

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***

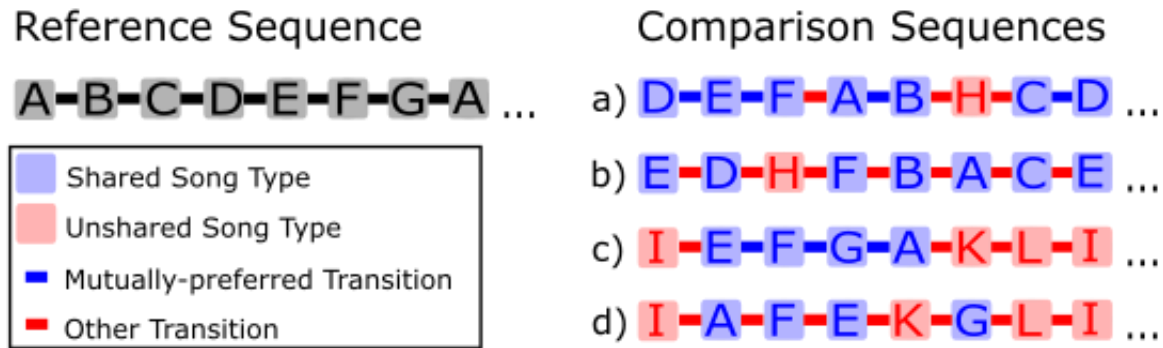
191 We define the term *preferred transition*, as a transition from one song type to another that  
192 occurs at statistically inflated rates relative to the overall rate of occurrence of the two  
193 constituent song types. Apart from preferred transitions, a dataset from a bird will typically  
194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

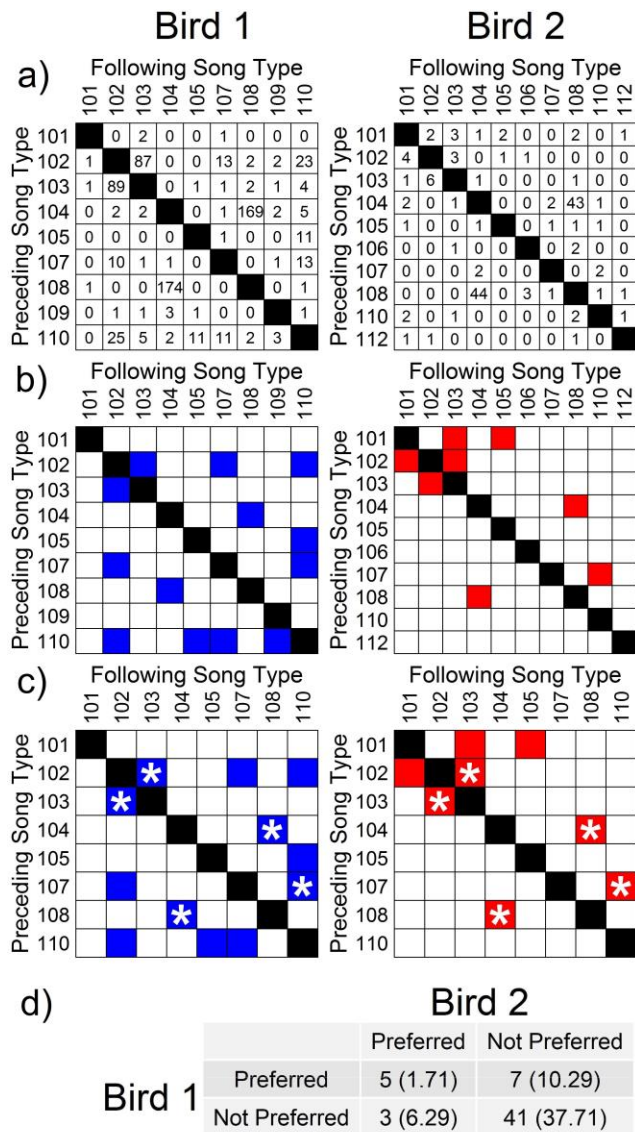
225

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  $2 \times 2$  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)*
<b>Adelaide's Warbler</b>	9	1035 $\pm$ 201	29 $\pm$ 4	14.6 $\pm$ 6.1
<b>Cassin's Vireo</b>	11	3461 $\pm$ 2018	51.4 $\pm$ 4.4	25.6 $\pm$ 4.4
<b>Rock Wren</b>	12	1535 $\pm$ 403	76.6 $\pm$ 17.6	31.8 $\pm$ 8.1
<b>Rufous-and-white Wren</b>	41	3651 $\pm$ 2447	8.1 $\pm$ 1.2	6.7 $\pm$ 1.2
<b>Marsh Wren</b>	2	450 $\pm$ 13	110 $\pm$ 0	100

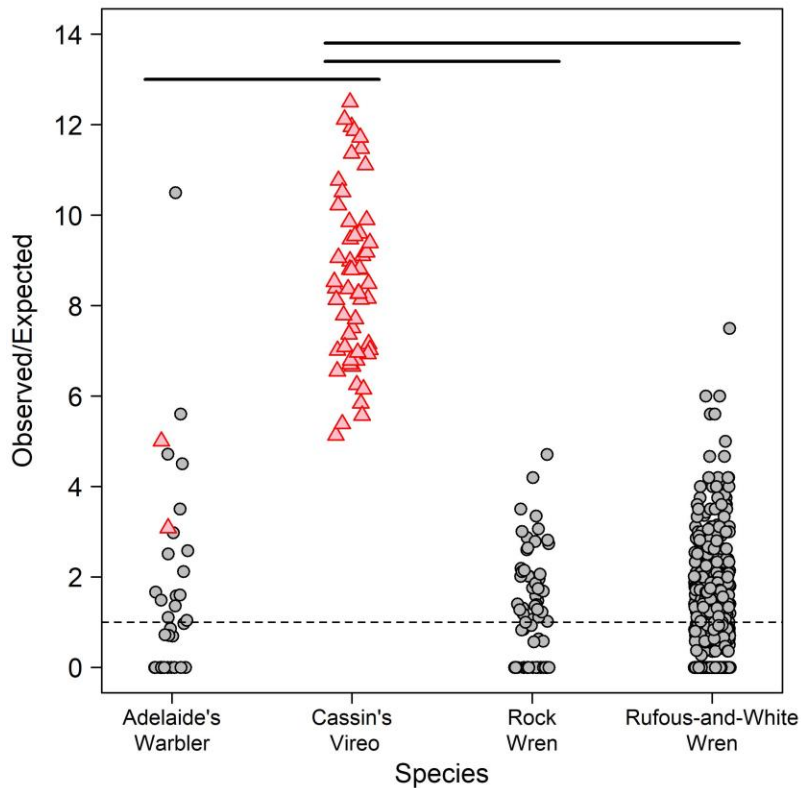
363 \* Calculated for all pairwise comparisons among individuals within a species.

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.

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