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Avian Behavior, Ecology, and Evolution

Song-type sharing between male Rock Wrens in northern Colorado

Uso compartido de tipos de canto entre los machos de *Salpinctes obsoletus* en el norte de Colorado

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ABSTRACT. We examined song-type sharing and song-type co-occurrence among broadcast songs in a migratory population of a songbird with large and highly variable repertoire sizes, the Rock Wren (*Salpinctes obsoletus*). Large song-type repertoires may offer a competitive advantage in intrasexual competition and provide opportunities for varied patterns of song-type sharing. We found that Rock Wrens in one population showed a general tendency to overproduce highly shared, i.e., popular, songs, and males with smaller repertoires sang more popular songs than males with larger repertoires. Song types with lower minimum frequencies and slower trill rates tended to be more popular, potentially enhancing song transmission. Using network analyses, we found non-random song sharing between pairs of males that does not seem to be mediated by location. Song-delivery rates of males were positively related to their song sharing with other males, and it is possible that both mediate male-male aggression or female preference. We also found that some pairs of song types co-occurred in birds' repertoires more than others, but the song co-occurrence network was not clustered, raising questions about what factors drive song co-occurrence and repertoire composition. Taken together, our results suggest that song sharing and singing locally popular songs may play an important role in social communication. The results support the notion that having a larger repertoire allows a bird to sing both rare and popular song types and use rare or unique song types that can be used in assessment by rivals, more often than birds with smaller repertoires.

RESUMEN. Examinamos el uso compartido de tipos de canto y la co-ocurrencia de tipos de canto entre los cantos emitidos en una población migratoria de un ave canora que tiene repertorios grandes y muy variables, el *Salpinctes obsoletus*. Los amplios repertorios de tipos de canto pueden ofrecer una ventaja competitiva en la competencia intrasexual y proporcionar oportunidades para variados patrones de tipos de canto compartidos. Encontramos que *S. obsoletus* en una población mostraba una tendencia general a sobreproducir cantos muy compartidos, es decir, populares, y que los machos con repertorios más pequeños cantaban más cantos populares que los machos con repertorios más grandes. Los cantos con frecuencias mínimas más bajas y tasas de trino más lentas tendían a ser más populares, lo que potencialmente favorecería la transmisión de cantos. Mediante el uso de análisis de redes, encontramos cantos compartidos no aleatorios entre pares de machos que no parece estar mediado por la ubicación. Las tasas de emisión de canto de los machos estaban positivamente relacionadas con su canto compartido con otros machos, y es posible que ambos factores influyan en la agresión entre machos o en la preferencia de las hembras. Asimismo, encontramos que algunos pares de tipos de canto aparecían más que otras en los repertorios de las aves, pero la red de coocurrencia de cantos no estaba agrupada, lo que plantea interrogantes sobre los factores que determinan la coocurrencia de cantos y la composición de los repertorios. En conjunto, nuestros resultados sugieren que compartir cantos y cantar cantos populares a nivel local puede desempeñar un papel importante en la comunicación social. Los resultados apoyan la noción de que tener un repertorio más amplio permite a un ave cantar tanto tipos de canto raros como populares y utilizar tipos de canto raros o únicos que pueden ser utilizados en la evaluación por parte de los rivales, con mayor frecuencia que las aves con repertorios más reducidos.

Key Words: *bird song; network analysis; rock wren; song sharing; song-sharing networks; wrens*

INTRODUCTION

Birdsong has long captured human interest and has been extensively studied in various contexts (Catchpole and Slater 2008). Songs can provide information about the singer and serve as signals of individual condition and intent (Dolby et al. 2005, Searcy and Beecher 2009, Lapierre et al. 2011). Individual birds often have a repertoire of song types, with repertoire size, i.e., the number of song types sung by a bird, and the extent of repertoire sharing with nearby conspecifics varying across species (Kroodsma 1977), populations (Hughes et al. 1998, Peters et al. 2000) and individuals within populations (Kroodsma 1975, Lapierre et al. 2011). Repertoire size and song sharing may, in some cases, influence intrasexual aggression (Beecher et al. 2000, Pitt 2018) and mate choice (Buchanan and Catchpole 1997, Nelson and Poesel 2013). The repertoire-size hypothesis (Beecher and Brenowitz 2005) posits that repertoire size positively reflects singer quality and larger repertoires are preferred by potential mates, whereas the general-sharing hypothesis, which is non-mutually exclusive with the repertoire-size hypothesis, says that song-matching or song-avoidance with nearby conspecifics is facilitated by a large repertoire and offers benefits in competition, as it does in Song Sparrows (*Melospiza melodia*; Beecher et al. 2000, Beecher 2008), and mating success, as it does in Indigo Buntings (*Passerina cyanea*; Payne et al. 1988).

Troglodyte wren species show considerable diversity in repertoire size and offer a good model for examining patterns of song-type repertoire use and sharing. Within this group, Rock Wrens

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(*Salpinctes obsoletus*) are sexually monomorphic (Benedict et al. 2021) territorial songbirds (Warning and Benedict 2015), with some migratory and some sedentary populations (Benedict et al. 2021). In the breeding season, they typically occupy open and arid habitats with rocky outcrops, cliffs, and/or escarpments, and build their nests in natural rock cavities (Warning and Benedict 2016, Benedict et al. 2021). Rock Wren males defend territories with song and sing with a flexible delivery pattern; song types are usually sung several times interspersed with other song types following no fixed pattern (Kroodsma 1975). Males show large and variable repertoire sizes (Kroodsma 1975, Benedict and Warning 2017). Whereas sympatric Canyon Wrens (*Catherpes mexicanus*) sing only five to six song types (Benedict et al. 2013), some Rock Wrens sing over 120 song types, with moderate repertoire sharing, e.g., ~42% of their repertoire shared with other birds in one study population (Benedict and Warning 2017). Playback experiments of larger Rock Wren repertoires elicited a greater response in singing by resident males, which suggests that repertoire size plays a role in male-male competition and territory defense (Pitt 2018), supporting the repertoire-size hypothesis. However, contrary to the expectation of the repertoire-size hypothesis that all song types should be sung in equal frequency, Rock Wrens sing some song types in their repertoires much more than others (Benedict and Warning 2017). These results highlight the value of a large repertoire while raising questions about what song types are most likely to be used and shared among individuals at the population level.

Network analysis has been used to examine transition patterns in song sequences of individual birds (Kaluthota et al. 2020) and is an effective method to examine song sharing (Potvin et al. 2019). We, therefore, used network analysis methods to examine song-type sharing among male Rock Wrens in northern Colorado; females of this species do not sing (Benedict et al 2021). We examined recordings of natural broadcast singing of male Rock Wrens in a migratory population after they returned in spring for breeding. In the same population, it was previously found that individual males use song types that maximize transmission in their environment (Benedict and Warning 2017) and that Rock Wrens order their song types in variable ways (Hedley et al. 2018). Detailed patterns of song-type sharing across the population, however, are yet to be examined. We aimed to answer three broad questions:

1. Are popular songs in the population preferred by individual birds?

According to the general-sharing hypothesis, overproducing song types that are sung by many birds in the population, i.e., popular songs (Table 1), may be beneficial by reducing aggression from conspecifics through the dear enemy effect (Briefer et al. 2008) and by allowing mutual assessment (Logue and Forstmeier 2008, Price and Yuan 2011). In this study population, Benedict and Warning (2017) found that individual Rock Wrens preferred different songs, with 10 of 12 birds having unique song types as their most used. Here, we expand on these analyses by asking, first, are most songs sung by many birds and, second, are popular songs sung more or less frequently than rare or unique songs by individual birds? Further, it is possible that not all birds follow the same strategy (Lapierre et al. 2011), so we examined the effect of repertoire size on the tendency to overproduce popular songs.

2. Is there non-random song sharing between bird repertoires, and what factors influence song sharing?

Song-type sharing might be more similar between immediate neighbors than others (Hill et al. 1999) and, if so, we expected similarity to decrease with increasing distance (Benedict et al. 2013). We constructed networks of song sharing between birds and examined whether some pairs of Rock Wrens shared more or less of their repertoire than expected by chance, hence non-random, and whether distance affected song sharing. Song sharing may be constrained by syntactic rules of song production or might reflect the complexity of repertoires (Benedict and Najar 2019, Searcy et al. 2023). Thus, we examined whether two measures of song production of individual birds affected song sharing in this dataset: the rate of singing songs, i.e., Delivery, and the proportion of song transitions that resulted in a switch in song type, i.e., Switching. We hypothesized that birds that sang at a faster rate and switched songs more often would be able to share more songs with other males.

3. Is there non-random co-occurrence of song types, and does it depend on song characteristics?

In the same population, individual males were found to preferentially sing songs from their personal repertoires that enhanced transmission: longer songs with lower frequencies, lower trill rates, and smaller bandwidths (Benedict and Warning 2017). Song types with these preferred characteristics may co-occur, i.e., such that both are present, within a bird's repertoire more than expected by chance, hence non-randomly. Accordingly, we examined whether song co-occurrence networks were non-random, and the effects of song duration, low frequency, bandwidth, trill rate, and frequency inflections, i.e., switches from ascending to descending frequency or vice versa (Benedict and Warning 2017), on song popularity. Popular songs may show the same trend as individual song usage and have enhanced transmission. Alternatively, because songs shared by more birds were of lower performance using some song metrics, like trill rate, in other birds (Cardoso and Atwell 2016, Podos et al. 2016), song popularity and performance measures including trill rate and number of frequency inflections may be negatively correlated.

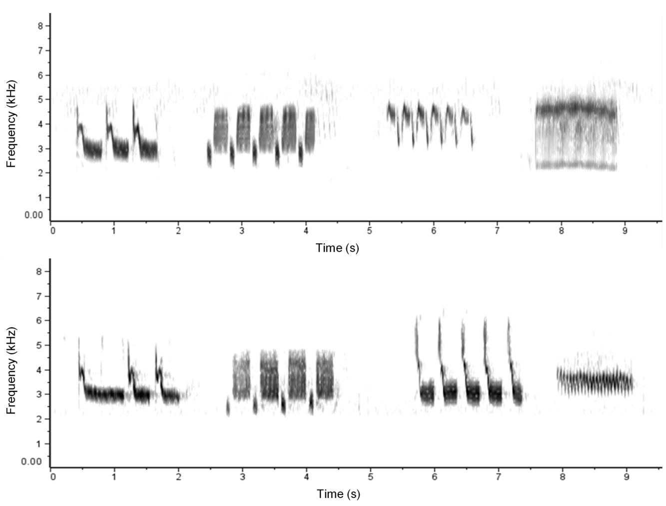
METHODS

Songs were recorded from 12 unbanded Rock Wrens in Larimer County, Colorado, USA, in spring 2013 and spring 2014. All the 12 birds were recorded in arid, exposed, and rocky habitats (Benedict and Warning 2017). Rock Wrens show high site-fidelity and large home ranges. Thus, we were confident about the identity of the singer while recording (Benedict and Warning 2017). Researchers recorded a mean of 1588 ± 418 (SD) songs per individual and categorized songs into 233 types based on visual appraisal of song characteristics, recorded song-type ordering through time, and measured acoustic song characteristics of each song type for every individual that sang it. Rock Wrens sing highly stereotyped songs that consist of repetitions of a single syllable or trill element, making them easy to classify to type visually based on syllable form (Figure 1). See Benedict and Warning (2017) for complete details on song recording and classification methodology; results reported here come from the same dataset, analyzed at the population rather than the individual level.

Table 1. Definition of terms and indices used in the analyses reported here.

Term	Type of measure/index name	Definition/interpretation
Top song type of the bird	Individual bird-level measure	The most commonly used (or sung) song type in the bird's repertoire.
Average proportion of usage of song type	Individual bird-level measure, averaged across birds	Proportion of total recorded songs per bird of that song type, averaged across birds when more than one bird sang the song type.
Popularity of a song type	Population-level measure	The number of birds in the population that sang that song type (varies from 1 to 12 in this dataset).
Popularity of the top song type of the bird	Population and individual bird-level measure	The number of birds in the population that sang the most commonly used song type of that bird.
Weighted popularity of a bird's songs	Population and individual bird-level measure	Proportion of total number of songs * popularity for each song type in a bird's repertoire, then summed across all song types. Similar to popularity of the top song type, but including all song types in the bird's repertoire.
Index 1	Adjusted Jaccard index	0 = no song-type sharing 1 = complete song-type sharing
Index 2	Weighted adjusted Jaccard index	0 = no song-type sharing 1 = complete sharing of song types, after accounting for song-type popularity
Index 3	Bray-Curtis dissimilarity index	1 = no song-type sharing 0 = birds sang the same song types with the same relative use frequencies
Index 4	Adjusted Jaccard index	0 = the two song types never occur in the same repertoire 1 = the two song types always occur in the same repertoires
Index 5	Bray-Curtis dissimilarity index	1 = no bird sang both song types 0 = birds which sang one song type, always sang the other song type, and they sang both with the same relative use frequencies

Fig. 1. Spectrograms illustrating four song types recorded from each of two Rock Wrens in Larimer County, Colorado. The first two songs in each recording represent shared types, whereas the second two are unique to each bird. A song type consists of repetitions of a single syllable that varies in length, i.e., ~1 to 3 seconds, and number of repetitions. In broadcast singing bouts, each song is typically followed by a brief, i.e., 2 to 5 seconds, period of silence, with pause durations reduced in the figure above for illustration purposes.



Popularity of a song type, its usage in individual birds, and the effect of repertoire size

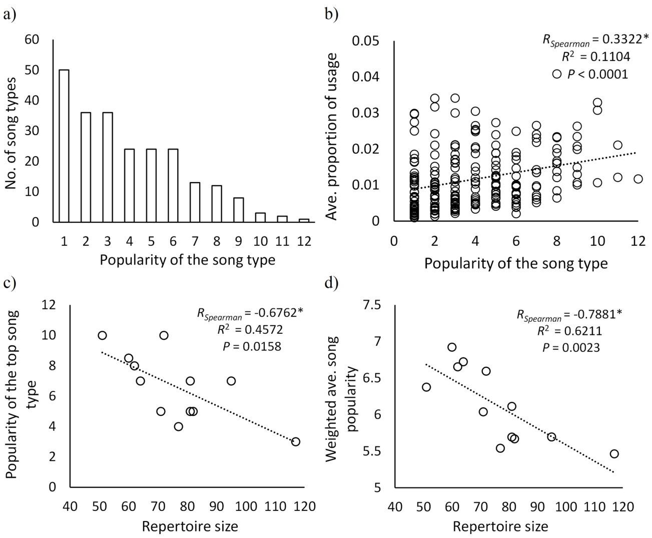
Popular songs in the population may have high or low song usage in individual birds. We plotted the number of song types that were sung by different numbers of birds, and correlated the number of birds that sang a song type, hereafter referred to as the "popularity of a song type," with the average proportion of usage, i.e., averaged across birds that sung the song (Table 1, Figure 2). If birds overproduced popular songs, we expected a positive correlation. If they instead preferred to sing unique songs, we expected a negative correlation. We also correlated the repertoire size of a bird with, first, the popularity of its top song type and, second, the weighted popularity of that bird's songs. These terms are detailed in Table 1. We performed Spearman's correlations in R version 4.2.3 (R Core Team 2023) for these comparisons.

Constructing song sharing and song co-occurrence networks and testing for non-randomness

We calculated three repertoire-level indices between all pairs of the 12 sampled Rock Wrens (Table 1) to measure song sharing between pairs of birds. *Index 1*, i.e., the Adjusted Jaccard index (Tracy and Baker 1999) = c / ((a + b + c) - d) where c is the number of shared song types, a is the number of song types unique to bird 1, i.e., number of song types in bird 1's repertoire not shared with bird 2, b is the number of song types unique to bird 2, and d is the (absolute) difference in repertoire sizes of the two birds. *Index 2* is a modification of the adjusted Jaccard index, where the songs were weighted by their popularity as $1 - Y_p$, with Y_p being the proportion of birds that sang that song type (Potvin et al. 2019), such that rarer songs weighed more than popular songs. These two indices measure similarity; a value of 1 indicates complete sharing and 0 means the birds shared no song types. Finally, *Index 3* is the Bray-Curtis dissimilarity index between pairs of birds (Bray and Curtis 1957). *Index 3* = $1 - ((2 * C_{12}) / S_1 + S_2)$, where C_{12} is the sum of lesser counts among bird 1 and bird 2 for each song type, summed across all song types, S_1 is total number of songs sung by bird 1, and S_2 is total number of songs sung by bird 2, again summed across all song types. *Index 3* accounts for the number of times that songs were sung, whereas indices 1 and 2 look at just the presence/absence of song types in a bird's repertoire, and is an index of dissimilarity, where 0 indicates the birds sang the same songs and in the same relative frequencies.

We also calculated co-occurrence indices between all pairs of the 233 song types, measuring how often they co-occur in the same bird's repertoire. *Index 4* or the Adjusted Jaccard index (Tracy

Fig. 2. (a) Frequency distribution of the popularity of the 233 song types; (b) popularity of a song, i.e., the number of birds that sang the song, and the average, i.e., if it is sung by more than one bird, proportion of its usage; (c) popularity of the top song type of a bird, i.e., the number of birds that sang the top song type of that bird, and the repertoire size of the bird; and (d) average weighted popularity of all songs sung by a bird and the repertoire size of the bird. Spearman's correlation coefficient and probability values are provided in the graphs. Significant correlations are marked with an asterisk.



and Baker 1999) $= c / ((a + b + c) - d)$, where c is the number of birds that sang both song types, a is the number of birds that sang song type 1 but not song type 2, b is the number of birds that sang song type 2 but not song type 1, and d is the (absolute) difference between the number of birds that sang song type 1 and the number of birds that sang song type 2. *Index 5* is the Bray-Curtis dissimilarity index between pairs of song types (Bray and Curtis 1957) $= 1 - ((2 * C_{12}) / S_1 + S_2)$, where C_{12} is the sum of lesser counts among song type 1 and song type 2 for each bird, summed across all birds, S_1 is the total number of times song 1 was sung, and S_2 is the total number of times song 2 was sung, summed across all birds. *Index 4* measures similarity and only looked at the presence/absence of one or both song types in a bird's repertoire. *Index 5* is a dissimilarity index that also takes into account the number of times the two song types were sung by different birds (Table 1).

We randomized the pre-network data, i.e., data-stream permutations, creating random repertoires for the 12 birds while keeping the number of birds that sang a song type the same as the observed dataset (Potvin et al. 2019) for all the 233 song types. We created 10,000 permuted datasets, with 10,000 flips per permutation, and compared the coefficient of variation, i.e., CV, of the five observed indices with corresponding permuted datasets. *P* values for permutations were calculated as 1- (Number of permutations where the observed value was greater than the corresponding permuted value / Number of permutations). If $P < 0.05$, the real or observed CV value was considered significantly greater than those in the permuted datasets, indicating that the network is non-random, with some pairs of birds sharing more of their songs than other pairs in the song-type sharing networks, and/or some pairs of song types tending to co-occur more than other pairs in the song co-occurrence networks.

All non-random networks were visualized, and network density, i.e., overall connectedness, modularity, i.e., how clustered the network is, and degree of non-random song co-occurrence networks were measured using Gephi version 0.10.1 (Bastian et al. 2009). For the Bray-Curtis dissimilarity indices, i.e., *Index 3* and *Index 5*, we used 1- index to visualize the networks, so that higher values represented higher similarity.

Effects of distance, delivery, and switching on song sharing

Using indices with non-random song sharing between birds, we examined the influence of several factors on song sharing. Distances between the central recording locations of birds were calculated in meters using GPS coordinates. We performed Mantel tests (Mantel 1967) to examine spatial patterns in song sharing. For each bird, we calculated Delivery, i.e., number of songs sung per minute of recording, and Switching, i.e., proportion of song transitions that resulted in a change in song type. These measures were previously found not to correlate with each other or with repertoire size in this dataset (Benedict and Najar 2019). We compared the observed Pearson's correlation coefficients between the average index of a bird and the bird's delivery and switching values to 1000 permuted datasets, permuted by node-label permutations, with 1000 flips of node labels in each permutation (Farine 2017). We expected birds with higher Delivery and Switching to have greater song sharing with others and, thus, positive correlations with *Index 1* and *Index 2*, and negative correlations with *Index 3*. If $P < 0.05$ (Appendix 1), the observed correlation was considered significant.

Effect of song characteristics on popularity

Using measurements of each song type from all birds, we calculated an average value of (1) song duration in seconds; (2) song low frequency in kHz; (3) song bandwidth in kHz; (4) trill rate in syllable/second; and (5) frequency inflections for each song type. We performed a zero-truncated negative-binomial regression, because our response variable, popularity, was a count that cannot have zero value and was overdispersed, looking at the main effects of the five song characteristics on the popularity of the song type using the VGAM package in R (Yee 2010). If songs are shared across birds because of the same motivation, i.e., of enhancing transmission, as song usage within birds (Benedict and Warning 2017), then we expect to find the same patterns for song sharing, or popularity of the song, and overall song usage. If, on the other hand, popular songs were favored because they were easy to sing then they are predicted to have lower performance than unpopular songs; specifically, we expected popularity to decrease with increasing song duration, increase with increasing low frequency, and decrease with an increase in song bandwidth, trill rates, and with frequency inflections.

Mantel tests were performed using the ecodist package (Goslee and Urban 2007). Data manipulations and permutations were performed in MATLAB version R2023a (The MathWorks Inc., 2023).

Table 2. Song sharing between birds and song-type co-occurrence, comparing observed and permuted datasets. All permutations were run with 10,000 permutations, and with 10,000 flips per permutation. Significant P values are bold.

Permutation	Index	Average ± SD (min - max) of index	CV in real dataset	Mean of CV in permuted datasets	No. of permutations where the CV of real > random	*P*
Between pairs of birds	*Index 1*	0.3184 ± 0.0796 (0.1860 - 0.5422)	0.2500	0.1482	10000/10000	**< 0.0001**
	Index 2	0.2386 ± 0.0681 (0.1367 - 0.4387)	0.2852	0.3215	1679/10000	0.8321
	Index 3	0.7320 ± 0.0575 (0.6049 - 0.8727)	0.0786	0.0603	9975/10000	**0.0025**
Between pairs of song types	*Index 4*	0.4065 ± 0.3878 (0.0000 - 1.0000)	0.9540	1.0049	0/10000	1.0000
	Index 5	0.8516 ± 0.1666 (0.0000 - 1.0000)	0.1956	0.1761	10000/10000	**< 0.0001**

RESULTS

Popularity of a song type, its usage in individual birds, and the effect of repertoire size

Most song types were sung by few birds (Average ± SD of popularity: 3.9185 ± 2.5659); frequency distribution in a, Figure 2, with 50, i.e., 21.5%, of the 233 song types sung by one bird and only one song type shared by all the 12 birds. The average proportion of usage was weakly, but significantly, positively correlated with the popularity of the song type; Spearman's rank correlation: $N = 233$, $R = 0.3322$, $P < 0.0001$ (b, Figure 2). The top songs of all the birds were also sung by other birds, and the repertoire size of a bird was negatively correlated with the popularity of its top song, i.e., Spearman's rank correlation: $N = 12$, $R = -0.6762$, $P = 0.0158$ (c, Figure 2) and with the weighted popularity of all songs, i.e., Spearman's rank correlation: $N = 12$, $R = -0.7881$, $P = 0.0023$ (d, Figure 2).

Constructing song sharing and song co-occurrence networks and testing for non-randomness

At the repertoire level between birds, we found moderate and generally consistent levels of song-type sharing; on average, they shared 37.5% to 48.3% of their repertoires with the other 11 birds. We similarly found moderate values using all three indices (Table 2), with all pairs of birds sharing some of their songs. We found that song-type sharing was non-random using *Index 1*, i.e., presence/absence of unweighted song types (Network in a, Figure 3), and *Index 3*, i.e., a dissimilarity index that included relative frequencies (Network in b, Figure 3), but not different from random using *Index 2*, i.e., presence/absence of song types, weighted by their popularity.

Song types co-occurred to different extents, with some pairs sharing no birds in common, and two pairs sharing all of them (Table 2). We found non-random song-type co-occurrence using *Index 5*, which reflects both the number of birds that sang both song types and the number of times each song type was used by those birds (Network in Figure 4), but not using *Index 4*, which looks only at presence/absence. The network (Figure 4) with 1- *Index 5* had dyads that had no similarity, i.e., 1- *Index 5* = 0, but was still a well-connected network, with a density of 0.6706, i.e., 18127 out of 27028 of all possible ties connected, and each song type co-occurring with many other song types (degree or number of connections: Average ± SD: 155.5966 ± 48.3220). The modularity of the network was low, i.e., 0.1920.

Effects of distance, delivery, and switching on song sharing

Distances between the 12 birds varied from 6.1049 meters to 18435.6900 meters (Average ± SD in meters: 3932.9293 ± 5832.6880). There was no significant effect of distance on the repertoire sharing similarity metric *Index 1*, i.e., Mantel test, Pearson's correlation, 1000 permutations: $N = 12$, $R = 0.0136$, P *(two-sided)* = 0.9290 (a, Figure 5), or on the repertoire sharing dissimilarity metric *Index 3*, i.e., Mantel test, Pearson's correlation, 1000 permutations: $N = 12$, $R = -0.2826$, P *(two-sided)* = 0.1620 (b, Figure 5).

Node-label permutations (1000 permutations) of the network with *Index 1* showed a positive correlation between Delivery and average index (c, Figure 5), and no correlation between Switching and average index (d, Figure 5; Appendix 1). Similar permutations of the network with *Index 3* showed a negative correlation between Delivery and average index (e, Figure 5), and no correlation between Switching and average index (f, Figure 5; Appendix 1).

Effect of song characteristics on popularity

The zero-truncated negative binomial regression results showed that songs with lower low frequencies and lower trill rates tended to be more popular (Table 3). Frequency inflections, duration and bandwidth had no effect on popularity (Table 3).

DISCUSSION

Rock Wrens in this migratory population shared many song types with each other, but only one song type was shared by all sampled birds. Rock Wrens have large repertoires and, hence, despite sharing many song types, pairs of Rock Wrens only had moderate song-sharing similarity indices. Song sharing was non-random in this population, with some pairs of males sharing more songs than others, but not because of geographic proximity. Small sample size of individual birds and, hence, incomplete sampling of the population are potential limitations of the study. However, the sample size ($N = 12$ birds) is comparable to other song-sharing networks, e.g., Potvin et al. (2019) constructed a syllable-sharing network with 12 male song sparrows. Further, given that distance did not affect song sharing in our analyses, it is unlikely that the observed trends are due to some individuals being farther away than others. Despite the small sample size of individuals, we found trends in song sharing that were affected by two different measures of song complexity: repertoire size and song delivery. We found non-random song sharing and song co-occurrence using some, but not other, indices.

Although few song types were sung by many birds (a, Figure 2), highly shared, i.e., popular, songs tended to be sung frequently by Rock Wren males in this population. Observed patterns of non-randomness in repertoire sharing are primarily driven by the sharing of popular songs, because song sharing was not different from random when we controlled for the popularity of the song in *Index 2*. These results suggest that birds in this population are singing the hits rather than emphasizing the unique parts of their

Fig. 3. Networks of song type sharing with 12 individual birds, indicated by different codes, as nodes, and different indices as edges; (a) using Index 1 reflecting presence/absence of song types in the repertoire by the index value; and (b) using (1-Index 3), reflecting presence and use frequency of song types in the repertoire, i.e., 1- index, value. In both networks, darker and thicker edges indicate higher weight and greater similarity.

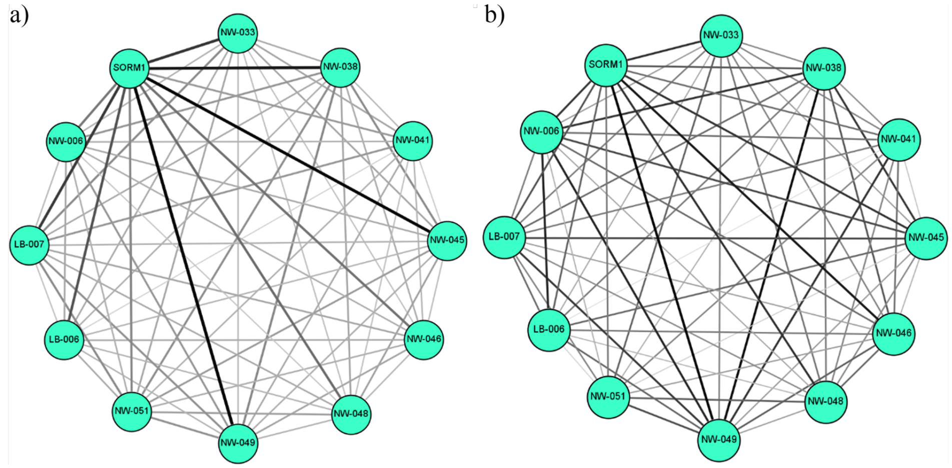
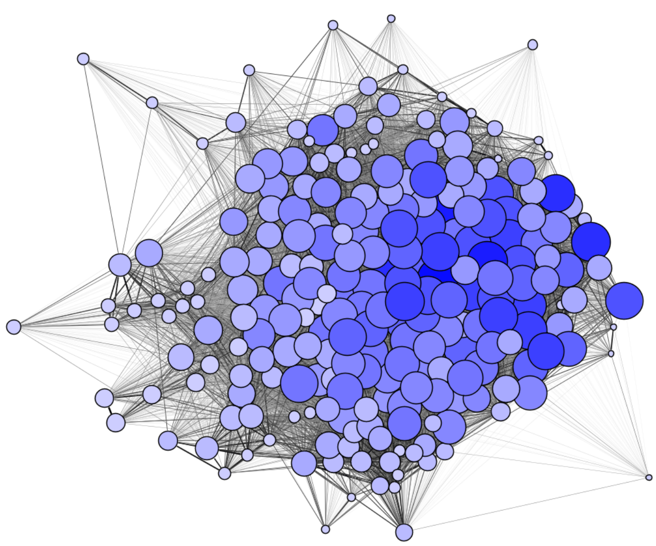


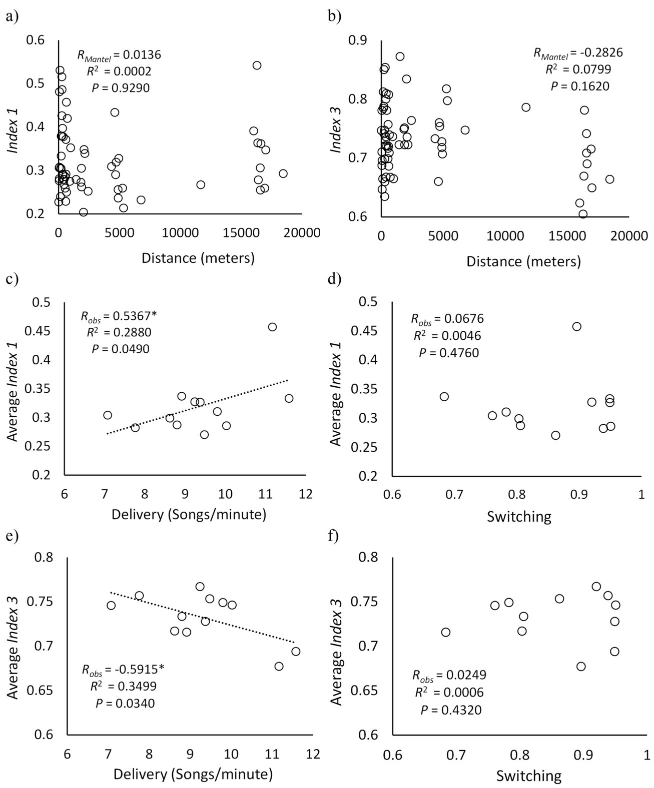
Fig. 4. Network of song co-occurrence with 233 song types as nodes, and (1- Index 5) as edges. The edges are weighted and colored, i.e., darker color indicates higher weight, by (1- Index) value and the nodes are sized by degree, i.e., number of song types with which the node has a non-zero (1- Index) value, with larger nodes having more connections, and colored by song type popularity, i.e., darker nodes are more popular. Darker and thicker edges indicate greater similarity. The network is well-connected and has no clear clusters, i.e., low modularity. Popular song types are, unsurprisingly, highly connected.



repertoires. However, all males did not sing popular songs to the same extent; males with smaller repertoires preferred singing more popular songs (Figure 2). Thus, whereas Rock Wren repertoire size seems to affect intrasexual competition and assessment (Pitt 2018), in line with the repertoire-size hypothesis, we find an overall tendency to overproduce popular songs, with birds singing the popular songs in their repertoire more often than the rare songs (b, Figure 2), supporting the general-sharing hypothesis. Lapierre et al. (2011) found that older, more competitive Song Sparrow males sang popular songs but we found the reverse, with the presumably less competitive males (Pitt 2018) singing the popular songs more than the competitive ones. Males preferentially singing popular local songs may face less aggression from other males (Beecher et al. 2000), making this strategy beneficial for males with smaller repertoires. Alternatively, males with smaller repertoires may possibly compensate for their repertoire-size disadvantage by singing popular songs that might be preferred by females, because females in other species are known to prefer males who sing locally common songs (Danner et al. 2011, Nelson and Poesel 2013). If female Rock Wrens prefer novel songs, males with larger repertoires could be singing preferred songs, but in Rock Wrens there is little evidence that females use song-repertoire sizes to choose mates (Pitt 2018). It would be interesting to examine the role of singing locally popular and rare/unique songs on direct measures of female choice.

We found non-random song-type sharing by Rock Wren males in two out of three indices, but song sharing was not strongly influenced by distance in this dataset. The lack of a clear relationship between distance and song sharing in this study may result from this being a migratory population or from frequent local movements (Benedict et al. 2021). It also raises questions about how age might affect repertoire size and usage of popular songs (Lapierre et al. 2011). Little is known about where and when Rock Wrens learn songs, because they do not seem to learn typically localized types, with most songs sung by only one bird (a, Figure 2). Further, spatial patterns of song sharing may vary at different spatial scales (Koetz et al. 2007, Rodríguez-Fuentes et al. 2022) and the sampled distances may not have been at the appropriate scale to capture the relationship.

Fig. 5. Distances and song-type sharing indices between pairs of rock wrens using (a) Index 1 and (b) Index 3, correlations of Delivery (c) and Switching (d) with average indices using Index 1, and correlations of Delivery (e) and Switching (f) with average indices using Index 3. Correlation coefficient and probability values of the corresponding statistical tests are provided in the graphs; significant correlations are marked with an asterisk.



We tested whether song-delivery patterns covaried with song-type sharing and found that one measure, delivery rate, was positively related to the average song-sharing index. This could result if birds singing at faster rates sing more songs in total, and consequently share more of their songs. However, we also saw this correlation with the adjusted Jaccard index that only looks at the presence and absence of song types. Therefore, we suggest that higher rates of singing and more song sharing may be related indicators of male quality, allowing individuals to sing locally popular song types that are shared with other males, being that during countersinging, male Rock Wrens have been known to song-match (Kroodsma 1975), which could then mediate male-male competition or female choice. Singing rates may be a signal of aggressive intent during male-male interactions (Szymkowiak and Kuczyński 2017), and male Rock Wrens sing at a greater rate in response to intruders (Pitt 2018). Thus, higher delivery of broadcast songs might directly play a role in competition, and/or affect it through influencing song sharing. Surprisingly, song-switching rate, which is also a signal in male-male interactions in some species (Deoniziak and Osiejuk 2020), was not related to song sharing in our study.

Table 3. Zero-truncated negative binomial regression results examining the effects of song characteristics on song popularity. Incidence rate ratios > 1 mean that an increase in the song-characteristic value is associated with increased popularity of the song type, while ratios < 1 mean that an increase in the song-characteristic value is associated with decreased popularity of the song type. Significant P values are bold.

Predictors	Incidence rate ratios	CI	*P*
Intercept 1	6.01	2.50 – 14.44	**<0.001**
Intercept 2 (overdispersion parameter)	3.43	2.09 – 5.63	**<0.001**
Duration	1.06	0.72 – 1.55	0.781
Low frequency	0.84	0.73 – 0.97	**0.017**
Bandwidth	0.98	0.89 – 1.08	0.656
Trill rate	0.97	0.95 – 0.99	**0.007**
Frequency inflections	1.01	1.00 – 1.03	0.130

Groups of Rock Wren song types did not markedly co-occur with each other more than with other types. Although a song co-occurrence network using the Bray-Curtis index was non-random (Figure 4), it was well-connected and not strongly modular or clustered. Consistent with the low modularity, we did not find strong relationships between song co-occurrence and song characteristics (Appendix 2). This result suggests that a few birds were not responsible for all of the song types in the population with particular acoustic properties, e.g., wide bandwidths or rapid trill rates. Rock Wren song types with lower low frequencies and lower trill rates were popular across birds, similar to what was found for within-bird song-type usage in Benedict and Warning (2017). Given the weak, positive correlation between the popularity of a song and its usage (b, Figure 2), it is unsurprising that we found similar trends at the population (this analysis) and individual (Benedict and Warning, 2017) levels. Low frequencies in a song type might be a potential signal of male body size and fighting ability (Benedict et al. 2012, Linhart and Fuchs 2015). By this metric, popular songs show higher performance. In contrast, higher trill rates are considered a signal of higher male quality in many species (Ballentine et al. 2004, Illes et al. 2006), and using trill rates as the metric, popular songs showed poorer performance. Thus, popular songs may have better transmission and carry variable performance information. Unlike the individual-level analysis in Benedict and Warning (2017), we did not find any significant relationship between popularity and song-type duration or bandwidth. This could be due to the small sample size for comparisons across birds, i.e., 12 birds, compared to within-bird song usage, i.e., hundreds of songs per bird. Alternatively, given that we find individual-level variation in song usage, it is possible that combining song-type usage across birds resulted in the non-significant relationships, highlighting that within-individual song use patterns do not always scale up to produce parallel population-level patterns. Thus, although individual birds prefer to sing the longer songs within their repertoires (Benedict and Warning 2017), those are not the most highly shared song types at the population level. More detailed studies on the relationship between song-type usage, popularity, and characteristics in different habitat types will help us understand whether birds of any species consistently preferentially share broadcast songs that enhance transmission.

Rock Wrens, with their large and variable repertoire sizes, present an interesting study system to examine song sharing. Individual Rock Wrens can have popular and rare songs in their repertoire and use them differently, and pairs of Rock Wrens can share their repertoires to different extents. Network analysis offers a holistic way to examine how those repertoires are shared across a population. As expected for a species with large repertoires, there was variation in song popularity, song sharing between pairs of males, and individual song-use patterns. Males with the smallest repertoire sizes were most likely to sing popular song types, prompting questions about the relative benefits of singing locally popular songs. Song popularity covaried with song form and song-sharing rates covaried with other measures of song behavior, such as delivery, providing insight into how song traits and song preferences of individual birds scale up to create population-wide patterns.

Author Contributions:

L. B. and K. P. conceived the study together. L. B. provided the data and K. P. performed data analyses. K. P. wrote the manuscript and L. B. edited the manuscript.

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Data Availability:

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.453v0 (Benedict and Warning 2017). Codes used in this paper are available on request.

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Appendix 1: Results of 1000 node-label permutations of song-sharing networks of 12 males with *Index 1* and *Index 3,* comparing observed and permuted correlations between the average index of a bird and two song metrics (Delivery and Switching). When we expected a positive correlation (with *Index 1*), the *P* value was calculated as 1- (Number of permutations where the observed correlation coefficient was greater than the permuted value /Number of permutations). When we expected a negative correlation (with *Index 3*), the *P* value was calculated as 1- (Number of permutations where the observed correlation coefficient was less than the permuted value /Number of permutations). Significant correlations are marked in bold.

Index	Song metric	$R_{observed}$	Average of $R_{permuted}$	No. of permutations where observed $R_{observed} > R_{permuted}$	*P*
Index 1	Delivery	0.5367	-0.0027	951/1000	**0.0490**
	Switching	0.0676	0.0094	524/1000	0.4760
Index 3	Delivery	-0.5915	-0.0233	966/1000	**0.0340**
	Switching	0.0249	-0.0255	568/1000	0.4320

Appendix 2. Mantel tests (1000 permutations, Pearson' correlation coefficient) between absolute differences in the average song characteristics and the co-occurrence indices (using *Index 5*). Significant correlations are marked in bold. There were no strong correlations.

Comparison	*N*	*R*	*P (two-sided)*
Difference in song duration and *Index 5*	233	0.1577	**0.0010**
Difference in song low frequency and *Index 5*	233	0.1440	**0.0010**
Difference in song bandwidth and *Index 5*	233	0.0252	0.2070
Difference in song trill rates and *Index 5*	233	0.0410	0.1530
Difference in song frequency inflections and *Index 5*	233	0.0590	**0.0250**