preferred transitions; 3) identification of shared
 230 song types and filtering of transition matrices to include only transitions between shared song
 231 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 $C \times C$ transition matrix to a 2×2 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 $M \times M$ 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 $E[i, j] = \frac{(\text{Row } i \text{ total}) * (\text{Column } j \text{ total})}{\text{Grand total}}$ (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	Repertoire Size	No. Shared Song
		Individual (mean \pm SD)	(mean \pm SD)	Types (mean \pm SD)*
Adelaide's Warbler	9	1035 \pm 201	29 \pm 4	14.6 \pm 6.1
Cassin's Vireo	11	3461 \pm 2018	51.4 \pm 4.4	25.6 \pm 4.4
Rock Wren	12	1535 \pm 403	76.6 \pm 17.6	31.8 \pm 8.1
Rufous-and-white Wren	41	3651 \pm 2447	8.1 \pm 1.2	6.7 \pm 1.2
Marsh Wren	2	450 \pm 13	110 \pm 0	100

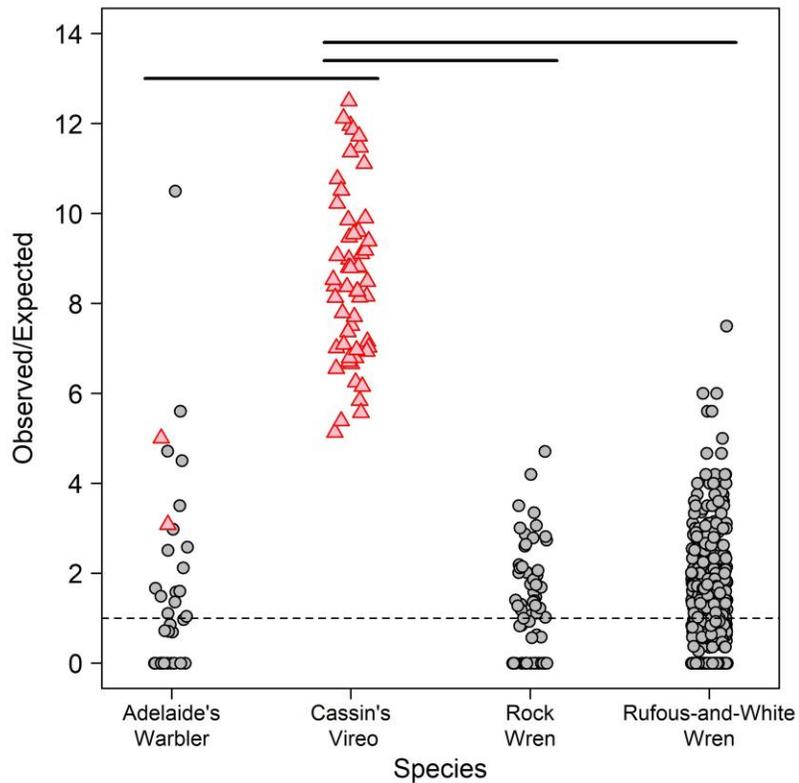
363 * Calculated for all pairwise comparisons among individuals within a species.

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



384 **Figure 3:** Summary of pairwise comparisons of song-type transitions among four species.

385 Pairwise comparisons that were deemed significant with the Benjamini-Hochberg procedure are
 386 displayed as red triangles, while non-significant comparisons are shown with grey circles.

387 Significant differences between species, as determined by post-hoc Mann-Whitney U tests, are
 388 indicated with black bars above the points. The horizontal dotted line indicates an

389 observed/expected value of one, the expected similarity if the song transitions of two birds were
 390 independently arranged. Higher observed/expected values indicate higher levels of similarity.

391 The single comparison between the two Marsh Wren individuals is not shown, but had an
 392 observed/expected value of 34.6.

393

394 **Table 2:** Summary of pairwise comparisons of song transitions among individuals within

395 each of the five species examined here.

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