



Assessing the similarity of song-type transitions among birds: evidence for interspecies variation

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In many species of songbird, individuals sing multiple song types, some of which are shared with their neighbours. Individuals may also share syntactical rules that govern the transitions between different song types, but few studies have attempted to study this kind of sharing. Progress has been inhibited by a lack of statistical tools to compare song-type transitions among individuals. We present a straightforward method for comparing song transitions based on Markov transition matrices. The method calculates the number of mutually preferred song-type-to-different-song-type transitions found in the song sequences of two birds, then assesses whether that number is significantly greater than would be expected if the two birds ordered their songs independently of one another. We applied this method to song sequences from five songbird species. All pairwise comparisons among male Cassin's vireos, *Vireo cassinii*, showed significant similarity in song transitions, as did a minority of comparisons among Adelaide's warblers, *Setophaga adelaidae*, and one pair of marsh wrens, *Cistothorus palustris*. In contrast, dyads of rock wrens, *Salpinctes obsoletus*, and rufous-and-white wrens, *Thryophilus rufalbus*, did not share song-type transitions at levels exceeding chance. Interterritory distance was not significantly related to our measure of song transition similarity in any of our study species. These results provide evidence that interindividual similarity in song-type transitions is a trait that varies considerably among species. We discuss the potential drivers of similarity in song transitions, but note that assessing its evolutionary breadth will require a larger sample of species. The application of our method to additional species will provide a more comprehensive understanding of signal use and vocal interaction in songbirds.

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Quantitative comparison of signal repertoires can advance research in animal communication (Kershenbaum et al., 2016). For example, conspecific animals living in close proximity often 'share' some or all of their vocal repertoires (Henry, Barbu, Lemasson, & Hausberger, 2015). Research into the function of shared vocal elements has demonstrated that conspecifics often deliver them preferentially during agonistic interactions (Krebs, Ashcroft, & Orsdol, 1981; Todt & Naguib, 2000; Vehrencamp, 2001), that they are likely to play a role in social bond formation and maintenance (Janik, 2000; Schulz, Whitehead, Gero, & Rendell, 2008) and that females can use them to evaluate male vocal performance (Ballentine, Hyman, & Nowicki, 2004). In songbirds, vocal

repertoire comparisons often begin and end at the level of the song type, but similarity may extend to other dimensions of singing behaviour. Below the level of the song type, birds may share parts of a song without sharing the entire song type (Anderson, Searcy, & Nowicki, 2008; Burt & Beecher, 2008). Above the level of the song type, transitions between song types may be similar, in which case similarity can be considered to occur at the level of the syntax governing each bird's transitions from one song type to another (Ivanitskii, Marova, & Antipov, 2017).

Reports of similarity in song transitions date back to a study of marsh wrens, *Cistothorus palustris*, in the state of Washington, U.S.A. (Verner, 1975). In western populations of this species, males sing repertoires of over 100 song types, most of which are shared between neighbours. Verner (1975) made three observations about the sequential ordering of songs: first, repetitions of the same song type in succession were rare; second, certain transitions from one song type to another were much more common (and others much

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less common) than expected by chance; and third, the order of song types was similar among males within the population (Verner, 1975). If one individual tended to transition from song type A to song type B, it was often the case that other nearby males tended to do the same. A subsequent laboratory study linked this similarity in song-type transitions to the learning process. By tutoring two male marsh wrens on the same song sequence, Kroodsmma (1979) found that the birds learned both the acoustic structure of the song types on the tape and their order of presentation. These results suggest that the patterns described by Verner (1975) in the field either resulted from one bird learning the songs and transitions from his neighbour early in life, or from both neighbours learning songs and transitions from a third party.

At least three other bird species have shown patterns similar to those Verner (1975) observed among marsh wrens. (1) Under laboratory conditions, the song sequences produced by common nightingales, *Luscinia megarhynchos*, were strongly influenced by the song order on their tutor tapes (Todt & Hultsch, 1998). When presented with linear sequences of song, the tutees appeared to divide the sequence into shorter chunks of several song types that were subsequently produced together. Since these chunks were often recombined in different ways during song production, the song sequences produced by the tutees were very similar, but not identical, to the sequences on the tutor tapes. (2) In congeneric thrush nightingales, *Luscinia luscinia*, individuals within a population delivered shared song types in similar orders (Ivanitskii et al., 2017). A sequence of five song types was identified in the song sequences of all 29 males whose repertoire included the five constituent song types. Shorter sequences of up to four song types were also widely shared. (3) Similarly, in a population of village indigobirds, *Vidua chalybeate*, transitions between song types showed little variation among individuals (Payne, 1979).

The similarity of song order was not analysed statistically in any of the aforementioned studies. Statistical comparisons would be valuable because some degree of similarity in transitions is to be expected by chance among birds that share song types. For example, the observation that two birds transition from song type A to B may simply reflect the finite repertoires from which the birds can select a successor to song type A. Moreover, the stochastic nature of transitions within birdsong sequences (Jin, 2013) may lead to occasional observations of transitions that are peripheral to the preferred syntax of a bird. The critical consideration, therefore, is not whether a particular transition occurs in the song sequences of both birds, but whether a transition is preferred by both birds, and whether the set of transitions that are preferred by both birds is larger than should be expected by chance given the repertoires of the two birds.

Without an objective statistical test to formalize comparisons of song ordering among birds, patterns of similarity remain anecdotal. This is not particularly troublesome in the above examples, since the patterns described are sufficiently striking that there is no reason to suspect they are spurious. Some species, however, might show subtler, yet still significant, levels of similarity, such that patterns are difficult to detect. If so, reports of similarity of song transitions in the literature may be biased towards the most extreme cases.

In this study, we examined interindividual similarity in song-type-to-song-type transitions. We present a statistical methodology for assessing whether two individuals show a significant tendency to transition between song types in similar ways. The method quantifies mutual preferences for certain song-type-to-song-type transitions, independent of rates of song sharing. It can be applied to species with stochastic or deterministic transitions. Although we focus on transitions between song types, our method could also be applied to assess similarity in transitions at other

levels of the hierarchy of song organization; for example, this method could be used to examine shared transitions between syllables within a song (Briefer, Aubin, Lehongre, & Rybak, 2008). The method could also be used to examine signal-type transitions in animals other than birds that possess signal repertoires. Here we apply this method to song sequences of five songbird species (Cassin's vireo, *Vireo cassinii*; Adelaide's warbler, *Setophaga adelaidae*; rock wren, *Salpinctes obsoletus*; rufous-and-white wren, *Thryophilus rufalbus*; marsh wren) to examine interspecific variation in song-type transition patterns. We also investigate whether interterritory distance explains variation in this metric.

METHODS

Song Sequence Data Sets

We used song recording data sets from four species: Adelaide's warbler, rock wren, rufous-and-white wren and Cassin's vireo. For each of these species, the song sequences were annotated according to a population-level song-type classification key (a separate key for each species) so that individual repertoires could be enumerated and rates of song sharing could be assessed. Spectrogram images are provided in [Supplementary Figs. S1–S4](#) to clarify what is meant by shared and unshared song types in each species. We calculated several summary statistics for each species, including the average number of songs recorded from each individual of each species, the song repertoire size of each bird and the average number of shared songs between males in each population. In addition to these four data sets, we analysed published transition networks for two marsh wrens that appear as Figures 11 and 12 in Verner (1975). Although the availability of only two individuals precludes broader conclusions about this species, marsh wrens were included as a means of comparing our quantitative approach with a historical, qualitative description of two birds with highly similar song-type transitions.

Adelaide's Warbler

We recorded nine colour-banded male Adelaide's warblers at the Cabo Rojo National Wildlife Refuge, Puerto Rico (17°58'48"N, 67°10'12"W) between March and June 2012. Males were recorded for 4 days each. Observations began 30 min before sunrise and continued until 3 h after sunrise. Recordings were collected with a portable solid-state recorder (Marantz PMD661) and a directional microphone (Sennheiser ME67). Songs were classified to song type according to their appearance on sound spectrograms in Syrinx PC v2.6f Sound Analysis Software (Fig. S1; J. Burt, Seattle, WA, U.S.A.). Trained observers labelled song types separately for each male. Later, two people independently chose 'holotypes' to define a population-level classification key, and classified song types across individuals. They did this separately at first, then discussed disagreements to come to a final decision. Finally, one person (D.M.L.) compared every song recording to the holotypes, corrected scoring errors, and reclassified (lumped) similar types, resulting in an annotated data set of 9499 songs. To estimate the repeatability of this final step, a second observer independently classified 22–23 randomly selected songs from each of nine males (total = 200 songs) using the population-level classification key. In total, 174 of 200 (87%) scores matched. For further details on this data set, see [Schraft, Medina, McClure, Pereira, and Logue \(2017\)](#).

Rock Wren

We recorded 12 male rock wrens in Larimer County, Colorado (40°28'12"–40°57'36"N, 105°9'–105°21'36"W) during May, June

and July 2012 and 2013. Most study subjects were not banded, but could be easily relocated because members of this species show strong territory fidelity (Warning & Benedict, 2015) and individual song patterning. At least 900 songs per individual were recorded over the course of one to three recording sessions on different days. All recordings were of unprovoked, natural broadcast singing of territorial males. Recordings were collected with a portable solid-state recorder (Marantz PMD 671) and a directional microphone (Sennheiser MKH-60). Songs for all individuals were classified to song type by one observer (L.B.) after visualizing recordings in Raven Pro Sound Analysis Software (Fig. S2; Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). To assess the repeatability of the classification of songs to song type, a second observer classified a subset of 10 songs from each of 10 individuals using a population-level classification key. The two observers agreed on the classification of 88 out of 100 songs (88%). For more information about this data set, see Benedict and Warning (2017).

Rufous-and-white Wren

We recorded 41 colour-banded male rufous-and-white wrens in Sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica (10°51'N, 85°36'W) between April and July 2003–2014. Songs were recorded from spontaneously singing birds using a portable solid-state recorder (Marantz PMD660 or PMD670) and a directional microphone (Sennheiser MKH70 or ME67). Songs were visualized and classified to song type based on their spectrotemporal properties according to a population-level classification key using Syrinx PC Sound Analysis Software. To assess the reliability of classification of songs to song types, two observers independently classified a sample of 200 songs (20 songs from each of 10 different males, selected randomly) using the population-level classification key. The two observers agreed on the classification of 193 out of 200 songs (96.5%). Additional details about this data set are provided in Harris, Wilson, Graham, and Mennill (2016).

Cassin's Vireo

We recorded 11 colour-banded Cassin's vireos in May and June 2014 at a site on private land in Amador County, California, U.S.A. (38°29'24"N, 120°37'48"W). Recordings were made opportunistically by one observer, by approaching the known territory of a male and recording song output until the bird moved out of the range of the microphone, stopped singing for a long period of time, or engaged in a close boundary dispute that made recording difficult. Songs were recorded using a portable solid-state recorder (Marantz PMD-661) and a directional microphone (Sennheiser MKH20-P48) with a Telinga parabolic reflector. Prior work on this species has referred to songs and song types as phrases and phrase types, respectively (Hedley, 2016b), but we use the former terms in this paper for consistency with the other species. Songs were annotated to song type by one observer (R.H.) by visually inspecting a spectrogram (Fig. S4) in the linguistics software Praat (Boersma & Weenink, 2014). Spectrogram inspection has been shown to give nearly identical results to automated methods of song-type classification in this species (Hedley, 2016b), and also shows over 99% repeatability from one human observer to the next (Hedley, Denton, & Weiss, 2017).

Terminology and Motivation for Statistical Approach

We define the term 'preferred transition' as a transition from one song type to another that occurs at statistically inflated rates relative to the overall rate of occurrence of the two constituent song

types. Apart from preferred transitions, a data set from a bird will typically include some transitions that are observed rarely and others that are not observed at all but which are possible given the bird's repertoire of song types. We combined rare and unobserved transitions under the category of 'nonpreferred transition', justified by the fact that rare transitions could result when a bird is interrupted, commits an error while producing a preferred transition or alters its song in response to external conditions. In other words, while preferred transitions show evidence of being intentionally delivered, rare transitions may result from mistakes that are likely to accumulate as recording proceeds. The binary classification of transitions as preferred or nonpreferred is sure to obfuscate some of the variation within each of these categories but has the benefit of simplifying subsequent analyses.

We define 'mutually preferred transition' as a transition that is preferred by two or more birds. Our analysis assesses whether the number of mutually preferred transitions in the song sequences of two birds is higher than expected, given the rate of song sharing and number of preferred transitions of the two birds. Pairs of birds whose mutually preferred transitions significantly exceed chance levels are considered to have similar song transitions.

Two birds who exhibit many shared song types may have many mutually preferred transitions (Fig. 1a) or few mutually preferred transitions (Fig. 1b). The null expectation is a low number of mutually preferred transitions if the sequencing tendencies of the two birds were developed independently of one another. Birds sharing few song types can still show evidence of higher-than-expected mutually preferred transitions (Fig. 1c), but individuals that do not share any song types cannot exhibit mutually preferred transitions.

Animal Welfare Note

Research on Adelaide's warblers was approved by the Institutional Animal Care and Use Committee at the University of Puerto Rico, Mayagüez (17 September 2010). Birds were captured under D.M.L.'s federal bird banding permit (no. 23696). The U.S. Fish and Wildlife Service granted permission to work at the Cabo Rojo Wildlife Refuge (permit 2012-01). Research on Cassin's vireos was approved by the Institutional Animal Care and Use Committee at the University of California, Los Angeles (ARC no. 2013-041-03A). Birds were captured under R.W.H.'s federal bird banding subpermit (no. 23809). Research on rock wrens was conducted under the University of Northern Colorado's Institutional Animal Care and Use permit no. 1506C, State of Colorado collecting permit no. TRb2041, and the United States Geological Survey's Bird Banding Laboratory permit no. 23741. Research on rufous-and-white wrens was approved by the University of Windsor Animal Care Committee (AUPP 09-06 and 13-15). Birds were captured under D.J.M.'s research permit from the government of Costa Rica (MINAE). As necessary, we obtained research permissions from local land management agencies. All research activities followed guidelines set forth by the ASAB/ABS and the Ornithological Council.

Statistical Methods

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

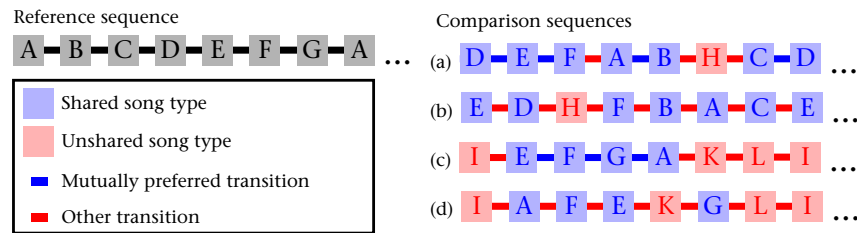


Figure 1. Simplified examples of four birds (a–d) that vary in the number of song types and mutually preferred transitions in common with a reference sequence (grey boxes). For simplicity, these hypothetical birds sing with a completely deterministic syntax, cycling linearly through their repertoire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

for a significant association between the transition matrices. These steps are explained in more detail below and are illustrated in Fig. 2.

The details of constructing a transition (or Markov) matrix, as required for step 1, have been described by Chatfield and Lemon (1970). Briefly, for a bird with repertoire size C , the transition matrix contains C rows and C columns corresponding to each of the song types in the bird’s repertoire. A cell in row i and column j is filled with a count of the number of times the bird transitioned from song type i to song type j in the recording sample (Fig. 2a). Diagonals in the matrix represent self-transitions, where a bird repeated the same song type consecutively, but it is often desirable to investigate transitions between types independent of repetitions (Hailman, Ficken, & Ficken, 1985). We opted to exclude entries along the diagonal because the tendency to repeat song types appears primarily to be a species-level trait with less variation among individuals of a species than between species. This has led to the common designation of species as singing with either eventual variety or immediate variety based on the frequency of repetitions in their song sequences (Kroodsmá & Verner, 1978). Moreover, a syntactic ‘rule’ designating a repetition is qualitatively different from one designating a transition between two song types. Repetitions could be underpinned by a rule like repeat(x), regardless of what x is. Transitions, in contrast, require association of different song types (e.g. transition from x to y). Efforts to model birdsong syntax have frequently shown that repetitions are not well described by the same processes that govern between-type transitions (Hedley, 2016a; Jin & Kozhevnikov, 2011; Kershenbaum, Bowles, Freeberg, Jin, & Lameira, 2014), suggesting that these two types of rules may be encoded differently within the avian brain. Therefore, we excluded repetitions in our primary analyses, but note that only slight modifications to our method are needed to include repetitions. Analyses with repetitions included are presented in Supplementary material 2.

In step 2, we examined each cell in the transition matrix to assess whether the transition occurred at statistically inflated rates given the number of occurrences of the two constituent song types. To do this, we used a cell-by-cell Fisher’s exact test. This test collapses the $C \times C$ transition matrix to a 2×2 contingency table for each cell $[i, j]$ where the margins represent the count in row i and not in row i on one margin, and the count in column j and not in column j on the other. A one-tailed Fisher’s exact test then tests whether the count in the cell $[i, j]$ exceeds that expected given the overall rate of occurrence of the constituent song types i and j . Cells with significantly inflated counts at a significance level of $P < 0.05$ were subsequently assigned a value of 1, and cells with counts that were not significantly inflated were assigned a value of 0 (Fig. 2b). This can be thought of as a thresholding step to eliminate rare transitions, where the threshold tends to be lower for transitions between rare song types than for transitions between common

song types. This differs from thresholding based on transition probabilities, because transition probabilities consider the overall rate of occurrence of the preceding song type alone, while our approach considers the rates of occurrence of both the preceding and following song types.

In step 3, we identified song types shared between the two birds. Rows and columns associated with shared song types were isolated from the matrix and arranged in an identical order in the matrices of the two birds. If the number of shared song types was M , this step resulted in two $M \times M$ transition matrices with the same column names and row names but which differed in terms of which cells contained ones and zeros (Fig. 2c). Each cell in these matrices can be thought of as a potential mutually preferred transition, given the repertoire of the two birds.

In step 4, we assessed whether the distributions of the preferred transitions of each bird were independent of one another. To do this, a 2×2 contingency table was produced, where the margins represented the transitions preferred and not preferred by bird 1, and those preferred and not preferred by bird 2 (Fig. 2d). Another one-tailed Fisher’s exact test conducted on this table assessed whether the number of mutually preferred transitions exceeded the expected number. To measure the magnitude of this association, we also divided the observed number of mutually preferred transitions by the expected number, where the expected number was calculated using the formula $E[i, j] = \frac{(\text{Row } i \text{ total}) \times (\text{Column } j \text{ total})}{\text{Grand total}}$ (Whitlock & Schluter, 2015). The rationale for this step is that, given the known repertoires of each bird and their number of shared song types M , there are $M(M - 1)$ possible transitions between shared song types (i.e. $M(M - 1)$ is the grand total). If both birds select their preferred transitions independently from this set of possibilities, the number of mutually preferred transitions is expected to be the product of the proportion of possible transitions that are preferred for each bird, multiplied by the grand total of possible transitions. Significant deviations from this expected value imply a lack of independence in the selection of preferred transitions of the two birds.

Data Analysis

We tested for significance at three levels: between dyads, at the species level and between species. At the dyad level, we calculated the number of mutually preferred transitions between each possible dyad in the population, as well as the effect size (observed number of mutually preferred transitions divided by expected, as above) and the P value comparing the number of mutually preferred transitions to the expected value for those two birds. To account for the large number of comparisons made within each species, we controlled the false discovery rate using the Benjamini–Hochberg procedure (Benjamini & Hochberg, 1995). In

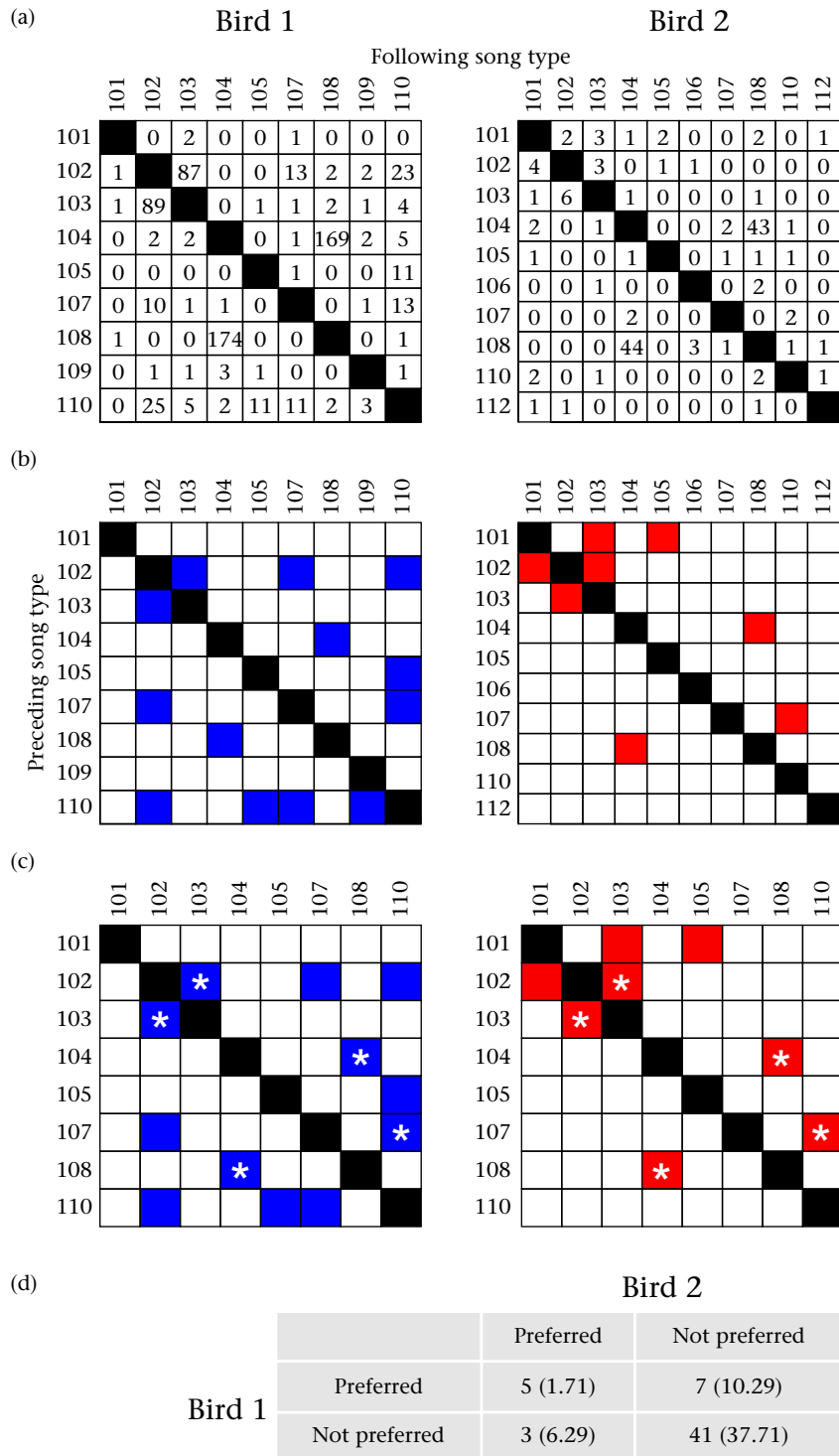


Figure 2. An illustration of our method for comparing song transitions, using two rufous-and-white wrens as an example. (a) First, a transition matrix is constructed from each bird's song sequences (left and right matrices). Cells contain the number of transitions from the preceding song type to the following song type. Self-transitions along the diagonal are ignored. (b) Each transition is determined to be preferred or not. It is not the absolute number of times that a transition is observed that determines whether or not it is preferred, but rather the number of times that a transition is observed relative to the number of times each of the two song types in the transition was sung within the data set as a whole. Blue and red cells show the preferred transitions for the two birds, and white cells show nonpreferred transitions. (c) Matrices are filtered to include only transitions between shared song types, such that the resulting matrices are the same size and have the same row and column song types (in this case the unshared song types 109 and 112 are removed). Mutually preferred transitions can then be identified (white stars) as transitions that are preferred by both birds, and this value can be compared against a null expectation. In this example, the two birds had five mutually preferred transitions in common: 102-to-103, 103-to-102, 104-to-108, 108-to-104 and 107-to-110. (d) A contingency table is produced summarizing the preferred and nonpreferred transitions of each bird. Observed values are given with expected values in parentheses. The five mutually preferred transitions among these two birds are more than the 1.71 that were expected by chance. A one-tailed Fisher's exact test showed a *P* value of 0.008 for this comparison. This *P* value, however, did not meet the threshold for significance once multiple comparisons among all rufous-and-white wrens included in the study were accounted for.

this method, P values are sorted from smallest to largest and assigned an index k from 1 to m , where m is the number of hypotheses tested. All null hypotheses with P values less than or equal to the largest k that satisfies $p_k \leq \frac{k}{m} \alpha$ are rejected. We used $\alpha = 0.05$. To compare whether the species as a whole showed a significant effect, we compared the effect sizes of all dyads for each species against a null expected value of 1 using a one-tailed Wilcoxon signed-ranks test. To make comparisons among species, we compared the effect size values among the five species using a Mann–Whitney U test.

We used GPS points from the birds' breeding territories to assess whether effect size was explained by the distance between the territories of two birds. To do this, we constructed two matrices for each species with rows and columns corresponding to the individuals of that species. The entry in cell $[i, j]$ of one matrix contained the effect sizes (observed/expected) for the comparison between bird i and bird j . Cell $[i, j]$ in the other matrix contained the distance between the territories of the two birds, in metres. We compared these two matrices using a Mantel test. The Mantel test randomly permuted the rows and columns of one matrix 10 000 times to assess whether the relationship between interterritory distance and effect size was significantly greater than expected by chance. All analyses were conducted in R version 3.3.1 (R Core Team, 2016). Data and code are available on Figshare (10.6084/m9.figshare.5379811). The R code reads in a set of transition matrices for a species and conducts comparisons at the dyad level, calculating the effect sizes and P values for all possible dyadic comparisons.

RESULTS

All five species exhibited large repertoires and high rates of song sharing (Table 1), allowing us to proceed with our comparisons of song-type transitions in the five species. At the dyad level, some species showed significant similarity in transitions but others did not. The results are summarized in Table 2 and visualized in Fig. 3. No comparisons were significant in rufous-and-white wrens or rock wrens when the Benjamini–Hochberg procedure was used to account for multiple comparisons. In Adelaide's warblers, an intermediate pattern was apparent, where 6% (2/36) of comparisons were significant. Cassin's vireos showed strong evidence of

Table 1
Summary characteristics of the songs of the five species analysed

| Species | Individuals (N) | Songs per individual (mean±SD) | Repertoire size (mean±SD) | No. shared song types (mean±SD) ^a |
|-----------------------|-----------------|--------------------------------|---------------------------|--|
| Adelaide's warbler | 9 | 1035±201 | 29±4 | 14.6±6.1 |
| Cassin's vireo | 11 | 3461±2018 | 51.4±4.4 | 25.6±4.4 |
| Rock wren | 12 | 1535±403 | 76.6±17.6 | 31.8±8.1 |
| Rufous-and-white wren | 41 | 3651±2447 | 8.1±1.2 | 6.7±1.2 |
| Marsh wren | 2 | 450±13 | 110±0 | 100 |

^a Calculated for all pairwise comparisons among individuals within a species.

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

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

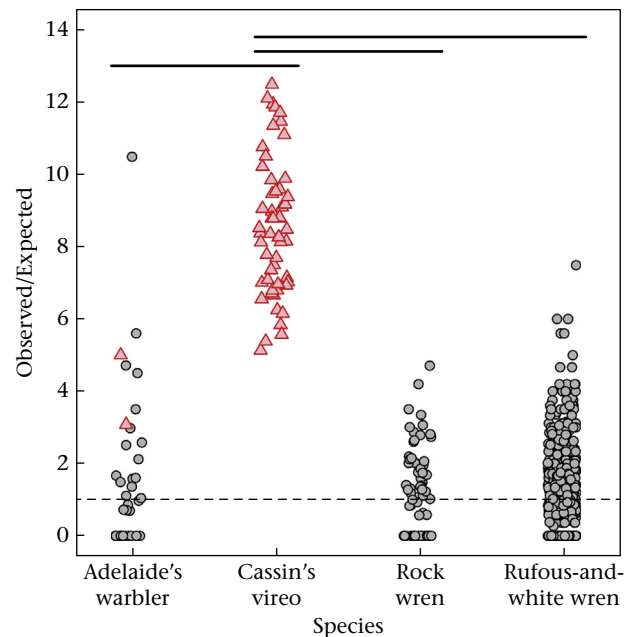


Figure 3. Summary of pairwise comparisons of song-type transitions among four species. Pairwise comparisons that were deemed significant with the Benjamini–Hochberg procedure are displayed as triangles, while nonsignificant comparisons are shown with circles. Significant differences between species, as determined by post hoc Mann–Whitney U tests, are indicated with black bars above the points. The horizontal dotted line indicates an observed/expected value of 1, the expected similarity if the song transitions of two birds were independently arranged. Higher observed/expected values indicate higher levels of similarity. The single comparison between the two marsh wren individuals is not shown, but had an observed/expected value of 34.6.

mutually preferred transitions in each of 55 pairwise comparisons. Effect sizes in this species ranged from 5.1 to 12.5, indicating that individuals shared mutually preferred transitions at several times the level expected by chance. The two marsh wren individuals showed the highest similarity of all, with an effect size 34.6 times the level expected by chance ($P < 0.0001$).

Inspection of Fig. 3 shows that some comparisons had high effect sizes but nonsignificant P values. This can be attributed to comparisons that had very low expected numbers of mutually preferred transitions. For instance, a comparison with an expected value of 0.1 and an observed value of 1 would not reach statistical significance, while one with an expected value of 1 and an observed value of 10 would, even though the effect size in both cases is 10. Accordingly, both the P values and effect sizes are important for proper interpretation of any dyadic comparisons.

At the species level, Cassin's vireos showed systematically greater-than-expected numbers of mutually preferred transitions ($W = 1540$, $P < 0.001$). Rock wrens showed significantly greater-than-expected numbers of mutually preferred transitions as well at the species level ($W = 1367$, $P = 0.047$). However, the effect was

slight (median effect size in rock wren was 1.25 times chance levels, compared to 8.38 times chance levels in Cassin's vireos), and not reinforced by statistical significance in any of the pairwise comparisons. Adelaide's warblers and rufous-and-white wrens showed no such effect at the species level (Adelaide's warbler: median: 1.04 times chance levels, $W = 385$, $P = 0.25$; rufous-and-white wren: median: 1.00 times chance levels, $W = 153\,610$, $P = 0.97$). Small sample sizes precluded species-level analysis of marsh wren data.

Effect sizes differed significantly between the five species tested (Kruskal–Wallis test: $\chi^2_4 = 164$, $P < 0.001$). Post hoc Mann–Whitney U tests with a Bonferroni adjustment showed that Cassin's vireos differed significantly from Adelaide's warbler ($U = 48$, $P < 0.001$), rock wren ($U = 3630$, $P < 0.001$) and rufous-and-white wren ($U = 44\,463$, $P < 0.001$). The latter three species did not differ from one another (Adelaide's warbler versus rock wren: $U = 1182$, $P = 1$; Adelaide's warbler versus rufous-and-white wren: $U = 15\,482$, $P = 1$; rock wren versus rufous-and-white wren: $U = 24\,054$, $P = 1$). Post hoc analyses of marsh wren observations were not conducted, since only one data point was available for that species.

Mantel tests revealed no significant relationship between interterritory distance and effect size within any of the species (Adelaide's warbler: $P = 0.46$; rock wren: $P = 0.50$; rufous-and-white wren: $P = 0.09$; Cassin's vireo: $P = 0.40$). A Mantel test could not be conducted for marsh wrens since this species was represented by just two birds.

DISCUSSION

Comparisons of Similarity of Song Order

We developed a method for comparing the similarity of transitions between shared song types of two birds. The method assesses the number of mutually preferred transitions in sequences of song from two individuals and compares this number to an expected value. We used this technique to show higher-than-expected numbers of mutually preferred transitions for all pairwise comparisons in a population of Cassin's vireo and for a small minority of pairwise comparisons in a population of Adelaide's warblers. In addition, we confirmed the high levels of similarity in the order of song delivery among marsh wrens that were described, but not statistically analysed, by Verner (1975). We did not find higher-than-expected numbers of mutually preferred transitions in the songs of rufous-and-white wrens or most Adelaide's warblers. Rock wrens showed slightly inflated levels of mutually preferred transitions overall, but no pairwise comparisons reached the threshold of significance.

One implication of these results is that interspecific variation in the similarity of song-type transitions can begin to be evaluated on a larger scale with the method presented here. Evidence of similarity in the delivery order of vocalizations has been described previously in a few species of birds and mammals (Ivanitskii et al., 2017; Kerstenbaum, Ilany, Blaustein, & Geffen, 2012; Payne, 1979; Verner, 1975). Cassin's vireo is one such species, where similarity in song order had been described but not analysed in depth (Hedley et al., 2017). The results of this study are therefore in line with previous descriptions for that species but provide a level of quantification that has been previously lacking. The negative results from rufous-and-white wrens in our study are also important, as no study had shown the absence of a pattern in any species before now, which raised the question of whether this pattern was widespread or phylogenetically restricted. These negative results, along with the variation between species in this study (Fig. 3), imply that similarity in song transitions is not ubiquitous, but instead varies considerably among species.

The negative results from Adelaide's warblers and rock wrens are more difficult to interpret. In Adelaide's warbler, some pairwise comparisons were significant, while average effect sizes across birds were not significantly different from chance expectations. In rock wrens, in contrast, no pairwise comparisons were significant, but the aggregate effect sizes were slightly greater than chance, albeit with marginal significance in a one-tailed test. More research would be worthwhile in these species to clarify how these results can best be interpreted. Regardless, it seems clear that average effect sizes in these species are not much different from chance expectations and are significantly lower than those of Cassin's vireo.

Although our results demonstrate variation across species in the similarity of song-type transitions, the nature of this variation remains poorly known. Is similarity in this trait between neighbouring birds common or restricted to a few species? Addressing whether the species examined in this study are representative of all songbirds will require a much larger sample. Descriptive studies of song are common in the literature and often include assessments of song sharing as a matter of course (Benedict, Rose, & Warning, 2013; Borror, 1987; Molles & Vehrencamp, 1999; Morton, 1987; Sosa-López & Mennill, 2014). We propose that assessments of similarity of song-type transitions can be included in such studies as well, which in time will reveal whether the patterns identified here are common or rare.

Our method for comparing song-type transitions should be applicable to any sequence data involving transitions between distinct behavioural states. For instance, courtship displays, such as the diving displays of hummingbirds (Stiles, 1982) or the dancing displays of manakins (Lukianchuk & Doucet, 2014) often involve transitions between discrete components, and the composition of these sequences differs among species (Clark, Feo, & Escalante, 2011). Transition matrices have also been frequently applied to the study of agonistic interactions (e.g. Chen, Lee, Bowens, Huber, & Kravitz, 2002; Ismayilova et al., 2013), so our method could find utility for comparing sequences of aggressive behaviours of any animal species in those contexts.

A further application of this method within the field of birdsong research would be to compare the duetting behaviours of different pairs of birds. In some songbird species, song duets are governed by stimulus–response rules called duet codes (Logue, 2006), in which the stimulus is a song type from the repertoire of one member of the pair, and the appropriate response is a different song type from the duetting partner's repertoire. A minor alteration to our method – where transition matrices are made to represent the stimulus–response transitions recorded from a pair of birds rather than the song-type transitions of a single bird – would allow an assessment of whether duet codes are shared between pairs beyond the level expected by chance. In a similar vein, rather than looking at differences between species, as we have done here (Fig. 3), this method could also be applied to investigate difference in singing behaviour between sexes of the same species, a topic which has been understudied in birds (Riebel, Hall, & Langmore, 2005).

Other approaches have been proposed for the task of comparing sequences and transition matrices (Vishwanathan, Schraudolph, Kondor, & Borgwardt, 2010), but our method has the advantage of offering a straightforward statistical comparison of song transitions that is suitable for a broad range of species and contexts. Ivanitskii et al. (2017) used an N -gram-based approach by scanning their sequences for chunks of up to five consecutive songs that were shared between individuals. Our approach can also be thought of as an N -gram-based approach, if rather than mutually preferred transitions being viewed as 'transitions' that are mutually preferred, they are viewed as 'bigrams' that are shared among birds. Where our approach differs from that of Ivanitskii et al. (2017) is by

providing a significance test to estimate the number of shared transitions that should be expected by chance.

Wu, Thompson, Bertram, and Johnson (2008) used Kullback–Liebler divergence between transition probability distributions to examine changes in the singing behaviour of captive zebra finches, *Taeniopygia guttata*, following surgery. Their metric of syntactic similarity was intended for cases where the repertoire remains constant but transition probabilities may change, as in a longitudinal study of a single individual. While their approach is useful for such contexts, our method appears more generally suitable to situations where repertoires and transition probabilities both differ between individuals, which is typical of many bird species.

Kershenbaum and Garland (2015) compared several methods for quantifying the similarity of sequences of vocalizations and advocated the use of edit distance as a suitable metric of similarity. Edit distance compares two sequences against an upper bound of perfect similarity (i.e. an edit distance of zero). A shortcoming of edit distance and other distance metrics, at least for the goals of this paper, is that dissimilarity (i.e. nonzero edit distance) is effectively unbounded and could emerge from differences in repertoire, syntax or sequence length. With three potential drivers of dissimilarity, it is not obvious what level of dissimilarity should be expected by chance between two birds, since their vocal outputs would likely differ in all three characteristics. Our proposed method, in contrast, controls for differences in repertoires and sequence length, and compares the similarity of transition matrices against a null expectation. This is not to say that our approach is superior to Kershenbaum and Garland's (2015) edit distance method, but only that they are fundamentally different. One scenario where edit distance would be more appropriate is for examining whether the song output of a single bird changes under different social contexts, seasonally or from one year to the next. Our proposed method is specifically suited to the task of comparing the song-type transitions of two individuals. The decision of which method to use should be made with a specific research question in mind.

Proximate Causes of Song Order Similarity

The tendency for individual Cassin's vireos, marsh wrens and some Adelaide's warblers to use similar song-type-to-song-type transitions implies that the development of these transitions may be controlled by factors common to multiple individuals within a population. One factor that may underlie shared behavioural patterns is a genetic underpinning to the behaviour. Genes might encode, for example, a rule such as 'B follows A' to underlie the sequence AB. Eastern phoebe, *Sayornis phoebe*, song appears to be innately encoded in this way, as birds raised without auditory feedback develop normal song sequences in this species (Kroodsma & Konishi, 1991). The species typically alternates its two song types (ABAB ...), suggesting that this simple sequencing rule, in addition to the acoustic structure of the song, is genetically determined.

While such a mechanism would seem reasonable for species that do not learn their songs, it is less plausible for the species investigated here, which are all oscine songbirds. Oscines are notable for the tendency of many species to develop elaborate songs through the process of social learning (Beecher & Brenowitz, 2005; Nottebohm, 1972). During the song learning process, exposure to song types is a crucial precondition for the development of a normal and high-quality adult song, and is essential for the development of shared song types. It seems unlikely that a sequencing rule such as 'B follows A' could be genetically encoded, when the acoustic structures of A and B are learnt. Thus, although

syntax, in the broad sense, may be influenced by genes, we do not find it likely that transitions from one specific song type to another are genetically encoded within our study species.

A second possibility is that different birds converge on similar transitions because of physiological constraints prohibiting the production of certain transitions. Although the influence of physiological performance constraints on syntax is worthy of further consideration, we do not find it a likely explanation for our results. Demonstrated performance constraints in other species occur within song types, rather than between them, and impact silent intervals that are only a fraction of a second in duration (Geberzahn & Aubin, 2014; Podos, 1997; Podos et al., 2016). In all species that showed significant similarity in song order in our analyses, songs were spaced out by 1 s or more of silence, which is probably more than sufficient for the vocal apparatus to reconfigure itself such that any song type might follow any other.

A final explanation for our results, and one that we find most likely, is that exposure to similar song sequences during the process of song learning may lead individuals in a population to deliver them in similar orders as adults. Laboratory experiments on marsh wrens (Kroodsma, 1979) and common nightingales (Todt & Hultsch, 1998) support this interpretation, since individuals adopted the sequencing patterns presented in a tutor tape. Song learning is much more challenging to document in the field, however, typically requiring inference based on observational rather than experimental evidence. Our reanalysis of the available marsh wren song sequence data from Verner (1975) confirmed a high similarity of song delivery order between nearby birds in that species, suggesting that the laboratory results can generalize to field conditions. It seems likely that similarity of song sequences in nearby individuals is driven by song learning in that species. It is tempting to generalize this learning ability to other species of wrens, given the close phylogenetic relationships, but our results suggest that rock wrens and rufous-and-white wrens do not learn to share song-type transitions in the same way that marsh wrens do. The three species of wrens use distinct song-ordering strategies, suggesting variability in song sequence learning even within members of the same family.

Nothing is known about if and how tutoring shapes song development in Adelaide's warbler and Cassin's vireo, which limits our ability to assess the role of learning in driving the patterns shown in our results. One expectation of this hypothesis is that the similarity of song order between tutor and tutee should be greater than between nontutor and tutee. This should give rise to pronounced declines in song order similarity as a function of geographical separation, provided tutors and tutees remain in close geographical proximity. Previous studies have documented this phenomenon, known as 'syntactic dialects', in birds (Balaban, 1988) and mammals (Kershenbaum et al., 2012). In those studies, the order of delivery of vocal elements, but not necessarily the vocal elements themselves, changed with increasing geographical distance. We did not find evidence of this in our data set, where all species lacked a clear relationship between our measure of song order similarity and the geographical distance separating their territories. This does not, however, rule out song learning as a driver of similarity in song order, since many songbirds learn songs prior to postfledging dispersal (Hultsch & Todt, 2004). If that is the case, dispersal may mask the pattern over short distances, but declines in similarity may still be apparent over larger distances. Our data were too geographically restricted to examine this, but an opportunity exists for future studies to examine this over a larger area or to track dispersal from hatching, to shed light on the mechanisms underlying these patterns.

Potential Roles for Similarity of Song Order in Vocal Interactions

The markedly different patterns in the similarity of song-type transitions between the four species examined here raise the question: why do some species show similarity in song transitions, while others do not? One possibility is that the ordering of songs might be important during countersinging in some species. Kroodsma (1979) showed that the song choices of two captive male marsh wrens were influenced by one another. Both individuals were tutored on the same song sequence and adopted similar song-type-to-song-type transitions as adults. During vocal interactions, the socially dominant bird consistently took a leading position in delivery of this shared sequence, and the subordinate bird consistently followed, engaging in a form of song matching akin to what has been described in several other species (Akçay, Tom, Campbell, & Beecher, 2013; Beecher, Campbell, Burt, Hill, & Nordby, 2000).

Cassin's vireos showed a similar behaviour in response to playback; birds responded to playback of one of the song types in their repertoire by singing the song type that normally follows it in their own song sequences (Hedley et al., 2017). As with the marsh wrens, this sometimes resulted in the responding bird taking a leading role in a song exchange, causing the singer to preempt an upcoming playback song type. Some authors have proposed that leaders and followers in vocal interactions reap asymmetrical benefits from eavesdroppers (Bartsch, Wenchel, Kaiser, & Kipper, 2014). If so, the tendency to deliver songs in similar orders as other birds in the population may allow a bird to take a leadership role in the delivery of a shared sequence, even without any prior familiarity with the other bird's singing tendencies. Our results from Cassin's vireos in this study suggest that they could interact with any other bird in the population in this way, since pairwise measures of song order similarity were high among all 11 individuals included in this study. Some Adelaide's warblers may do the same, but many would not, and no rock wrens or rufous-and-white-wrens would accrue this potential benefit within countersinging exchanges.

Another possible reason that nearby individuals might show similarity in song transitions is to facilitate individual identifications or to signal group membership. Briefer et al. (2008) demonstrated that skylark, *Alauda arvensis*, songs contained shared sequences (referred to as phrases) that varied from one group to the next. Playback experiments revealed that birds responded less aggressively to sequences containing phrases typical of their group, regardless of the identity of the singer, and more aggressively to sequences whose order had been altered (Briefer, Rybak, & Aubin, 2013). This implies that the order of syllables, rather than the acoustic structure of the constituent vocal units, was the basis upon which discrimination occurred. Contrary to this hypothesis, Cassin's vireos did not respond differently to playback of song sequences arranged according to population norms and those deviating from population norms (Hedley et al., 2017), suggesting that the order of song does not convey information pertaining to group identity.

Alternatively, the patterns observed here might emerge as a by-product of song learning without any functional consequences later on. Todt and Hultsch (1998) proposed that birds memorize large repertoires by subdividing the tutor songs into chunks of several song types during learning, and they showed that these chunks re-emerge in similar orders during song production. Perhaps, if this is extended to the population level, it could lead to all individuals transitioning between song types in similar ways, even if the order of song delivery has no relevance in communication. We find this possibility unlikely, given the apparent role for similar song delivery order in countersinging interactions in Cassin's vireos (Hedley et al., 2017) and marsh wrens (Kroodsma, 1979; Verner,

1975). Moreover, despite possessing large repertoires of over 70 song types, rock wrens showed little evidence of similarity in song-type transitions, suggesting that at least in some species, constraints on memorizing large repertoires are not the sole determinant of this pattern.

In conclusion, the technique we presented to quantify the similarity of song transition matrices revealed marked variation among five species of songbirds. Cassin's vireos and marsh wrens showed clear tendencies to transition between shared song types in similar ways, as did a few dyads of Adelaide's warblers. Dyads of rock wrens and rufous-and-white wrens showed no such tendency. These results highlight an underexplored axis of behavioural variation among songbird species. Although we have proposed various hypotheses regarding the proximate and ultimate causes of this variation, few conclusions can be firmly drawn without further study. The method we have presented can be applied to a broad array of behavioural sequence data to illuminate the consequences of similarity in song-type transitions in animal communication.

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Supplementary material

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