Community algorithms reveal song type themes in Adelaide's warbler song type sequence networks

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Abstract

Some New World Warblers (Family: Parulidae) sing with immediate variety during the dawn chorus and eventual variety during daytime song. We used network analysis, including a community clustering algorithm, to further characterize song type sequences during the dawn chorus and daytime song in male Adelaide's warblers (*Setophaga adelaidae*). Networks had longer path lengths than expected by chance, indicating that song type transitions were constrained. Community analysis revealed the presence of "themes," or groups of song types that individuals deliver in close sequential proximity. To our knowledge, this is the first report of song type themes in Parulidae. Males did not cycle through their repertoires efficiently, as would be expected if large repertoires were attractive to females. Themes might emerge from the learning process or from interactions with neighbors. Themes may function to improve vocal performance or organize song types with similar functions. Relative to dawn chorus networks, daytime song networks had longer paths and stronger community structure. We hypothesize that song type networks are more structured during daytime song because song delivery is optimized for vocal warm-up during the dawn chorus, males frequently switch among intended receivers during the dawn chorus, or females prefer extended themes during daytime song.

Keywords

Bird song, community analysis, dawn chorus, network analysis, Parulidae

The sequential order with which songbirds (Suborder: Passeri) deliver their song types can vary by context (Hedley 2016a; Hedley et al. 2018; Suzuki et al. 2019). This variation has been shown to affect receivers' behavior, suggesting that song order can have functional consequences (e.g., Taylor et al. 2017). A classic example of contextual variation in song delivery occurs in certain New World warblers (Family: Parulidae) that deliver songs differently during the dawn chorus than they do during daytime song (Spector 1992). Previous studies have used traditional song type delivery metrics like switch rate and diversity to characterize differences in song type delivery between these two singing modes. While useful, these metrics ignore potentially important axes of variation, such as the orderliness of song type sequences and the tendency of certain song types to be delivered in close sequential proximity. We addressed this gap in knowledge by using network analysis to characterize and compare song type delivery during dawn chorus and daytime singing in a New World Warbler.

Network analysis has proven to be a powerful tool for the analysis of song type sequences (Allen et al. 2019; Deslandes et al. 2014; Hedley 2016b; Kaluthota et al. 2020; Sasahara et al. 2012; Taylor et al. 2016; Weiss et al. 2014; Zsebők et al. 2021). In a typical song type sequence network, song types are represented by nodes (objects in the network) and first-order transitions between song types are represented as directed edges (arrows connecting nodes). Metrics developed for network analysis can be used to quantify the properties of song type sequences. For example, the network metric "minimum average path length" (hereafter, "path length") measures the mean distance in number of edges between pairs of nodes. Applied to song type sequence networks, a long path length implies structure borne of constraint: birds choose certain transitions and avoid others (Kaluthota et al. 2020). In addition to generating metrics like path length, song type sequence networks can also reveal whether groups of song types tend to cluster together in sequences.

Community clustering algorithms assign the nodes of a network to subgroups called "communities" (Agrawal and Patel 2020; Yang et al. 2016). In song type sequence networks, these algorithms identify clusters of song types that tend to be delivered in ordinal proximity to one another (Opaev and Kolesnikova 2022). We use the term "themes" to describe these clusters (following Cody et al. 2016; Ivanitskii and Marova 2022; Pandolfino and Hedley 2019). Other authors have called sequentially associated song types "packages" (e.g., Todt and Hultsch 1998). We view these terms as synonyms. The probability of transitioning to a song type within the same community, theme, or package exceeds the probability of transitioning to a song type that belongs to a different one.

We analyzed communities in male Adelaide's warbler (*Setophaga adelaidae*) song type sequence networks. Males in our study population sing repertoires of 29.0 ± 4.0 discrete song types, each of which is a frequency modulated trill (Fig. 1; Kaluthota et al. 2019a). Patterns of song type delivery vary by context. During the breeding season, males participate in a dawn chorus, during which they sing at high rates in switch mode. Most males deliver their dawn chorus from high up in one or two tall trees on their territory. For mated males, the dawn chorus ends when the female joins the male (unpublished data). Members of our group have observed the end of many dawn choruses, but we have never seen pair mates copulate, so copulation is probably not common at that time. After the female joins the male, the pair typically patrols the territory borders and engages in border conflicts with neighbours. After the dawn chorus, song rates are lower, and males sing in repeat mode. Unmated males, which we excluded from the present study, continue dawn-like singing throughout the morning (Staicer 1996b).

Like many New World warblers, Adelaide's warblers' repertoires comprise two song categories – Category A and Category B (sometimes called Type 1 and Type 2, respectively; Kaluthota et al. 2019a; Spector 1992; Staicer 1996a). The defining differences between the categories are patterns of song delivery. Males sing Category A songs throughout the year, in repeat mode, with long latencies between songs. In contrast, they sing Category B songs only in the breeding season, in switch mode, and with short latencies between songs. The dawn chorus, which occurs only during the breeding season, comprises almost entirely Category B songs. After the dawn chorus males sing a mix of Category A and B songs. Two studies defined song categories based on these differences in song delivery and then compared their acoustic structures. One study reported that relative to Category B songs, Category A songs tend to be longer, with more notes (Kaluthota et al. 2019a; b), while the other found Category A songs have a less complex structure, higher overall frequency, and broader frequency bandwidth (Staicer 1996a). Both studies reported that a given song type might be used in Category A by one male, but in Category B by another. Further complicating matters, Kaluthota et al. (2019) concluded that category membership may be a continuous property (such that a given song type might fall on a spectrum from A to B) rather than a discrete one. In the present study, we sidestep these complications by focusing on the distinction between the dawn chorus and daytime singing (everything after the end of the dawn chorus), rather than song categories.

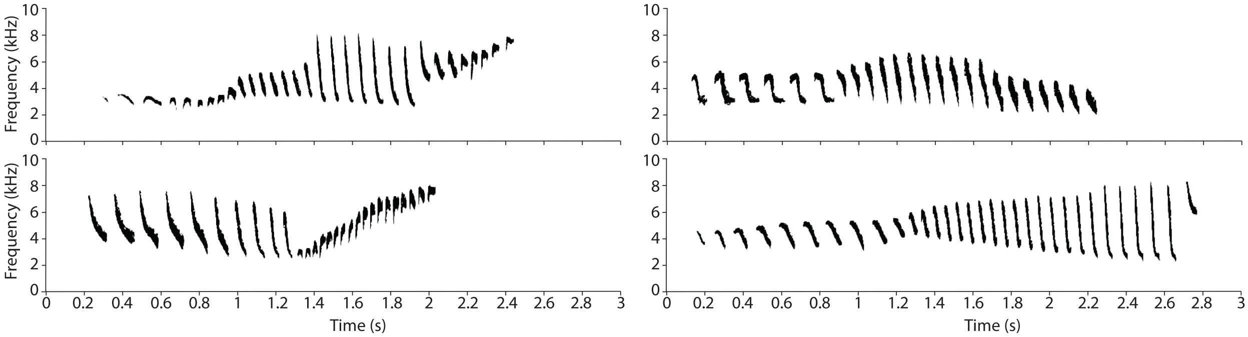

Figure 1. Sound spectrograms of four song types from male Adelaide's warblers (Hann window, 512 points / sample). Copied from Vazquez-Cardona et al. (2023) with permission from the authors.

The goals of this descriptive study are to characterize and compare individuals' song type sequence networks during the dawn chorus and daytime song. We analyzed networks based on natural singing from individually marked male Adelaide's warblers. We then used the results to generate hypotheses about the proximate and functional constraints that might have generated the observed differences between song type sequence networks from the dawn chorus and daytime song.

Materials and Methods

Field work

Mated male Adelaide's warblers were recorded at the Cabo Rojo National Wildlife Refuge, Puerto Rico (17°59′N, 67°100′W) in 2012, 2017, and 2018. All birds used in this study were captured with mist nets and acoustic lures and marked with a unique combination of plastic colored leg bands and a numbered metal band prior to recording. Recordings were made with Marantz PMD-661 digital recorders (Marantz, Sagamihara, Japan) and Sennheiser ME66 "shotgun" microphones (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) and saved as .wav files (sampling rate 44.1 kHz; bit depth 16 bits). In 2012, nine males were recorded for 4 days each. Recordings began 45min before sunrise and ended 2h 45min after sunrise. In 2017 and 2018, birds were recorded for 4.2 ± 2.02 days (avg. ± SD), from the first song of the day until approximately two hours after sunrise.

Field work was conducted with permission from the U.S. Fish and Wildlife Service (permits 2012-01, 41521-2016-11), the Departamento de Recursos Naturales y Ambientales de Puerto Rico (permit 2016-IC-068-1), the University of Puerto Rico at Mayagüez Animal Care and Use Committee (September 17, 2010), and University of Lethbridge Animal Welfare Committee (protocol #1605). Bird handling was conducted under D.M.L.'s master bird banding license (no. 23969).

Scoring and analysis

Adelaide's warblers' sing repertoires of discrete song types, but there is also some variation within types. The main sources of within-type variation in our population are the number of notes in each part (syllable) of the song, and the presence or absence of short introductory, or more commonly, terminal elements. The goal of our song type analysis was to split types and lump variants within a type. For all years, two songs were considered to belong to the same type if they were judged to be 80% similar with respect to overall frequency contour (the shape of the outline of the song on a spectrogram) and note shape. Although less common, consistent, large differences in the number of notes in each phrase were also grounds for splitting song types. The presence or absence of short introductory or terminal elements was not used to separate types. Hybrid songs, comprising part or all of two song types without a silent gap between them, were treated as unique song types, but these were rare (< 1% of songs). Using these criteria, it was straightforward to assign songs to song types within an individual's repertoire. Assigning songs to types among individuals is more challenging, but we did not need to do that for the present study. Annotators visualized 2012 recordings in Syrinx PC v.2.6 (Burt 1995-2006) and entered data into a spreadsheet. After all scoring was complete, one observer (D.M.L.) reviewed all song types. The recordings from 2017 and 2018 were annotated in Raven Pro 1.6.1 (Center for Conservation Bioacoustics 2019). After scoring was complete, one person (P.C.M. for 2017, S.W.K. for 2018) reviewed all song types.

We used song type sequences to generate song type sequence networks. We first removed sequential repetitions of song types. For example, we would have converted the song type sequence "A-A-A-B-B-A-A-C-C" to "A-B-A-C." We omitted sequential repetitions because (1) differences in repetitions between dawn chorus and daytime song have already been characterized in this population, as we discussed above (Kaluthota et al. 2019a; C Staicer 1991; Staicer 1996a), (2) repetitions have no effect on the metrics path length or reciprocity, as they are typically calculated, and (3) repetitions distort community clustering, because they are always within-cluster transitions. The third point merits elaboration. If we had included repetitions, clusters would be defined primarily by birds' tendency to repeat song types (which is already known to differ between the dawn chorus and daytime song) rather than their tendency to sing sets of song types in sequential proximity (which is not yet known). Because birds sing repetitively during daytime song, the modularity (strength of clustering) would be much higher during daytime song than during the dawn chorus if we included repetitions, but we would not know whether that difference indicated a difference in their tendency to sing sets of song types in sequential proximity during those time periods.

The time that the dawn chorus ends varies by day and individual. We therefore wrote an algorithm to define the end of the dawn chorus in a way that was consistent and repeatable. We developed this algorithm by experimenting with different policies until we found one that produced reasonable results for almost all our recordings. The winning policy ignored the first ten songs, because song is often sporadic when birds begin singing. After that point, the cut-off was placed at the midpoint of the silent gap just before either of the following conditions were met: (1) three consecutive silent gaps between songs were all ≥ 45 s, or (2) there were ≥ 10 consecutive songs without a song type switch (Fig 2.). Song type sequences before this cut-off were labelled "dawn chorus" and song type sequences after the cut-off were labelled "daytime song."

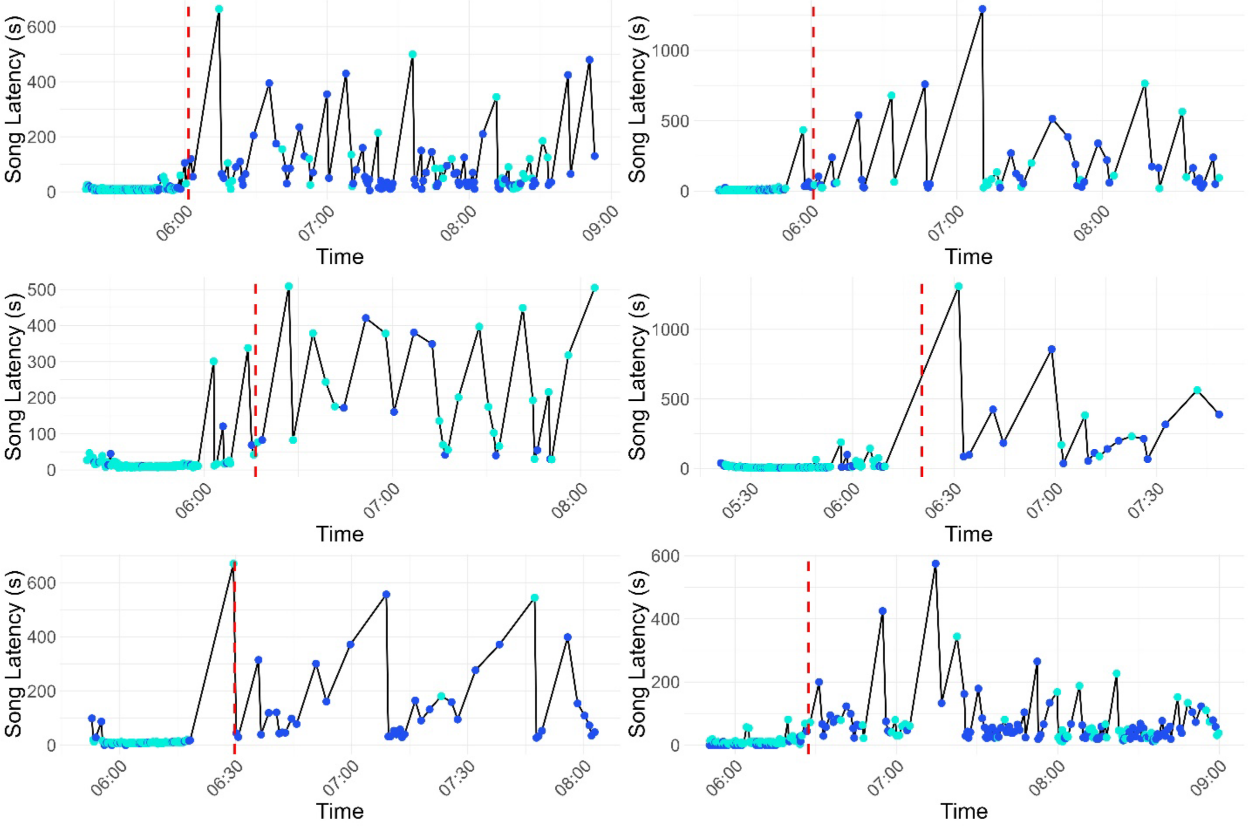

Figure 2. Example plots based recordings of male Adelaide's warblers from each year of the study (top row: 2012, middle row: 2017, bottom row: 2018). Dark blue dots represent songs that belong to the same song type as the previous song, and light blue dots represent songs that do not. The red dotted line indicates the cutoff between the dawn chorus and daytime singing. See text for details.

We used these sequences to construct directed, weighted song type sequence networks. The word "directed" means that each edge describes one or more transitions *from* a particular song type *to* another song type (in a non-directed network, edges do not specify a direction). Any two nodes in a network could be directly connected by zero edges (no transitions), one edge (transitions from A-to-B only), or two edges (transitions in both directions). Edges were weighted by the observed number of transitions. Each network comprised all the song types and song type transitions (regardless of the presence of silent gaps) recorded from one individual, on one day, during one time period (dawn chorus or daytime song).

Network analysis can, in principle, be applied to networks with any number of nodes (song types) > 1. However, variation in the number of nodes will bias some network metrics. We statistically account for the effects this variation in our analyses (below). It is important to construct networks from a sufficient number of samples (songs), because network structure is less stable when samples are small. We therefore omitted networks with fewer than 100 songs from the analysis (n < 100 networks). We were left with 125 networks to analyze (Table 1). Most individuals contributed more than one network to our analyses.

We chose the walktrap clustering algorithm because it is effective for a variety of cluster densities and network sizes (de Sousa and Zhao 2014; Pons and Latapy 2006; Yang et al. 2016). The walktrap algorithm identifies communities from random "walks" through the network. Beginning at one node, which we call the "home node," the algorithm takes a short random walk of predetermined length (walk length = 4 steps in the present study) and records which node it lands on (we call this node the "destination"). It repeats this process many times, then moves on to the next home node and does it again, until it has generated a distribution of destinations from random walks from each node. Frequent occurrences of a node as a destination are taken as evidence that it is in close proximity to the home node. The algorithm then uses hierarchical clustering to identify communities.

We scored the following metrics from each song type sequence network: path length, reciprocity, number of communities, and modularity. As described above, path length is the mean number of steps required to connect any two nodes in the network. In a song type sequence network, high values indicate structure born of constraint – certain sequence are more common, and others are less common, than would be expected in a random network (Kaluthota et al. 2020). Reciprocity describes the probability that the reciprocal of a directed edge (that is, an edge that connects the same two nodes in the opposite direction) is also present in the graph. In song type sequence networks, reciprocity measures the bidirectionality of song type transitions. The number of communities is simply a count of communities identified by the walktrap algorithm. Modularity measures the strength of community structure. A high score indicates a high ratio of intra-community connections to inter-community connections.

We ran Monte Carlo simulations to test whether observed network properties differed from null expectations. We first averaged the variable of interest over all networks for a given period (dawn chorus, daytime song), for each individual (e.g., the average reciprocity of male DgDgY's dawn chorus networks). This step ensured that all individuals were weighted equally. We then averaged these within-individual averages over all individuals for a given period to arrive at the observed test statistic (e.g., the observed mean path length of dawn chorus networks). Next, we randomized the order of song type sequences (after eliminating sequential repeats) to generate 10,000 random sequences. We designed our randomization algorithm to avoid generating song type sequences with sequential repetitions, because the observed edited sequences did not have repetitions. We used each random sequence to make a song type sequence network, which we subjected to the walktrap algorithm. Our randomization procedure preserved the number of song types (nodes) and song type transitions from the observed data while randomly redistributing the transitions. This approach did not always preserve the number of edges from the observed networks, because the number of edges does not necessarily correspond to the total number of transitions in a weighted song type transition network. Finally, we used the random song type sequence networks to generate a null distribution of test statistics (i.e., network metrics), which we compared to the observed test statistic to calculate a realized p-value.

We built generalized linear mixed models (GLMMs) to test whether network properties vary by time of day. Data were the raw (unaveraged) network parameters. Models used Gaussian error distributions and estimated parameters with maximum likelihood. Each model included time period, number of songs, and number of song types as independent variables. The number of songs and song types were included as covariates because they can affect network metrics (e.g., the number of song types limits the path length). Individual and day (nested within individual) were included as random variables to account for the non-independence of networks from the same individual as well as those from a given individual in the same day. We tested whether time period influenced network metrics by looking at the bootstrapped confidence intervals from the GLMM output. We also conducted likelihood ratio tests by removing the variable of interest from each model and comparing the full model to the reduced model with the *anova* function. To be conservative, we concluded that there were contextual differences for variables in which both the confidence intervals and the likelihood ratio tests indicated a difference.

All analyses were conducted in R x64 4.1.0. (R Core Team 2018), running the R Studio development environment (RStudio Team 2021). Network analyses relied on the *igraph* package (Csardi and Nepusz 2006). We used *lme4* for linear modeling. Data and code are available at (*put data repository information here*).

Results

Our networks included 22,236 songs from 28 males (Table 1). The walktrap algorithm divided networks into communities, each of which contained a set of song types that the focal male tended to deliver in ordinal proximity to one another (Fig. 3). Two recordings did not meet either of our cut-off conditions, but visual analysis indicated they included both a dawn chorus and daytime song. We set the dawn chorus cut-offs manually for those recordings.

Table 1. Descriptive statistics from Adelaide's warbler song type sequence networks.

	Males	**Networks**	**Duration (min)***	**Latency (s)***	**Songs***	**Transitions***	**Song Types***
Dawn Chorus	28	91	39.4 ± 20.7	13.0 ± 5.5	181.8 ± 47.6	59.5 ± 15.5	14.8 ± 3.2
Daytime Song	17	34	158.1 ± 36.3	70.4 ± 25.4	145.7 ± 37.2	24.6 ± 12.9	10.7 ± 3.7

* Data represent avg. ± SD of within-individual averages.

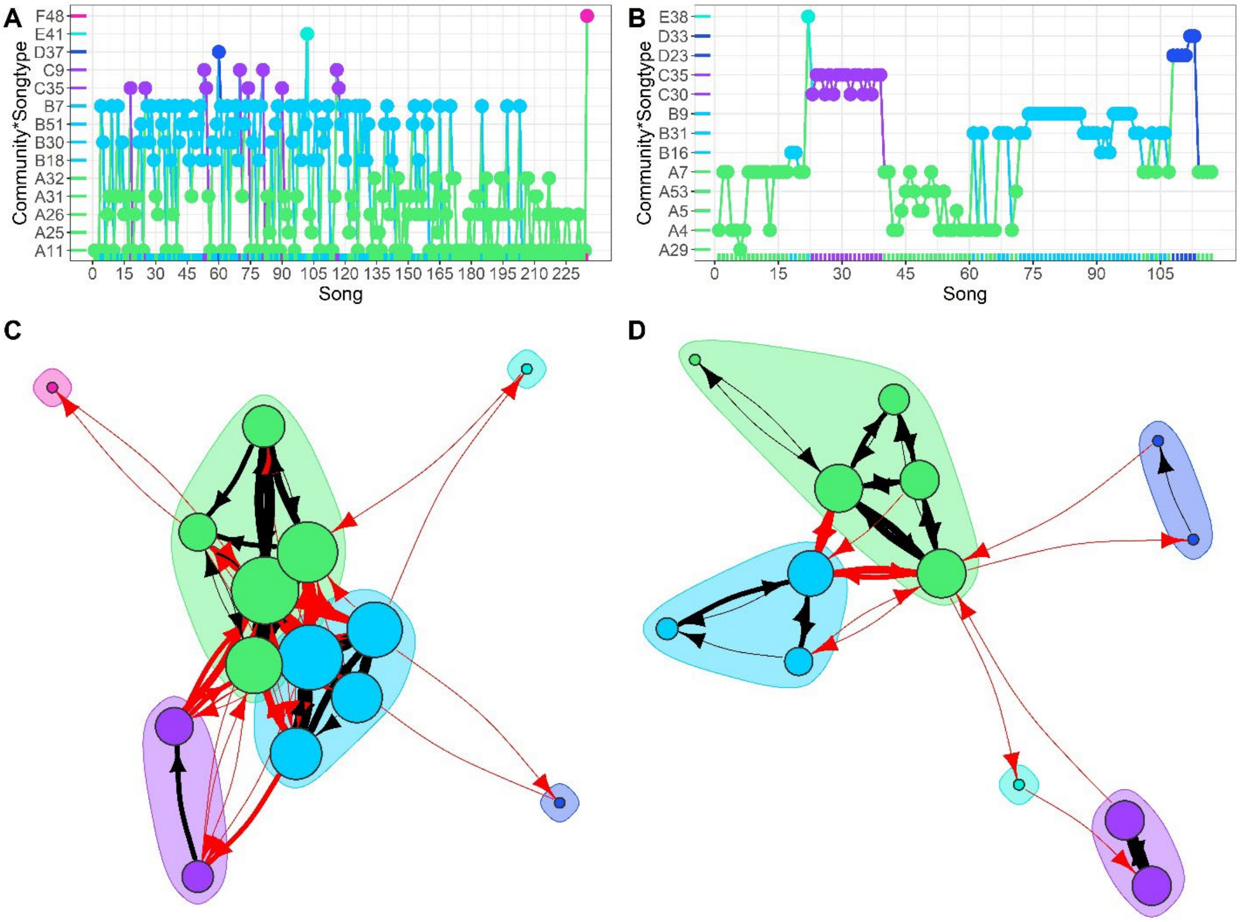

Figure 3. Scatterplots (A & B) and networks (C & D), representing one song type sequence from the dawn chorus (A &C) and another from daytime song (B & D). These two sequences are from different males. They were chosen because their modularity scores were close to the average modularity scores for the dawn chorus (A & C), and daytime song (B & D) networks, respectively. In A and B, colors represent communities identified by the walktrap community clustering algorithm. In C and D, nodes (circles) represent song types, and edges (arrows) represent first-order transitions between song types. Node size indicates the number of songs of each type and edge weight (thickness) indicates the number of transitions. The translucent shapes describe communities and the colors of these shapes and the nodes correspond to community ID. Black edges show transitions within communities and red edges show transitions among communities. The placement of nodes and communities is intended to make connections easy to discern. Community proximity is not a proxy for modularity.

Table 2. Summary of network metrics from Adelaide's warbler song type sequence networks. Values were first averaged within individual, then averaged among individuals. Values based on randomized data are in parentheses.

	Path Length	**Reciprocity**	**Communities**	**Modularity**
Dawn Chorus	1.16 ± 0.27 (0.94 ± 0.0037)	0.62 ± 0.10 (0.59 ± 0.0057)	3.43 ± 1.48 (1.76 ± 0.098)	0.13 ± 0.10 (0.048 ± 0.004650)
Daytime Song	1.64 ± 0.53 (0.70 ± 0.0053)	0.68 ± 0.12 (0.72 ± 0.0090)	2.90 ± 1.00 (1.39 ± 0.12)	0.31 ± 0.14 (0.025 ± 0.0067)

The Monte Carlo analyses indicated that all network variables differed significantly from null expectations (all $p < 0.0001$). For both dawn chorus and daytime song networks, observed values of path length, number of communities, and modularity, exceeded null expectations. The observed reciprocity greater than expected during the dawn chorus, but lower than expected during daytime song (Table 2). The effect sizes for reciprocity were small.

The confidence intervals produced by the GLMMs indicated that path length and modularity were significantly higher during daytime song than they were during the dawn chorus (Tables 2, 3; Fig. 4). The confidence intervals for reciprocity and number of communities straddled zero, indicating no significant difference. The likelihood ratio tests, however, indicated significant differences in all four network parameters (path length: $\chi^2 = 106.03$, df = 1, $p < 0.0001$; reciprocity: $\chi^2 = 0.023$, df = 1, $p < 0.0001$; communities: $\chi^2 = 1.218$, df = 1, $p = 0.0001$; modularity: $\chi^2 = 63.031$, df = 1, $p < 0.0001$).

We combined the results of these two tests with our evaluation of group means and distributions to interpret our findings. We concluded that, compared to the dawn chorus networks, daytime song networks were characterized by moderately higher path length and much higher modularity. We did not interpret the differences in reciprocity or number of communities across time periods because the effect sizes were small, and the significance tests were equivocal.

We included number of songs and number of song types as covariates in our GLMMs (Table 3). The number of songs covaried negatively with path length and positively with reciprocity. The number of song types scaled positively with path length, communities, and modularity, and negatively with reciprocity.

Table 3. Parameter estimates and 95% confidence intervals (in parentheses) from GLMM's that test the effect of time of day on Adelaide's warbler song type sequence networks. See text for details.

	Path length	**Reciprocity**	**Communities**	**Modularity**
Intercept	1.20 (1.045, 1.35)	0.79 (0.73, 0.84)	1.50 (0.55, 2.35)	0.15 (0.069, 0.23)
Period (relative to daytime song)	-0.69 (-0.80, -0.60)	-0.0027 (-0.044, 0.036)	-0.32 (-0.85, 0.21)	-0.23 (-0.27, -0.18)
# songs	-0.0030 (-0.0037, -0.0024)	0.00093 (0.00067, 0.0011)	-0.0025 (-0.0068, 0.0021)	-0.00031 (-0.00066, 0.000032)

# Song Types	0.082 (0.071, 0.094)	-0.022 (-0.026, -0.019)	0.18 (0.12, 0.24)	0.018 (0.013, 0.023)

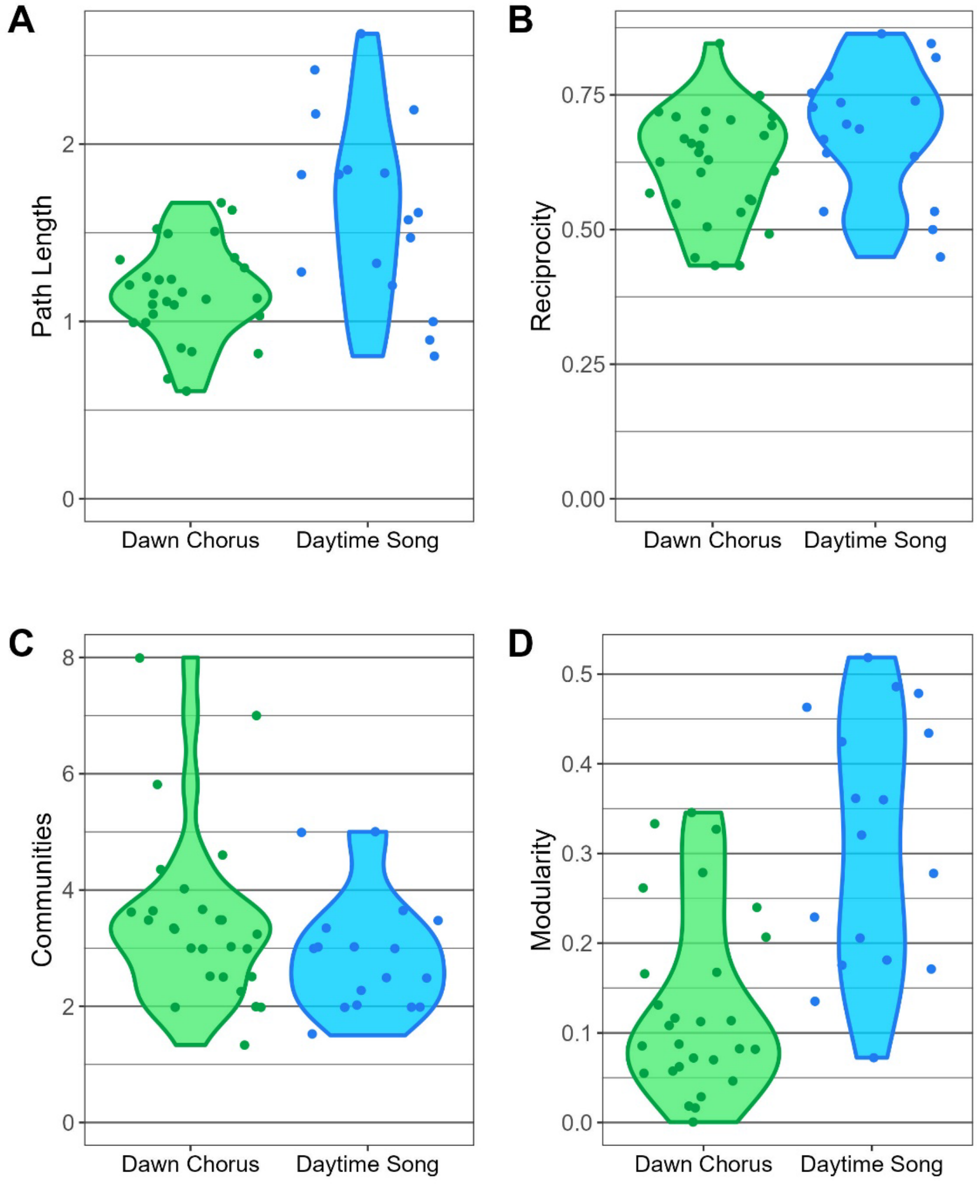

Figure 4. Violin plots comparing network metrics derived from male Adelaide's warblers' song type sequences recorded during the dawn chorus and daytime song.

Discussion

We used network analysis to characterize and compare male Adelaide's warblers' song type sequences during the dawn chorus and daytime song. Our analyses revealed stronger evidence of structure (i.e., longer path lengths, more communities, and higher modularity) than would be expected from random sequences. We interpret this finding to mean that song transitions are constrained, such that individuals tend to favor certain transitions and avoid others. The network metric reciprocity was slightly, but significantly, higher than expected by chance. Walktrap community analysis revealed the existence of distinct communities. Collectively, these findings indicate that male Adelaide's warbler song type sequences are structured into themes, rather than being delivered randomly, or linearly as in some other species (Hedley 2016a; Kroodsma 1979).

We propose four non-exclusive hypotheses to explain why Adelaide's warblers deliver song types as themes. First, song learning could underlie the emergence of themes. Vocal units that are learned together tend to cluster together during song delivery in nightingales (Luscinia megarhynchos; Hultsch and Todt 2004) and zebra finches (Taeniopygia guttata; Williams and Staples 1992). Second, organizing songs into clusters may be an adaptation to facilitate efficient recall. It would be interesting to test whether birds sing with higher vocal performance when transitioning within versus between themes (Logue et al. 2020; Sierro et al. 2023). A third hypothesis is that vocal interactions among countersinging males, like song type matching and song advancing, interact with male's endogenous song type sequencing rules such that themes emerge (Logue 2021). This appears to be the case during the dawn chorus, when multiple neighbouring males converge on song type themes (Logue et al. unpublished data). Our fourth hypothesis is that community structure emerges from the adaptive clustering of song types into functionally distinct themes. If different song types function differently (e.g., Trillo and Vehrencamp 2005), it may be adaptive for birds to group songs with similar functions into themes. If certain song types function in aggressive interactions, for example, we would expect many transitions among those types during agonistic encounters.

Our results allow us to reject the hypothesis that male Adelaide's warblers efficiently showcase the size of their song type repertoires. Although males deliver songs with immediate variety during the dawn chorus, they do not run through their full repertoire quickly in a way that might impress female receivers who prefer large repertoires (as in Searcy et al. 2022). Rather, they sing from one theme for a while before moving on to another theme (Fig. 3). As further evidence against this hypothesis, some song types are only sung rarely (unpublished data).

Why does song delivery differ between the dawn chorus and daytime song?

There are many hypotheses about the functions of the dawn chorus, but little in the way of consensus (Gil and Llusia 2020; Schlicht et al. 2023; Staicer et al. 1996; Vazquez-Cardona et al. 2023). Our findings add to a long list of differences between song delivery during the dawn chorus and daytime song. Relative to daytime singing, the dawn chorus has a much higher song rate and song type switch rate, less pronounced structure (shorter path length and lower modularity), and uses a different part of the song type repertoire (Kaluthota et al. 2019a; CA Staicer 1991; present study). Any coherent hypothesis about dawn chorus function in Adelaide's warbler must be compatible with all these differences.

One potential explanation for the observed contextual differences relates to the finding that male Adelaide's warblers warm up their voices during the dawn chorus (Schraft et al. 2017; Vazquez-Cardona et al. 2023). Perhaps rapidly switching between themes warms up the voice more efficiently than singing one theme for a long time. The social environment also differs between the dawn chorus, when males are alone and relatively stationary, and daytime song, when they patrol the borders of their territory with their mates. Based on the hypothesis that males use different song types to communicate with different neighbours, they may rapidly switch from one intended receiver to another during the dawn chorus but communicate at length with one receiver before moving on to the next during daytime song. Finally, it may be the case that males sing in repeat mode with extended themes during daytime song because that is what females prefer. This hypothesis is consistent with the recent findings that repetitive singing improves consistency in male Eurasian blue tits (*Cyanistes caeruleus*), and females prefer songs with high vocal consistency (Sierro et al. 2023).

The differences we observed between song type sequence networks from the dawn chorus and daytime song cannot be explained by the direct effects of higher song type switch rates during the dawn chorus because we eliminated sequential repetitions before generating networks. There may, however, be indirect effects of song type switch rates on song type sequences. For example, the number of sequential repetitions of a song type could influence the time lag until a singer returns to that type (Searcy et al. 2019). The finding that modularity was higher during daytime song does not necessarily mean that birds adhere more strictly to themes during daytime song. Theme switching generates between-cluster transitions that reduce modularity scores, so high levels of theme switching, rather than low adherence to themes, may explain why modularity was lower in the dawn chorus.

Comparable studies

This is the latest in a string of recent studies that use community clustering to identify themes in song type sequence networks in California thrashers (Toxostoma redivivum; Cody et al. 2016; Taylor et al. 2017), grey-crowned warblers (Phylloscopus tephrocephalus; Opaev and Kolesnikova 2022), and now Adelaide's warblers (present study). It appears that song type themes are widespread and common in songbirds with medium and large song type repertoires.

It is instructive to consider the different ways that community clustering algorithms have been applied to animal signal sequences. We used the walktrap community algorithm, but other studies used the Newman algorithm (Cody et al. 2016; Sánchez Castellanos et al. 2015), the spinglass algorithm (Paul et al. 2021), or an unspecified algorithm (Allen et al. 2019; Opaev and Kolesnikova 2022). We chose the walktrap algorithm because of its simplicity and robustness. We found that it was easy to implement, the results were straightforward to interpret and visualize, and the clusters corresponded to groups of songs that were delivered together in song type sequences (e.g., Fig. 3). One limitation of the walktrap approach, however, is that a node (song type) cannot be assigned to more than one cluster. Some studies of signal sequence networks might benefit from a community algorithm that allows nodes to occur in more than one cluster.

Another important difference among studies that apply community analysis to acoustic signal sequence networks is the scale of analysis. Some analyses apply clustering algorithms to a smaller scale to identify clusters of acoustic subunits (e.g., syllables) within songs (Allen et al. 2019; Paul et al. 2021). It is also possible to apply community analysis at a broader scale, as in Opaev and Kolesnikova (2022), which combined song sequences of individual grey-crowned warblers to identify themes at the population level.

We found the number of songs and song types covaried with several network metrics. Had we not included these covariates, our results would have been biased by uncontrolled variation in the number of songs and song type. We recommend including the number of songs and song types as covariates in most studies of song type sequence networks.

One limitation of our study is that we only examined first-order transitions in song type sequences. Our networks show the frequency with which a song type at position X is followed by another song type at position X + 1. They do not show the frequency with which a song type at position X is followed by another song type at position X + Y, where Y > 1. Similarly, our analysis does not show how combinations of song types might influence subsequent song type choices. We can imagine, for example, that song type C is more likely to follow the song type sequence A-B, than it is to follow D-B, but our analysis does not address this possibility. There is evidence of such “higher-order dependencies” in bird song sequences (Hedley 2016b; Searcy et al. 2022). Although we did not directly examine higher order dependencies, our application of community clustering algorithms to first-order signal sequence network models is a simple way of asking which song types are associated with one another, whether or not first-order transitions generate that association.

We used song type sequence networks to describe patterns of song type delivery, but we do not view them as Markov models of the process that generates song type sequences. We reject the generative interpretation because Markov chains seem to be poor models of signal choice in animals (Kershenbaum et al. 2014). One reason for this mismatch is that sequences are probably influenced by exogenous factors in addition to internal rules. In particular, it is likely that neighbours’ songs influence individuals’ song type sequences (Logue 2021; CA Staicer 1991). A full accounting of song type sequences probably requires a communication network approach in which multiple signalers are recorded simultaneously.

Conclusion

The finding that male Adelaide’s warbler song type sequences are characterized by themes improves our understanding of acoustic communication in this species and opens avenues for additional research on the origin and function(s) of song type themes. Song type sequences were more structured (constrained) during daytime song than they were during the dawn chorus. This finding is one of several differences between dawn chorus and post-dawn singing, all of which must be accounted for by a coherent theory of song function in this species. We believe this is the first study to show evidence of themes in New World Warblers’ song type sequences, and the first to show that the community structure of song type sequences varies across contexts.

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Declaration of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to have influenced the work reported in this report.

AI Statement

We used ChatGPT to assist with syntax and debugging in R.

References

Agrawal S and Patel A (2020) Clustering algorithm for community detection in complex network: a comprehensive review. *Recent Advances in Computer Science and Communications (Formerly: Recent Patents on Computer Science)* **13**(4)**,** 542-549.

Allen JA, Garland EC, Dunlop RA and Noad MJ (2019) Network analysis reveals underlying syntactic features in a vocally learnt mammalian display, humpback whale song. *Proceedings of the Royal Society B* **286**(1917)**,** 20192014.

Burt J (1995-2006) Syrinx ver 2.6. Seattle, WA.

Center for Conservation Bioacoustics (2019) Raven Pro: Interactive Sound Analysis Software ver 1.6.1. Ithaca, NY: The Cornell Lab of Ornithology.

Cody ML, Stabler E, Sánchez Castellanos HM and Taylor CE (2016) Structure, syntax and "small-world" organization in the complex songs of California Thrashers (Toxostoma redivivum). *Bioacoustics* **25**(1)**,** 41-54.

Csardi G and Nepusz T (2006) The igraph software package for complex network research. *InterJournal, complex systems* **1695**(5)**,** 1-9.

de Sousa FB and Zhao L (2014) Evaluating and comparing the igraph community detection algorithms. In: *2014 Brazilian Conference on Intelligent Systems.* IEEE.

Deslandes V, Faria LR, Borges ME and Pie MR (2014) The structure of an avian syllable syntax network. *Behavioural processes* **106,** 53-59.

Gil D and Llusia D (2020) The bird dawn chorus revisited. In Aubin T and Mathevon N (eds), *Coding strategies in vertebrate acoustic communication.* Springer Nature, 45-90.

Hedley RW (2016a) Composition and sequential organization of song repertoires in Cassin's Vireo (Vireo cassinii). *Journal of Ornithology* **157**(1)**,** 13-22.

Hedley RW (2016b) Composition and sequential organization of song repertoires in Cassin's Vireo (Vireo cassinii). *Journal of Ornithology* **157,** 13-22.

Hedley RW, Logue DM, Benedict L and Mennill DJ (2018) Assessing the similarity of song-type transitions among birds: evidence for interspecies variation. *Animal Behaviour* **140,** 161-170.

Hultsch H and Todt D (2004) Approaches to the mechanisms of song memorization and singing provide evidence for a procedural memory. *Anais da Academia Brasileira de Ciências* **76,** 219-230.

Ivanitskii V and Marova I (2022) The syntactic organization of bird song. *Biology Bulletin* **49**(8)**,** 1158-1170.

Kaluthota C, Logue D and Rendall D (2020) Conventional and network analyses of song organization and complexity in northern House Wrens (Troglodytes aedon parkmanii). *Journal of Field Ornithology* **91**(4)**,** 375-392.

Kaluthota CD, Medina OJ and Logue DM (2019a) Quantifying song categories in Adelaide's Warbler (Setophaga adelaidae). *Journal of Ornithology* **160**(2)**,** 305-315.

Kaluthota CD, Medina OJ and Logue DM (2019b) Quantifying song categories in Adelaide's Warbler (*Setophaga adelaidae*). *Journal of Ornithology***,** 1-11.

Kershenbaum A, Bowles AE, Freeberg TM, Jin DZ, Lameira AR and Bohn K (2014) Animal vocal sequences: not the Markov chains we thought they were. *Proceedings of the Royal Society B: Biological Sciences* **281**(1792)**,** 20141370.

Kroodsma DE (1979) Vocal dueling among male marsh wrens: Evidence for ritualized expressions of dominance / subordinance. *The Auk* **96,** 506-515.

Logue DM (2021) Countersinging in birds. *Advances in the Study of Behavior* **53,** 1-61.

Logue DM, Sheppard JA, Walton B, Brinkman BE and Medina OJ (2020) An analysis of avian vocal performance at the note and song levels. *Bioacoustics* **29**(6)**,** 709-730.

Opaev A and Kolesnikova Y (2022) Song theme sharing in the grey-crowned warbler Phylloscopus tephrocephalus. *Bioacoustics* **31**(2)**,** 191-207.

Pandolfino ER and Hedley RW (2019) Structure of Lark Sparrow Song in California. *Western Birds* **50**(2).

Paul N, Thompson MJ and Foote JR (2021) Characterising the flight song: repeatable individual variation of Ovenbird song features. *Bioacoustics* **30**(2)**,** 232-251.

Pons P and Latapy M (2006) Computing communities in large networks using random walks. *J. Graph Algorithms Appl.* **10**(2)**,** 191-218.

R Core Team (2018) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

RStudio Team (2021) RStudio: Integrated Development for R. RStudio, Inc.

Sánchez Castellanos H, Vallejo E and Taylor C (2015) PajaroLoco: a suite of programs to study the grammatical structure of bird songs. In: *Proceedings of the Twentieth International Symposium on Artificial Life and Robotics.*

Sasahara K, Cody ML, Cohen D and Taylor CE (2012) Structural design principles of complex bird songs: a network-based approach. *PloS one* **7**(9)**,** e44436.

Schlicht L, Schlicht E, Santema P and Kempenaers B (2023) A dawn and dusk chorus will emerge if males sing in the absence of their mate. *Proceedings of the Royal Society B* **290**(2011)**,** 20232266.

Schraft HA, Medina OJ, McClure J, Pereira DA and Logue DM (2017) Within-day improvement in a behavioural display: wild birds 'warm up'. *Animal Behaviour* **124,** 167-174.

Searcy WA, Ocampo D and Nowicki S (2019) Constraints on song type matching in a songbird. *Behavioral ecology and sociobiology* **73,** 1-10.

Searcy WA, Soha J, Peters S and Nowicki S (2022) Long-distance dependencies in birdsong syntax. *Proceedings of the Royal Society B* **289**(1967)**,** 20212473.

Sierro J, de Kort SR and Hartley IR (2023) Sexual selection for both diversity and repetition in birdsong. *Nature Communications* **14**(1)**,** 3600.

Spector DA (1992) Wood-warbler song systems: a review of paruline singing behaviors. *Current ornithology***,** 199-238.

Staicer C (1991) The role of male song in the socioecology of the tropical resident Adelaide's warbler (*Dendroica adelaidae*). Ph.D., Department of Zoology, University of Massachusetts.

Staicer CA (1991) The role of male song in the socioecology of the tropical resident Adelaide's Warbler (Dendroica adelaidae). Ph.D. Dissertation, University of Massachusetts.

Staicer CA (1996a) Acoustical features of song categories of the Adelaide's Warbler (Dendroica adelaidae). *The Auk* **113**(4)**,** 771-783.

Staicer CA (1996b) Honest advertisement of pairing status: evidence from a tropical resident wood-warbler. *Animal Behaviour* **51**(2)**,** 375-390.

Staicer CA, Spector DA and Horn AG (1996) The dawn chorus and other diel patterns in acoustic signaling. In Kroodsma D and Miller EH (eds), *Ecology and evolution of acoustic communication in birds.* Cornell University Press, 426-453.

Suzuki TN, Griesser M and Wheatcroft D (2019) Syntactic rules in avian vocal sequences as a window into the evolution of compositionality. *Animal Behaviour* **151,** 267-274.

Taylor C, Vallejo E and Sánchez H (2016) PajaroLoco: A suite of programs to study complex adaptive properties of animal language. An example of a Cassins vireo syntax network. In: *ALIFE 2016, the Fifteenth International Conference on the Synthesis and Simulation of Living Systems.* MIT Press.

Taylor CE, Brumley JT, Hedley RW and Cody ML (2017) Sensitivity of California thrashers (Toxostoma redivivum) to song syntax. *Bioacoustics* **26**(3)**,** 259-270.

Todt D and Hultsch H (1998) How songbirds deal with large amounts of serial information: retrieval rules suggest a hierarchical song memory. *Biological cybernetics* **79**(6)**,** 487-500.

Trillo P and Vehrencamp S (2005) Song types and their structural features are associated with specific contexts in the banded wren. *Animal Behaviour* **70**(4)**,** 921-935.

Vazquez-Cardona J, Bonnell TR, Mower PC, Medina OJ, Jiskoot H and Logue DM (2023) Vocal performance increases rapidly during the dawn chorus in Adelaide’s warbler (Setophaga adelaidae). *Behavioral Ecology***,** arad030.

Weiss M, Hultsch H, Adam I, Scharff C and Kipper S (2014) The use of network analysis to study complex animal communication systems: a study on nightingale song. *Proceedings of the Royal Society B: Biological Sciences* **281**(1785)**,** 20140460.

Williams H and Staples K (1992) Syllable chunking in zebra finch (Taeniopygia guttata) song. *Journal of Comparative Psychology* **106**(3)**,** 278.

Yang Z, Algesheimer R and Tessone CJ (2016) A comparative analysis of community detection algorithms on artificial networks. *Scientific reports* **6**(1)**,** 1-18.

Zsebők S, Herczeg G, Laczi M, Nagy G, Vaskuti É, Hargitai R, Hegyi G, Herényi M, Markó G and Rosivall B (2021) Sequential organization of birdsong: relationships with individual quality and fitness. *Behavioral Ecology* **32**(1)**,** 82-93.