



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, Kroodsma (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

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