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SURVIVAL AND SONG-TYPE SHARING IN A SEDENTARY SUBSPECIES OF THE SONG SPARROW[1]

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Abstract. The extent and spatial pattern of song-type sharing among neighboring males in one subspecies of Song Sparrow, *Melospiza melodia cooperi,* were examined in two San Diego County populations. Repertoire size averaged 9.6 song types per male (range 7 to 14). Song-type sharing was greatest between neighbors and declined with distance between territories. Adjacent neighbors shared an average of 22% of their song types. Variation in the amount of sharing between adjacent territory owners was high, ranging from 0% to 86% repertoire overlap. Results are consistent with the expected pattern produced by age-restricted learners that attempt to establish territories near tutors. The probability of a male surviving and remaining on his territory through the breeding and nonbreeding season increased as the fraction of song types shared with adjacent neighbors increased. The amount of song-type sharing may therefore be an indicator of a male's competitive ability to obtain a preferred territory near his tutors, or it may determine a male's effectiveness in using shared and unshared song types to communicate aggressive intentions.

Key words: Melospiza melodia cooperi, *repertoire overlap, song learning, Song Sparrow, territory tenure.*

INTRODUCTION

Many songbirds learn their repertoire of songs by copying whole song types from neighbors or other adults (Kroodsma 1996). This learning strategy often results in song-type sharing among neighboring birds, or repertoire overlap in species with multiple song types per male. The extent of repertoire overlap varies enormously among species. Neighboring males share all or most of the song types in species such as the Tufted Titmouse (*Baeolophus bicolor*; Schroeder and Wiley 1983) and Village Indigobird (*Vidua chalybeata*; Payne 1985). Intermediate levels of repertoire overlap have been found in species such as the Great Tit (*Parus major*; McGregor and Krebs 1989) and American Redstart (*Setophaga ruticilla*; Lemon et al. 1994). Whole song-type sharing, although present, is rare (< 5%) in migratory populations of Eastern Towhees (*Pipilo erythrophthalmus*; Ewert and Kroodsma 1994) and Sedge Wrens (*Cistothorus platensis*; Kroodsma et al. 1999).

Inter- and intraspecific variation in the level of song-type sharing is attributed to different learning strategies, timing and duration of the critical learning period, seasonal migration, and dispersal patterns (Slater 1989). The spatial pattern of song-type sharing with distance between males is indicative of these strategies. When open-ended learners modify their repertoire of song types to contain neighbor song types, there is little variation in the level of song-type sharing among close neighbors and sharing falls off rapidly with distance (Fig. 1a). The Great Tit (McGregor and Krebs 1982, 1989) and American Redstart (Lemon et al. 1994) show this type of pattern. A second spatial pattern is characterized by moderate but variable sharing among close neighbors and a general linear decline with distance (Fig. 1b). This pattern can arise in age-restricted learners that preferentially attempt to establish territories close to their tutors if vacancies arise but otherwise disperse farther. Sedentary Washington state Song Sparrows (*Melospiza melodia morphna*) are believed to learn and disperse in this way (Beecher 1996). Other species showing this pattern include the Bewick's Wren (*Thryomanes bewickii*; Kroodsma 1974) and *Thryothorus* wrens (Morton 1987, Molles and Vehrencamp 1999). The third type of distribution is expected when there is either non-ran-

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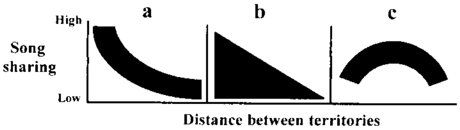

FIGURE 1. Three models for the relationship between the repertoire overlap of two territorial males in a population and the distance between their territories. See text for an explanation of the factors producing each pattern.

dom dispersal in age-restricted learners or active avoidance of sharing with close neighbors in open-ended learners. Sharing is high at intermediate distances and low at both shorter and greater distances (Fig. 1c). This pattern has been found in the Cirl Bunting (*Emberiza cirlus*; Kreutzer 1979), Common Nightingale (*Luscinia megarhynchos*; Hultsch and Todt 1981), and a Cactus Finch (*Geospiza conirostris*; Grant 1984).

Little evidence exists for a fitness advantage to males having higher sharing levels with their neighbors. Payne (1982, 1983) found that yearling male Indigo Buntings (*Passerina cyanea*) who copied their single song type from an adult neighbor had higher survival and reproductive success than yearlings who did not copy. However, buntings are open-ended learners with the ability to change their song in different social and ecological contexts. Males are more likely to copy their neighbors and maintain residency in competitive, high-quality habitats, but fail to copy and sometimes abandon territories in low-quality habitats (Payne et al. 1988). McGregor and Krebs (1984) and Cosens and Sealy (1986) found no effect of song-type sharing level on reproductive success in Great Tits and Yellow Warblers (*Dendroica petechia*), respectively, both age-unrestricted learners. Female Great Reed Warblers (*Acrocephalus arundinaceus*) could be using song element sharing to discriminate against immigrant males (Bensch et al. 1998). Species with moderate to high levels of song-type sharing clearly use matching song types in strategic ways during countersinging, and song-type matching is associated with subsequent aggressive or dominant behavior in several species (Lemon 1974, Kroodsma 1979, Krebs et al. 1981).

The Song Sparrow (*Melospiza melodia*) has been characterized as a species with low whole-song sharing, although song elements are often shared (Hughes et al. 1998 and references therein). Laboratory studies of song learning indicate that Song Sparrows are age-restricted learners that often improvise new song types by combining elements of their tutors' songs (Mulligan 1966, Marler and Peters 1987). However, males of sedentary populations in the Pacific Northwest copy whole songs and share several song types on average with their neighbors (Beecher et al. 1994, Nordby et al. 1999). Substantial song-type sharing also has been reported in southern California populations, but sharing between neighbors has never been rigorously measured (Eberhardt and Baptista 1977, Nielsen and Vehrencamp 1995). Our objectives were to quantify the fraction of shared song types between male Song Sparrows in a southern Californian subspecies (*M. m. cooperi*), examine how sharing levels varied with distance between territories, and evaluate whether sharing level was related to repertoire size, pairing status, territory size, and territory tenure.

METHODS

We determined song-type repertoires of male Song Sparrows from two non-migratory San Diego County populations separated by approximately 20 km. One population was located in the Los Peñasquitos Canyon Preserve (LPCP). Sparrow territories were aligned along a creek bed containing bulrushes (Cyperaceae), cattails (Typhaceae), and mule fat bushes (*Baccharis glutinosa*). The heavily grazed flood plain habitat on both sides of the creek did not support breeding territories of Song Sparrows, although floaters occasionally sang from these areas. Although the population was studied from 1989–1993, accurate information on territory location, repertoire size, and survival was only available for the eight contiguous color-banded males monitored in 1991. The second population was located in Kit Carson Park, Escondido (KCP). We color-banded and monitored 16 males between January and June of 1997, 1998, and 1999. Birds defended territories along pond banks occluded by cattails and gum trees (*Eucalyptus globulus*). The habitat on three sides of the study area consisted of mowed grass and *Eucalyptus* trees, marginal habitat for Song Sparrows, but the fourth side was contiguous with an extensive freshwater marsh containing a high density of Song Sparrows. We located territory boundaries at both sites by observing disputes

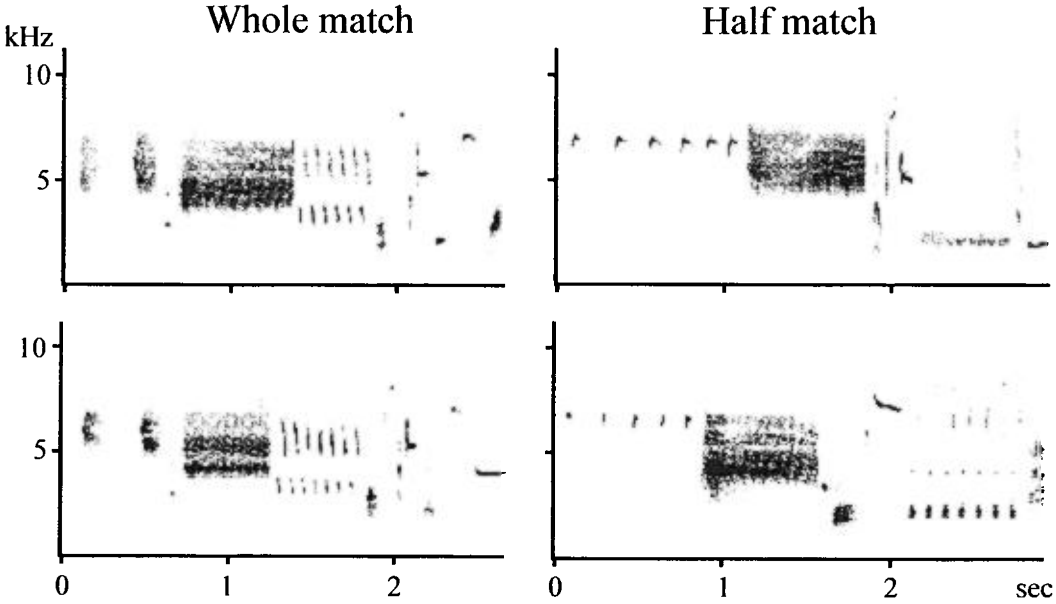

FIGURE 2. Examples of song-type matches between two males. Left: whole match. Right: half match.

between neighbors and intrusions by floaters. At KCP, adjacent territory centers were separated by approximately 47 m and territory size averaged 0.114 ± 0.044 ha.

We recorded a minimum of 300 songs from each bird to obtain complete repertoires as recommended for this species (Searcy et al. 1985). Recordings were made with a Sennheiser MKH816 shotgun microphone and either a Marantz PMD420 cassette tape recorder or a Teac DA-P20 digital tape recorder. Spectrograms of all songs were produced using either SoundEdit Pro (Walker 1991) or Canary (Charif et al. 1995) sound analysis software. Songs were grouped into song types based on possession of a common introduction plus other internal notes and occurrence within the same bout. Completeness of repertoires was verified by plotting the cumulative number of song types encountered against the number of songs recorded. Cumulative song types reached an asymptote from the 200th to 300th song in most cases. We found no evidence of new song types in birds that were monitored for two or more consecutive years. The song types of each bird were visually compared to the song type of every other bird by at least two people to determine whether the songs were matching types. Two song types were considered whole matches if they shared at least two thirds of the total number of phrases. If the song types shared between one half and two thirds of the phrases, we considered them half matches (Fig. 2). Both whole and half matches were required to share the same introduction notes. Our criteria are consistent with the criteria employed by Hughes et al. (1998) and Hill et al. (1999) for other Song Sparrow subspecies.

We assessed the spatial pattern of repertoire overlap at the two sites by comparing repertoire overlap and distances between territory owners. Repertoire overlap was computed for every pair of males in the population using the standard song sharing index $S = 2N_S/(R_1 + R_2)$, where N_S is the number of song types two birds share and R_1 and R_2 are the birds' repertoire sizes (McGregor and Krebs 1982). The sharing index was calculated using both whole matches only and the sum of whole matches (each scored as 1.0) and half matches (each scored as 0.5). The distance between two males was measured as the number of territories separating them (adjacent neighbors were separated by one territory). The significance of the sharing versus distance relationship in each study year was tested with Mantel correlation analysis using Permute! 3.4 with 4,999 permutations (Philippe Casgrain; http://alize.ere.umontreal.ca/~casgrain/en/labo/permute/).

Annual survival of focal males was monitored to determine whether territory tenure was related to the level of sharing with neighbors. Males

TABLE 1. Song sharing indices between adjacent neighbors and between all territorial male Song Sparrows in two populations of San Diego County.

Population	Whole and half matches			Whole matches		
	Mean	Min	Max	Mean	Min	Max
Adjacent neighbors						
LPCP 1991	0.242	0.067	0.381	0.207	0.000	0.381
KCP 1997	0.167	0.000	0.864	0.123	0.000	0.727
KCP 1998	0.243	0.000	0.864	0.182	0.000	0.875
All males						
LPCP 1991	0.153	0.000	0.474	0.133	0.000	0.421
KCP 1997	0.069	0.000	0.864	0.044	0.000	0.727
KCP 1998	0.123	0.000	0.864	0.086	0.000	0.750

studied in a given spring and summer breeding season were scored as surviving one year if they were present on their territories at the beginning of the following breeding season (March). Males not present the following March were considered dead or displaced. We also examined the relationships among survival, repertoire size, pairing status, territory size, and repertoire overlap. For this analysis, we computed an average value of repertoire overlap between each male and his immediately adjacent neighbors (usually two) using the whole- plus half-match sharing index. Seven males banded at KCP in 1997 that survived to the next breeding season were included in the 1998 cohort, because most had acquired new neighbors. We performed logistic regression analyses on JMP 3.2 (SAS Institute 1997) when the dependent variable consisted of two categories such as survived and died, and report the whole-model likelihood-ratio χ^2 statistic. All other statistical tests were analyzed with StatView 5.0 (SAS Institute 1998). Nonparametric tests were used when variables could not be transformed to meet the distribution requirements of parametric tests. All tests are two-tailed and are considered significant at the 0.05 level. We report means ± SD throughout the paper.

RESULTS

Mean repertoire size for combined years and sites was 9.6 ± 1.7 song types. Repertoire size did not differ significantly between the LPCP site (8.9 ± 1.5 song types, range 7 to 12) and the KCP site (9.9 ± 1.7 song types, range 7 to 14; t-test, $t_{20} = 1.49$, $P = 0.15$). Repertoire overlap between adjacent neighbors for the combined years and sites was approximately 22% (Table 1); 17% was attributed to whole-song matches, and 5% to half matches. There were only three birds, one per year, that did not share whole songs with any immediate neighbors. In two of those three cases, the male shared whole songs with other nearby males. Repertoire overlap among all territorial males in a given population averaged 12% (9% whole and 3% half matches) (Table 1). Unique song types (those that were not shared with any other bird in the population) comprised an average of 29.6% of a male's repertoire in the LPCP population and 28.6% of the repertoire at KCP (t-test, $t_{20} = 0.094$, $P = 0.93$).

We found a significant negative correlation between the percentage of song types shared between two males and their proximity at all three site-years (LPCP 1991: Mantel $r = -0.41$, $P < 0.05$; KCP 1997: $r = -0.32$, $P < 0.05$; KCP 1998: $r = -0.40$, $P < 0.005$; see Fig. 3). Repertoire overlap between adjacent neighbors showed a large degree of variation (LPCP 1991: CV = 0.95; KCP 1997: CV = 1.50; KCP 1998: CV = 1.48) that ranged from 0 to 47% at LPCP and from 0 to 86% overlap at KCP. At LPCP in 1991, one of seven pairs of adjacent males shared no whole songs. Non-sharers at KCP numbered 5 of 13 and 7 of 16 male pairs in 1997 and 1998, respectively.

At both sites combined, the probability of territory owners surviving until the onset of the next breeding season was 64.5% ($n = 31$ bird-years). The probability of surviving increased significantly as the average repertoire overlap with adjacent neighbors increased (Logistic likelihood ratio, $\chi^2_1 = 6.26$, $P < 0.02$). To provide a more heuristic sense of the magnitude of the survival effect, males sharing less than the me-

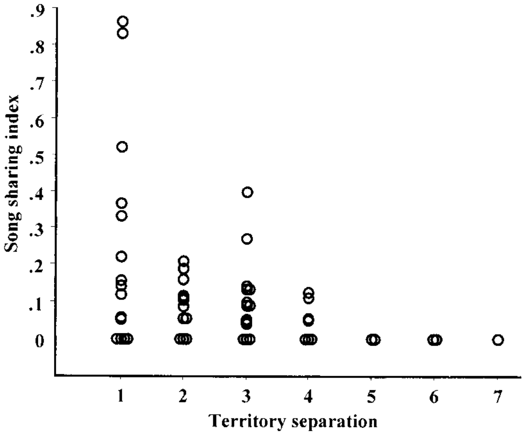

FIGURE 3. Song-sharing index, or repertoire overlap, between pairs of territorial males versus the number of territories separating them in the KCP population in 1998. Overlapping points have been shifted right or left for clarity.

dian average fraction of song types with their neighbors (average $S < 0.2$) had a 43% chance of survival compared to 82% survival for males with higher repertoire overlap (average $S \geq 0.2$).

Because an earlier study of Song Sparrows found that repertoire size was positively associated with territory tenure (Hiebert et al. 1989), we examined the role of this possibly confounding factor. Although a bird's average level of sharing with his neighbors was significantly correlated with his repertoire size ($r = 0.45$, $n = 24$, $P < 0.05$), there was no relationship between repertoire size and annual survivorship in our population (Logistic likelihood ratio, $\chi^2_1 = 0.0004$). Neither pairing status nor territory size were related to survival, repertoire size, or repertoire overlap (all P-values > 0.15). Age does not appear to be a confounding variable, because repertoire size and composition do not change with age in this species (Hiebert et al. 1989). We observed a slight but nonsignificant increase in mean repertoire overlap with neighbors for the seven KCP males present in both years (from 0.212 in 1997 to 0.235 in 1998; paired t-test, $t_6 = 0.58$). Thus sharing level is the only significant correlate of territory tenure in our populations.

Of the 11 male disappearances, 2 occurred during the March–June breeding period and the remainder occurred during the July–February nonbreeding season. Although we cannot rule out the possibility that some of these males moved to new sites, territory relocation of established males is rare in Song Sparrows and documented cases involved short-distance movements one or two territories away (Arcese 1989, M. Beecher, pers. comm; this study). Common territory acquisition strategies employed by young birds are to squeeze between two established territorial males separated by a strip of marginal habitat, take over a portion of an established male's territory, or subdivide the territory of a male that has disappeared. These males vigorously defend their small territories and often acquire mates and reproduce. However, only those young males with high repertoire overlap persisted through the breeding and subsequent nonbreeding period, and then typically enlarged their territory to the normal size by the beginning of the next breeding season.

DISCUSSION

Despite the assertion that the Song Sparrow neither copies whole song types nor shares song types with neighbors (Hughes et al. 1998), western U.S. populations in fact exhibit significant levels of song-type sharing among neighboring males. San Diego, California, populations exhibit somewhat lower mean sharing levels between adjacent neighbors (17–24%) than those found in Seattle, Washington (21–40%), but higher than those reported for Pennsylvania (3%) (Hughes et al. 1998, Hill et al. 1999). Some additional West Coast subspecies also show substantial song sharing, but others do not (Vehrencamp et al., unpubl. data). Subspecific differences in song sharing may therefore vary as much as morphology in this widespread and highly differentiated species.

The microgeographic spatial pattern of song-type sharing in our two San Diego populations indicates that sharing levels are higher between close neighbors than between distant birds. The average level of song sharing falls off quickly with distance. In addition, there is a large variance in repertoire overlap between close neighbors. Some were found to share up to 86% of their repertoires, whereas others shared no song types. Because many males share few or no song types with neighbors, the pattern of sharing versus distance is more consistent with the dispersal and learning model of Figure 1b than with the one in Figure 1a.

The results of this study corroborate the observations of Beecher et al. (1994) and Nordby et al. (1999) that song learning occurs in a floater's home range before territory acquisition and that first-year males settling near their tutors share more song types with their neighbors than males dispersing farther. As in Seattle populations, San Diego males appear to copy whole song types from a set of adjacent tutor males during the first few months after fledging. The number of unique song types in our populations (29%) was higher than that reported for Seattle sparrows (8.7%). We concur that these unique song types are primarily a consequence of dispersal into the population by foreign birds rather than of song improvisation. The small size of our study populations may be partially responsible for the higher fraction of unique song types. San Diego Song Sparrows probably also prefer to learn common song types as described for Seattle sparrows (Beecher et al. 1994), and employ overproduction and selective attrition of types as in the Field Sparrow *Spizella pusilla* (Nelson 1992). Both strategies serve to maximize the likelihood that young males share songs with their neighbors.

The slightly lower sharing levels in San Diego compared to Seattle sparrows is most likely the result of quantitative rather than qualitative differences in territory turnover rates and dispersal distances. San Diego sparrows experience higher annual mortality and a patchier distribution of optimal habitat than Seattle birds (M. Beecher and J. Burt, pers. comm.). As long as there are always more yearling floaters than available vacant territories, an increase in adult mortality causing more territory openings is predicted to result in longer mean dispersal distances (McCarthy 1997). Longer dispersal distances lead to lower sharing levels in an age-restricted learner such as the Song Sparrow. These subspecies differences mirror the interpopulation differences we found between our two local populations (KCP had slightly lower sharing and higher annual mortality than LPCP).

The high variation in sharing levels among adjacent males indicates that territory establishment does not require birds to share songs. However, our data suggest that there is a strong effect of the number of songs a male shares with his neighbors on his ability to defend his territory in the long term. Similar survival effects have been found in Seattle sparrows (Beecher et al., in press). Although repertoire size was found to be correlated with age on Mandarte Island because of the attrition of young birds with small repertoires (Hiebert et al. 1989), the true determinant of territorial persistence may have been repertoire overlap which is correlated with repertoire size. McGregor et al. (1981) and Cosens and Sealy (1986) also reported positive correlations among repertoire size, repertoire overlap, and reproductive success in Great Tits and Yellow Warblers, but partial correlation analyses indicated that the true determinant of high reproductive success was repertoire size. Great Tits and Yellow Warblers, however, can learn to sing new song types as adults and can adjust repertoire overlap to the optimal level (sharing pattern depicted in Fig. 1a). Repertoire overlap does not appear to operate as a constraint on or predictor of reproductive success or survival in open-ended learners as it does in age-restricted learners.

There are at least three non-exclusive hypotheses for the association between sharing level and male survival in age-restricted learners. One hypothesis is that shared song types are required for effective territory defense. Song Sparrows strategically use their shared and unshared song types when responding to neighbors versus strangers (Beecher et al. 1996) and aggressive response is stronger to playback of shared than to unfamiliar song types (Nielsen and Vehrencamp 1995). Song-type matching is both a predictor of subsequent sender aggression and a stimulus that produces a strong aggressive approach response in receivers (Burt 1999, Vehrencamp et al., unpubl. data). Any male lacking the required vocabulary may be less effective at managing territorial conflicts and subsequently lose his territory.

Another hypothesis is that repertoire overlap with neighbors is an honest indicator of male quality, dominance, or fighting ability. This linkage will only occur if sharing level is inversely correlated with dispersal distance from the tutor-floater area, and if more capable males acquire closer territories. The inverse relationship between song sharing and dispersal distance has already been demonstrated for Song Sparrows (Nordby et al. 1999). Two factors could reduce the strength of the correlation: annual fluctuation in territory vacancies, and joint long-distance dispersal of several birds from the same tutor-floater area. Nevertheless, in sedentary populations of age-restricted learners with moderate to high levels of song-type sharing, sharing level should still be a reasonably reliable index of a bird's dispersal distance (Vehrencamp 2000). McCarthy's (1997) competitive dispersal model predicts that dominant competitors, like early dispersers in a sequential dispersal system, achieve shorter dispersal distances than subordinate competitors. Arcese and Smith (1985) showed that male Song Sparrows differ consistently in competitive ability at feeders, and that dominant first-year males are more likely to acquire and retain a territory than subordinate males. Furthermore, observations and playback experiments on our KCP sparrows indicate that non-song-sharing birds are aggressively harassed by their neighbors whereas song-sharing birds do not readily approach each other during vocal exchanges (Wilson and Vehrencamp, unpubl. data). The key predictions for the hypothesis that song sharing is an index of fighting ability are therefore met.

The third hypothesis is that birds are more successful in defending and maintaining a territory in a familiar neighborhood, resulting in a spurious correlation between song sharing and survivorship. In other words, song-sharing level is an index of dispersal distance, but it has no direct implications for a bird's quality or ability to vocally defend its territory. Evidence for such a familiarity effect has been suggested for the Florida Scrub-Jay (*Aphelocoma coerulescens*), a well-studied nonmigratory species with intense year-round competition for territorial space like western Song Sparrows. Both male and female scrub-jays that disperse $>$ 2 territories away from their natal territory exhibit a decrease in annual survivorship for the first two years as a breeder, compared to birds that disperse 0 to 2 territories away (Fitzpatrick et al. 1999). However, the reproductive success of these same birds does not decrease with distance dispersed, arguing against a role of quality or condition as a cause of the reduced survival. A major source of mortality in scrub-jays is predation during territorial displays and encounters. Birds dispersing close to home are familiar with both the habitat and the neighboring birds as a result of frequent pre-dispersal forays into these areas. Territorial disputes with known rivals may be less frequent or less intense than disputes with unfamiliar birds, and birds dispersing only one territory away experience little aggression along the border with their parents. Arcese and Smith (1985) provided evidence against a familiarity effect in territory acquisition for Song Sparrows. A group of early-hatching birds that were placed in captivity for most of the breeding season and denied the opportunity to interact with resident birds nevertheless succeeded in acquiring territories as well as their field-experienced age-mates. Thus, inherent dominance or competitive ability appears to play a stronger role than familiarity for territorial success in Song Sparrows.

In conclusion, the association between song sharing and survival in Song Sparrows is either a direct result of shared song types providing stronger threat signaling effectiveness, and/or an indirect consequence of more dominant yearlings gaining territories closer to their tutors. The differences in mean song-sharing level among the divergent subspecies of the Song Sparrow are likely to be an outcome of different degrees of competition for territorial space.

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