

## Song-type sharing in a population of Song Sparrows in the eastern United States

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**ABSTRACT.** Male Song Sparrows (*Melospiza melodia*) sometimes interact with neighboring territory owners by song-type matching or repertoire matching. In some Song Sparrow populations, levels of song sharing are high and most neighbors can interact by matching, but levels of song sharing are much lower in other populations, limiting the degree to which males can match their neighbors. One explanation for variation in sharing levels is that the importance of song-type and repertoire matching, and therefore the extent of song sharing, varies geographically in North America, being greater in western populations than eastern populations. However, to date, two studies of eastern populations have provided conflicting evidence concerning levels of song sharing by Song Sparrows. Thus, we measured sharing of whole songs and introductory phrases of songs between males with adjacent territories in another population of Song Sparrows in the eastern United States (North Carolina), near the eastern and southern limits of the species' breeding range. Males ( $N = 17$ ) in our study shared an average of only 8.7% of their song types with neighbors, and more than half of neighbor pairs shared no whole songs. Sharing of introductory phrases was more common (mean = 22.8%). The level of whole song sharing in our study is the second lowest yet reported for any Song Sparrow population, supporting the hypothesis that sharing is generally lower in eastern than in western populations.

**RESUMEN. Tipo de canto compartido en una población de *Melospiza melodia* en la parte este de los Estados Unidos**

Los machos del Gorrión melódico (*Melospiza melodia*) en ocasiones interaccionan con los dueños de territorios vecinos, pareando la canción tipo o el repertorio. En algunas poblaciones del gorrión, el nivel de canciones compartidas es alto y muchos vecinos pueden interactuar pareando el mismo, pero en otras poblaciones, el nivel de canciones compartidas es mucho menor, limitando el grado de pareo del canto de sus vecinos. Una explicación para la variabilidad en el nivel de compartir es que la importancia del tipo de canto, pareo del repertorio, y por ende la extensión de compartir las vocalizaciones, varía geográficamente en Norte América, siendo mayor en las poblaciones del oeste que en las del este del continente. Sin embargo, al presente, dos estudios de poblaciones del este han provisto evidencia conflictiva sobre los niveles del compartir del canto en el Gorrión melódico. Por ende, medimos el compartir de canciones completas y de frases de introducción entre machos de territorios adyacentes en otra población del este, en Carolina del Norte, cerca del límite este y sur del área de reproductiva geográfica de esta especie. Los machos ( $N = 17$ ) en nuestra área de estudio tan solo compartieron un promedio del 8.7% de su canto con los vecinos, y más de la mitad de los vecinos, no compartieron nada de la canción. El compartir las frases introductorias resultó más común (promedio = 22.8%). El nivel de compartir la canción completa, es el segundo más bajo informado para población alguna del Gorrión melódico, lo que apoya la hipótesis, de que el compartir del canto, por lo general, es más bajo en las poblaciones del este que en las del oeste.

*Key words:* animal communication, bird song, *Melospiza melodia*, song matching

Shared song types play an important role in signaling interactions in songbirds in general and Song Sparrows (*Melospiza melodia*) in particular. Song-type matching, where one singer replies to a rival with the same song type the rival has just sung, is a common form of interaction in some populations of Song Sparrows (Stoddard et al. 1992, Anderson et al. 2005) and in many other species of songbirds (Krebs et al. 1981,

Schroeder and Wiley 1983, Falls 1985, Rogers 2004). Song Sparrows also interact using repertoire matching, where one singer replies to a rival using a shared song type other than the one the rival has just sung (Beecher et al. 1996, 2000a). Song-type matching has been hypothesized to be an aggressive signal in songbirds (Krebs et al. 1981, Searcy and Beecher 2009) and, in some Song Sparrow populations, song-type matching and repertoire matching function together as components of a hierarchy of threatening signals (Burt et al. 2001, Beecher and Campbell 2005,

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Akçay et al. 2013). Song sharing facilitates matching, but may also function in other ways, for example, as a signal of quality to other males (Rothstein and Fleischer 1987) or to females (Poesel et al. 2012).

Song sharing has previously been examined in other Song Sparrow populations. In general, sharing seems to be low in eastern populations (Borror 1965, Harris and Lemon 1972, Hughes et al. 1998, Stewart and MacDougall-Shackleton 2008) and high in western populations (Cassidy 1993, Hill et al. 1999, Wilson et al. 2000, but see Baker 1983). Among western populations, song sharing between pairs of neighbors averaged 33% in British Columbia (Cassidy 1993), 17% in California (Wilson et al. 2000), and 24% and 37% in two Washington populations (Hill et al. 1999), whereas sharing averaged 3% in an eastern population in Pennsylvania (Hughes et al. 1998). In addition, the number of songs males shared with neighbors was found to be positively correlated with measures of territory tenure (and thus with fitness) in two western populations (Beecher et al. 2000b, Wilson et al. 2000), but not in an eastern one (Hughes et al. 2007). These results suggest that natural selection has favored song sharing by Song Sparrows in western populations, but not eastern populations.

The hypothesis of a simple east/west difference in sharing levels of Song Sparrows was cast into doubt, however, when Foote and Barber (2007) measured song sharing in a population of Song Sparrows in eastern Canada (Nova Scotia) and found mean sharing between pairs of neighboring males to be 33%, one of the highest levels of sharing yet found in any Song Sparrow population. The high level of sharing in an eastern Canada population suggests that the low sharing level in a Pennsylvania population (3%, Hughes et al. 1998) might not be representative of eastern populations as a whole. Thus, one objective of our study was to determine if the amount of song sharing in another eastern population of Song Sparrows is more similar to the low level found in Pennsylvania or the high level in Nova Scotia.

Playback experiments in both western (Burt et al. 2002) and eastern (Anderson et al. 2005) North America have revealed that male Song Sparrows not only match whole songs, but also match songs that share only the introductory phrase with one of their own song types. Thus,

sharing of introductory phrases may to some extent substitute for whole song sharing in interactions between male Song Sparrows. Providing some support for this hypothesis, Hughes et al. (1998) found that sharing of introductory phrases was more common in their Pennsylvania population than was sharing of whole songs. To further examine the possibility that matching introductory phrases might be important in Song Sparrow signaling, a second objective of our study was to measure sharing of introductory phrases in another eastern population.

## METHODS

We measured song sharing with adjacent neighbors for 17 male Song Sparrows in Forest Hills Park in Durham, North Carolina (35.980N, 78.914W). Territories of Song Sparrows were located mainly in riparian vegetation along a small stream. Recordings were made from 7 to 28 May 2010 using a digital recorder (PMD 660, Marantz, Mahwah, NJ) and a microphone (ME62, Sennheiser, Wedemark, Germany) in a parabolic reflector (330, Sony Corporation, Tokyo, Japan).

Male Song Sparrows have repertoires of ~5–13 song types, with some geographic variation in mean repertoire sizes (Peters et al. 2000). Previous work indicates that recording 300 songs is sufficient to obtain a male's complete repertoire (Searcy et al. 1985). To classify songs to song types, we produced spectrograms of all recorded songs using Syrinx (J. M. Burt, [www.syrinxpc.com](http://www.syrinxpc.com)). Spectrograms for each male were visually sorted into song types to determine repertoire sizes. As a check on whether we obtained full repertoires, we calculated the Pearson product moment correlation between the number of songs recorded and repertoire size. Male Song Sparrows vary successive renditions of songs within song types, most often by adding, subtracting, or altering notes and syllables at the ends of songs (Saunders 1924, Stoddard et al. 1988, Podos et al. 1992). For each male, we identified all variants and counted the number of times each variant of each song type was represented in our sample. We then identified the most common variant of each song type in each male's repertoire and used these most common variants in our assessments of song sharing. Basing assessment of song sharing on the most common variant should provide a

more accurate assessment of sharing than basing estimates on randomly chosen variants.

Song Sparrow songs are made up of two types of phrases: trills and note complexes (Mulligan 1963, Podos et al. 1992). A trill is a series of repetitions of a single syllable, whereas a note complex is a group of un-repeated notes. Songs usually begin with a trill, and the two phrase types alternate thereafter. Given the complexity of Song Sparrow songs, determining if two song types are similar enough to be considered shared is difficult, and various criteria have been used in making such judgments (Cassidy 1993, Hughes et al. 1998, Hill et al. 1999). We used the criteria proposed by Hill et al. (1999) and subsequently adopted by Foote and Barber (2007), i.e., two song types are considered shared if they share two-thirds or more of their phrases. Trills are considered shared if the component notes are similar in shape, frequency, and timing. Note complexes are considered shared if they share half or more of their notes. Judgments about sharing were made independently by two observers, and any disagreements were resolved by consulting a third independent observer. Hill et al. (1999) provided sonograms illustrating examples of songs that were shared and not shared based on the above criteria.

The sharing metric we used is the sharing index  $2N_i/(R_1 + R_2)$ , where  $N_i$  is the number of song types shared by males 1 and 2, and  $R_1$  and  $R_2$  are the numbers of song types in their respective repertoires (Harris and Lemon 1972, McGregor and Krebs 1982). For each of our 17 focal males, we estimated sharing with each neighbor with an adjacent territory and whose repertoire we also recorded. Finally, we calculated the average sharing index value for each male across his neighbors, so that the final number of sharing values was equal to the number of subjects.

## RESULTS

We recorded an average of 354 songs from each male Song Sparrow (range = 306–498, Table 1). Mean repertoire size was 9.6 song types (range = 7–12). Repertoire size was not correlated with the number of songs recorded ( $r = -0.09$ ,  $P > 0.10$ ), suggesting that we recorded enough songs to obtain complete repertoires of our focal males.

Males sang an average of 5.0 variants (range = 1.8–11.3) of each song type (Table 1). Although these numbers suggest considerable within-song-type variation, one variant tended to dominate for each song type. On average, the most common variant constituted 60% (range = 42–85%) of the renditions of any given song type (Table 1).

Male Song Sparrows at our site shared few whole songs with neighbors (Table 1), with a mean sharing index per male of 0.087 (range = 0–0.239). On average, males shared one or more whole songs with fewer than half of their neighbors (Table 1). Three males shared no whole songs with any neighbor, and most males (14 of 17) shared no whole songs with at least one neighbor. The highest sharing index between any pair of neighbors was 0.40.

Male Song Sparrows were more likely to share the first trills of their songs (Table 1), with a mean sharing index per male of 0.228 (range = 0.081–0.436). Males shared at least one first trill with more than 80% of their neighbors (Table 1), and no male failed to share a first trill with at least one neighbor.

## DISCUSSION

Male Song Sparrows in our North Carolina population shared an average of 8.7% of their songs with neighbors, a somewhat higher percentage than in another eastern population in Pennsylvania (3%; Hughes et al. 1998), but considerably lower than in a third eastern population in Nova Scotia (33%; Foote and Barber 2007). The North Carolina population has the second lowest sharing level of the seven Song Sparrow populations for which such measurements have been made (Table 2), and a lower sharing level than in any western population.

Our results provide a more complete picture of geographic variation in song-type sharing in Song Sparrows, but do not produce convincing support for any of the hypotheses proposed to explain such variation. These hypotheses can be characterized as offering either proximate or ultimate explanations of sharing levels. Proximate hypotheses suggest some aspect of life history or demography that varies between populations and might affect sharing levels directly, e.g., by affecting the stability of associations between territory owners. Song Sparrows incorporate in

Table 1. Repertoire sizes, variants per song type, number of neighbors, and sharing of whole songs and first trills for 17 male Song Sparrows in Durham, North Carolina.

Male	No. of songs recorded	No. of song types	Variants per song type	Proportion most common variant	No. of neighbors	Whole song sharing index	Percentage of neighbors sharing $\geq 1$ whole song	First trill sharing index	Percentage of neighbors sharing $\geq 1$ first trill
1	342	10	3.3	0.66	1	0.21	100	0.26	100
2	373	9	7.9	0.51	2	0.11	50	0.13	50
3	331	12	3.9	0.55	2	0.00	0	0.11	50
4	328	7	4.6	0.60	2	0.00	0	0.17	100
5	324	8	4.7	0.57	4	0.06	25	0.23	75
6	338	11	4.9	0.55	6	0.05	33	0.11	67
7	368	9	3.2	0.64	6	0.04	17	0.15	67
8	395	9	11.3	0.42	4	0.24	100	0.39	100
9	392	11	1.8	0.85	5	0.10	60	0.28	100
10	328	10	5.6	0.55	4	0.17	75	0.32	75
11	330	11	4.0	0.64	2	0.05	50	0.10	100
12	306	10	7.0	0.46	3	0.20	100	0.44	100
13	383	9	7.5	0.42	4	0.02	25	0.08	75
14	328	12	3.1	0.82	4	0.12	75	0.34	100
15	317	8	3.7	0.63	4	0.03	25	0.24	100
16	335	8	3.9	0.64	3	0.00	0	0.17	67
17	498	9	3.8	0.63	4	0.10	50	0.36	100
Mean	354	9.6	5.0	0.60	3.5	0.09	46	0.23	84
SD	46	1.5	2.3	0.12	1.4	0.08	35	0.11	19

Table 2. Measures of whole song-type sharing relative to migratory status, latitude, and longitude in seven populations of Song Sparrows.

Location	Sharing level	Repertoire size	Migratory status	Latitude	Longitude	Reference
Washington (Gold Creek)	37%	8.0	Altitudinal migrants	47°	121°	Hill et al. (1999)
Nova Scotia	33%	9.2	Partial migrants	45°	64°	Foote and Barber (2007)
British Columbia	33%	8.2	Residents	49°	123°	Cassidy (1993)
Washington (Seattle)	24%	8.2	Residents	48°	122°	Hill et al. (1999)
California	17%	9.6	Residents	33°	117°	Wilson et al. (2000)
North Carolina	9%	9.6	Partial migrants	36°	79°	This study
Pennsylvania	3%	7.9	Partial migrants	42°	80°	Hughes et al. (1998)

their repertoires songs learned after natal dispersal and thus after young males have moved to areas where they will establish a territory (Beecher et al. 1994, Nordby et al. 1999). Once adulthood is reached (at 1 yr), males do not change their repertoires (Searcy et al. 1985, Cassidy 1993, Nordby et al. 2002). Because adult males cannot adjust their repertoires to match those of new neighbors, movement of territory owners between breeding seasons (breeding dispersal) should lower sharing levels. A simulation model indicates that increased mortality of territory owners might also reduce sharing (Goodfellow and Slater 1986).

One life history trait that may affect the stability of territorial associations is seasonal migration. Migratory populations of terrestrial birds do not necessarily have higher adult mortality than resident populations (Sandercock and Jaramillo 2002), but do tend to exhibit greater breeding dispersal (Paradis et al. 1998). If breeding dispersal distances are greater in migratory populations, then levels of song sharing should be lower. Lower sharing in migratory than resident populations has previously been found in some within-species comparisons (Ewert and Kroodsma 1994, Yoon et al. 2013) and by an across-species comparison of New World

sparrows and their relatives (Handley and Nelson 2005). In Song Sparrows, however, studies of three resident populations have revealed a mean sharing level of 25%, which is similar to the mean sharing level of 21% for the four migratory or partially migratory populations (Table 2). Thus, variation in song-type sharing among Song Sparrow populations is not explained by migratory status.

A second proximate factor that might affect sharing is breeding latitude. Survival rates may be lower for populations at higher latitudes, resulting in more turnover. In addition, the short duration of breeding seasons at high latitudes may limit the opportunity for males to learn songs from territorial neighbors (Handley and Nelson 2005). Given these factors, sharing might be expected to decrease with latitude. However, the results of studies to date (Table 2) reveal a weak positive correlation between sharing and latitude (Spearman's rank correlation = 0.63).

A final proximate factor hypothesized to affect sharing is song repertoire size (Handley and Nelson 2005). How repertoire size should affect sharing is not intuitively obvious, but computer simulations (Williams and Slater 1990) indicate that, under realistic conditions, larger song repertoires lead to lower sharing between neighboring males. Our results support the predicted effect, with repertoire sizes relatively large in our study population (9.6 song types per male) and sharing relatively low (8.7%). The predicted pattern does not hold across studies (Table 2), however, with essentially no correlation between repertoire size and sharing ( $r_s = -0.14$ ).

Ultimate explanations of sharing levels are hypotheses about selective factors affecting the evolution of sharing. Selection might alter sharing by adjusting aspects of song learning, such as its timing relative to dispersal or the propensity to copy whole songs versus parts of songs. Consistent with ultimate hypotheses about song sharing, there is evidence of variation in learning strategies among Song Sparrow populations. Studies indicate that copying of parts of songs predominates in eastern Song Sparrows (Marler and Peters 1987, 1988), whereas copying of whole songs predominates in western Song Sparrows (Beecher et al. 1994, Nordby et al. 1999). Unfortunately, this difference can also be explained as an artifact of how learning has been studied, using captive birds for eastern Song

Sparrows (Marler and Peters 1987, 1988) and free-living birds for western ones (Beecher et al. 1994, Nordby et al. 1999).

Selection may favor song-type sharing in some Song Sparrow populations, but not others. Song sharing levels affect the ability of singers to interact through song-type matching. Although matching occurs in both western and eastern Song Sparrows (Stoddard et al. 1992, Anderson et al. 2005), it appears to be more important as a signal in western populations. Matching has been found to be a reliable signal of aggressive intentions in a western population of Song Sparrows (Akçay et al. 2013), whereas matching was not predictive of aggressive escalation in an eastern population (Searcy et al. 2006, 2013). Thus, sharing and matching may play a more important role in territorial signaling in western populations than eastern ones. As predicted by this hypothesis, the level of sharing between males and their territorial neighbors was found to be correlated with territory tenure in two western populations (Beecher et al. 2000b, Wilson et al. 2000), but not in an eastern population (Hughes et al. 2007). The low level of sharing we found in North Carolina supports the hypothesis that selection for sharing is weaker in eastern populations, but the hypothesis is undermined by the high sharing found in another eastern population in Nova Scotia (Foote and Barber 2007). To further test this hypothesis, sharing levels should be examined in additional populations in conjunction with studies of the importance of matching interactions and the relationship between sharing and territory tenure.

In our study, sharing of introductory phrases was more common than sharing of whole songs, as also reported in another eastern population (Hughes et al. 1998). Song Sparrows have been found to match playback of partially shared songs in both western and eastern populations (Burt et al. 2002, Anderson et al. 2005), so sharing of introductory phrases or other parts of songs may to some extent substitute for sharing of whole songs. However, it has not been shown for any population that partial matching is a reliable signal of aggression, and sharing of introductory phrases was not correlated with territory tenure in the one (eastern) population where this relationship has been examined (Hughes et al. 2007).

Overall, our finding of relatively low levels of song sharing in an eastern population of Song

Sparrows is consistent with a previously proposed pattern of lower song sharing in eastern populations compared to western populations in this species. Further work on sharing in additional populations is needed to identify the explanation for variation in levels of sharing across populations.

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