

## ORIGINAL ARTICLE

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## Song sharing in two populations of song sparrows (*Melospiza melodia*)

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**Abstract** Sharing song types with immediate neighbors is widespread in birds with song repertoires, and sharing songs may confer a selective advantage in some cases. Levels of song sharing vary between different geographical populations of several bird species, and ecological differences often correlate with differences in singing behavior; in particular, males in migratory subspecies often share fewer songs than males in resident subspecies. The song sparrow (*Melospiza melodia*) appears to fit this pattern: resident song sparrows in western North America generally share 20–40% of their repertoire (of about eight songs) with each neighbor, while migratory subspecies from eastern North America often share 10% or less. We compared song sharing in two populations within a single subspecies of song sparrow (*M. m. morphna*) in Washington State. These populations, separated by only 120 km, nonetheless differ in migratory tendencies and several other ecological and life history variables. We recorded complete song repertoires from 11 male song sparrows in a high-elevation, migrating population at Gold Creek in west-central Washington, and compared them to two samples ( $n = 15$  and  $n = 36$ ) from a coastal, resident population at

Discovery Park, Seattle, Washington. Despite major differences in habitat, population density, and migratory tendencies, song sharing among Gold Creek males was as high as that among Discovery Park males. In both populations, sharing was highest between immediate neighbors, and declined with distance. We conclude that at the within-subspecies level, neither migration nor population density affect song sharing in song sparrows, a song repertoire species.

**Key words** Song sharing · Song repertoire · Migratory · Resident · Song sparrow · *Melospiza melodia*

### Introduction

Geographic variation in the singing behavior of songbirds has attracted attention as an indicator of song function. If separate populations of a species sing differently, and if the change in singing styles parallels changes in ecological or social variables, the correlations can provide clues to the evolution of singing behaviors and the functions of song. Comparative studies between populations of a species, or between closely related species, can thus provide insights into the function of bird song that studies of one population in isolation cannot.

A promising area of research into song function is the sharing of song types between neighboring males. Much of the focus on song type sharing has concerned regional dialects involving sharing among all individuals in an area (e.g., Baker and Cunningham 1985). However, the scale at which interactions using song take place is between individuals, most often territorial neighbors, and sharing of song types between neighbors can be common even in non-dialect species (Schroeder and Wiley 1983; McGregor and Krebs 1989; Beecher et al. 1994b). Evidence for fitness benefits of song sharing is mixed. Indigo buntings (*Passerina cyanea*) that share songs with neighbors have higher reproductive success than buntings with songs that differ from their neighbors (Payne

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1982; Payne et al. 1988), and song sharing is correlated with mating success in brown-headed cowbirds (*Molothrus ater*; Dufty 1985), but such a relationship between song sharing and fitness has not been documented for other species. In fact, in large cactus finches (*Geospiza conirostris*), having the same song type as a neighbor sometimes correlates with lower reproductive success (Grant 1984).

Despite the paucity of studies relating song sharing to fitness, several indirect lines of evidence suggest there may be advantages to sharing song types with neighbors. First, many species with repertoires of multiple song types engage in matched countersinging with territorial neighbors using similar or identical song types, which is possible only when neighbors share songs. Two patterns have been noted: birds may respond to playback (or a singing neighbor) by answering with the same song type, called "type matching" (Verner 1965; Krebs et al. 1981; Falls 1985; Shackleton et al. 1991; Stoddard et al. 1992a), or they may respond to playback of a neighbor's song with a song matching not the playback but another song type shared between the two neighbors, called "repertoire matching" (Beecher et al. 1996). A second observation suggesting a value for shared songs is that species that can add and drop songs after their first summer often change their repertoires in ways that increase sharing with their neighbors (Payne and Payne 1977, 1993; Jenkins 1978; Payne 1985; McGregor and Krebs 1989; O'Loughlen and Rothstein 1993; Lemon et al. 1994). Tufted titmice (*Baeolophus bicolor*), which apparently do not add whole song types between years, do modify the details of songs in ways that increase the songs' similarity with neighbors' songs (Schroeder and Wiley 1983). Finally, recent evidence shows that songbirds in their first year may shape their repertoires by preferentially learning or retaining those songs that are most similar to their territorial neighbors (Nelson 1992; Bell et al. 1998; Nordby et al. 1999), a finding which has reawakened interest in sharing with neighbors as a factor in song learning.

Studies of sharing between neighbors in a repertoire species (where each male sings multiple song types) are more difficult than studies of some other aspects of song such as repertoire size, because sharing is harder to measure than repertoire size (see Discussion). Perhaps because of this difficulty, few comparative studies of song sharing have been undertaken. Two comparative studies have addressed population differences in song type sharing between neighbors, and they suggest a common cause for those differences. Each study contrasted a sedentary, dense population with a migratory, less dense population. In each study, sharing was lower in the migratory, less dense population. Resident (non-migratory) eastern towhees (*Pipilo erythrophthalmus*) in Florida have larger repertoires and share more song types with neighbors than do towhees in migratory populations that breed in New York and Massachusetts (Ewert and Kroodsma 1994). In a comparison between *Cistothorus* wrens, resident marsh wrens (*Cistothorus palustris*) and tropical resident sedge wrens (*C. platensis*)

share more with neighbors than do nomadic temperate sedge wrens (Kroodsma 1996; Kroodsma et al. 1998).

Thus, in *Cistothorus* wrens and eastern towhees, migratory behavior is associated with reduced song type sharing between neighbors. However, those results do not distinguish between proximate and ultimate causes for the correlation. Have birds in resident, dense populations evolved tactics to learn shared songs because shared songs are especially useful in defending a year-round territory against many close neighbors? Or is it simply that year-round exposure to the same tutors, or shorter natal dispersal in non-migrants cause the observed differences in song sharing, with no underlying genetic differences in the birds themselves? Laboratory tutoring experiments have shown that different subspecies of marsh wrens and white-crowned sparrows (*Zonotrichia leucophrys*) learn songs differently in response to identical song-tutoring regimes (Kroodsma and Canady 1985; Nelson et al. 1995; also see discussion in Baptista 1996), confirming that evolved genetic differences can play a part in song learning. Our study compares two populations of the same subspecies, in close geographical proximity but exposed to different ecological and social pressures, and investigates the extent to which several proximate ecological differences shape singing behavior in birds that are presumably genetically similar.

As with wrens and towhees, song sparrows (*Melospiza melodia*) also show a correlation between ecology and song learning. Song sparrow males have an average repertoire size of about eight songs. Each song consists of two to six phrases, with each phrase consisting of a note complex or trill. Songs are sufficiently complex that two males will not converge on a near-identical song by chance. On the rare occasions that distant males share songs in a Washington State population, it is the result of one bird learning its songs in one neighborhood and moving to establish a territory elsewhere (Nordby et al. 1999). Nonetheless, whole-song sharing between neighbors is widespread in this species – in all studies of which we are aware, whole-song sharing between neighbors has been documented (Nice 1943; Borror 1965; Mulligan 1966; Harris and Lemon 1972; Eberhardt and Baptista 1977; Baker 1983; Kramer and Lemon 1983; Cassidy 1993; Nielsen and Vehrencamp 1995; Hughes et al. 1998), but the amount of sharing varies between different geographic areas. Males in some resident populations in western North America tend to share multiple songs with each adjacent neighbor (Cassidy 1993; Beecher et al. 1994b), while sparrows in migratory populations in eastern North America share fewer songs (Harris and Lemon 1972; Kramer and Lemon 1983; Hughes et al. 1998; see Discussion for consideration of other studies relating to this point).

Here we compare song sharing in two different populations, both of the same western subspecies, *M. m. morphna* (Jewett et al. 1953; American Ornithologists' Union 1957). Because these two populations are separated by only 120 km, with continuous suitable and occupied song sparrow habitat between them (Smith

et al. 1997), they are presumably genetically quite similar. Nonetheless, they differ greatly in migratory habit, population density, and territory size. The population in Discovery Park, Seattle, Washington, is resident year-round at sea level, with high population density, while the population at Gold Creek, Kittitas County, Washington is montane and migratory, with much lower density and correspondingly larger territory size. We use these two populations to test the importance of two proximate factors, migration and population density, on song sharing. If either of these factors affects song sharing, we expect Gold Creek sparrows to share fewer songs than Discovery Park sparrows. If, on the other hand, migration and density are unimportant, we expect to find little difference between the two populations, at which point our attention should shift to other environmental factors or perhaps genetic differences in song learning propensities to explain the observed east-west differences in song sharing in song sparrows.

## Methods

### Study sites

Our first study site, Discovery Park, Seattle, Washington, is an undeveloped wooded park. Elevations range from sea level to 100 m. Song sparrow habitat, in the understory of deciduous and mixed woods, is nearly continuous, with only occasional mowed fields providing small (<100 m) uninhabited gaps. Territories are small (0.2–0.4 ha) and dense (30–40/10 ha). The approximately 200 pairs of sparrows at Discovery Park are resident and territorial year round.

Our second site, at Gold Creek, Kittitas County, Washington, is 120 km east of Discovery Park, at 1000 m elevation. Occupied habitat includes streamside willow thickets and open or shrubby wet meadows. Territories are larger (0.4–1.6 ha) and sparser (2–8/10 ha) than at Discovery Park, and large (>300 m) tracts of uninhabited dense coniferous forest separate patches of suitable habitat. Sparrows breeding at Gold Creek leave the breeding area for the winter. Deep snow cover persists through March; returning sparrows arrive during April.

### Banding and recording

At Discovery Park, since 1989, males have been mist netted and individually color banded when they arrive on site or establish a territory for the first time, usually in the fall of their first year or the spring of their second year (Beecher et al. 1994b). For this study, we color banded and recorded 11 birds at Gold Creek during the 1996 nesting season. We selected two sets of birds from Discovery Park to compare with the Gold Creek sample. Because the birds recorded at Gold Creek had a scattered distribution, and not all were contiguous neighbors, we chose a sample of 15 Discovery Park birds that replicated the spatial arrangement of the Gold Creek birds as closely as possible. We also included a second, larger sample ( $n=36$  subjects plus their adjacent neighbors) of Discovery Park birds from 1992, when one of us (S.E.C.) had measured song sharing across the whole park. One bird appears in both the 1992 and 1995 Discovery Park samples.

### Recording songs

Male song sparrows sing discrete song types, and deliver them with eventual variety, usually singing 5–20 iterations of a song type

before switching to the next type. We tape recorded each male through at least 19 type switches, a criterion that ensures recording of the complete repertoire (Kroodsma 1982; C.R. Wilkerson, J.C. Nordby and M.D. Beecher, unpublished data). Two birds at Gold Creek were included in sharing analyses although we recorded only 16 and 17 switches from them (repertoire sizes of six and eight songs respectively). Given the chance that we may have missed recording a song type for them, we excluded these two birds from analyses of song repertoire size. Recordings were made onto cassette tapes, using Sennheiser ME-88 shotgun microphones and Sony TC-D5 M tape recorders. Tapes were analyzed on a Kay DSP 5500 sonograph. We printed sonograms of all song types, and all major variants of each type.

### Determination of sharing

Song sparrow songs generally consist of two to six phrases, most often three or four. Introductory phrases usually consist of two to ten repeated notes or pairs of notes; succeeding phrases include trills, buzzes, and (usually at the end of the song) “note complexes,” series of short notes and/or buzzes (see Fig. 1 for examples). Each sparrow sings variations on each song type in its repertoire, and major variants usually involve omission of one or more of the phrases in the song, or substitution of different phrases, especially toward the end of the song.

In the Gold Creek sample, we compared song types from each male to songs of all other males by visual inspection. Songs were considered shared if so identified by a consensus of three independent judges. We measured sharing in the 1995 Discovery Park sample in the same way. Sharing in the second, larger, 1992 Discovery Park sample was judged by one of the three judges (S.E.C.) used in the smaller comparison, and each bird was compared only with its adjacent neighbors. To be considered shared, two songs had to match 2/3 or more of their component phrases. Introductory phrases, trills and buzzes were considered to match if they were similar in note shape, timing, and frequency; note complexes were considered to match if they shared half their component notes, regardless of order. In borderline or equivocal cases, the judges put more weight on the more invariant portions of the song (i.e., introductory phrases) and less on later parts of the song, which are more variable and less important in individual recognition (Nice 1943; Horning et al. 1993). We considered all recorded variations when looking for shared types.

The percentage of repertoire shared between two birds was calculated as the sharing index, equal to  $2N_S/(R_1 + R_2)$ , where  $N_S$  is the number of shared songs and  $R_1$  and  $R_2$  are the repertoire sizes of the two birds (McGregor and Krebs 1982). For each bird, we calculated its average sharing index with all adjacent neighbors. Then for each sample (Gold Creek 1996, Discovery Park 1992 and 1995), we calculated the average sharing index of all birds. At the population level, the sharing index is equivalent to mean number of shared songs/mean repertoire size.

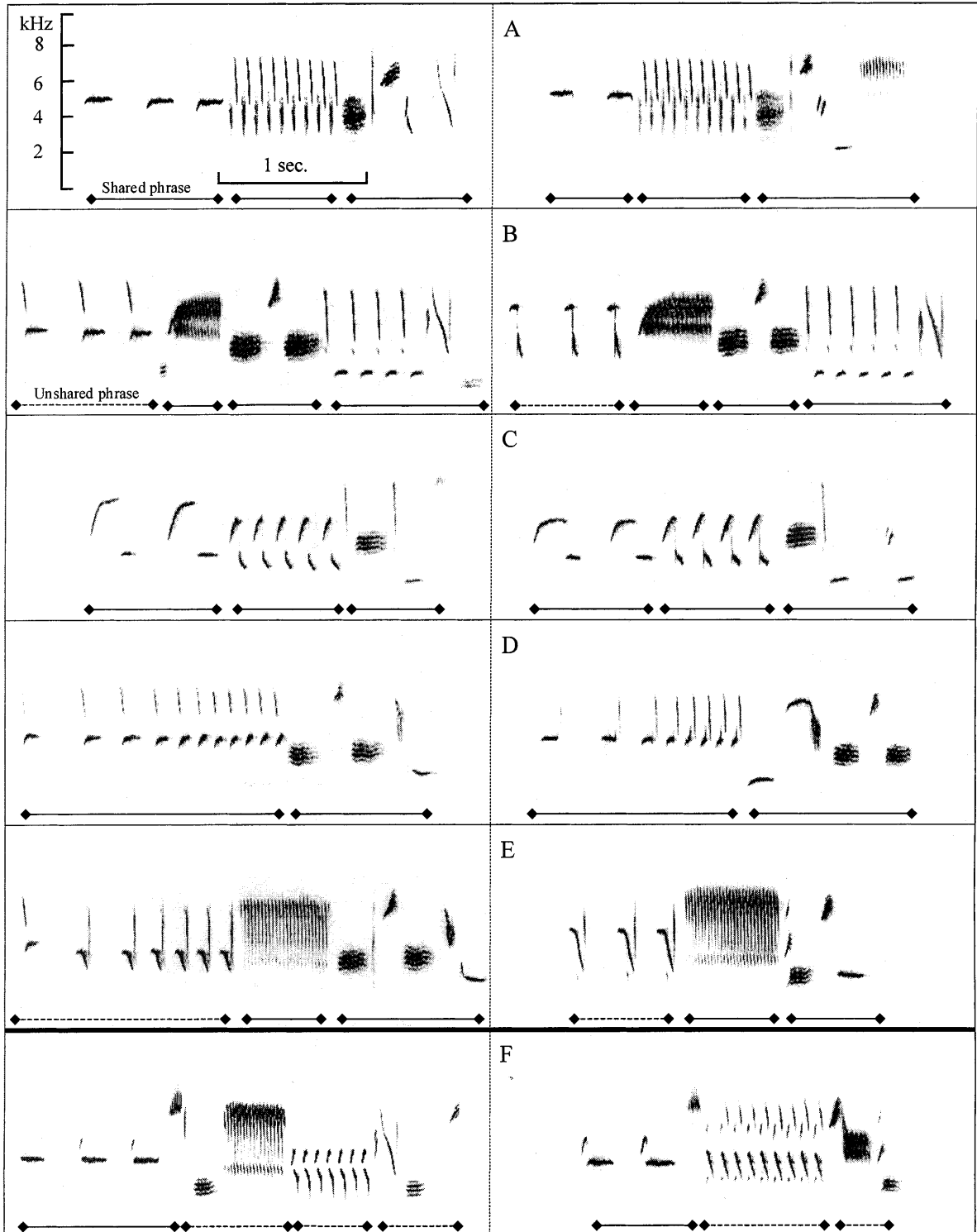
### Comparisons between sites and years

We used a small subset of the total data to test for differences in sharing across sites and years, for the following reason. Although recordings of neighborhoods of adjacent birds are necessary to understand the spatial patterning of song sharing, most birds in such a data set are involved in multiple comparisons with different neighbors, so observations of sharing are not strictly independent. Therefore, to ensure that each bird was used in only one pairwise comparison, we randomly chose one neighbor of each subject and calculated the sharing index between that pair. We continued randomly choosing pairs of subjects and neighbors until all birds had been used in one pairwise comparison. This reduced the sample size to 33 independent pairwise comparisons (5 at Gold Creek, 21 and 7 at Discovery Park in 1992 and 1995, respectively). We then performed an analysis of variance to compare average sharing in the three samples.

Spatial pattern of sharing

For the Gold Creek and the 1995 Discovery Park birds, we calculated sharing indices between all birds in the sample, no matter how distant. We then used two methods to test the hypothesis that sharing between adjacent neighbors was more common than sharing between distant birds, which has been questioned in another population of song sparrows (Hughes et al. 1998). First, we used Mantel's test to examine the hypothesis that sharing decreases

with distance. Mantel's test determines the relationship between two distance matrices (Mantel 1967). For the sparrows, the first matrix contained the physical distances between each pair of birds in the sample, measured as the number of territory boundaries separating them, and the second matrix contained song-sharing indices between the same pairs of birds. High values of the Mantel test statistic indicate that the two distance measures are positively correlated. Statistical significance of the correlation is tested by a permutation procedure. We used the ADE-4 analysis package, with



1000 permutations (Thioulouse et al. 1997) to perform the Mantel test.

Another way of examining the spatial patterning of song sharing is to simply compare sharing with neighbors to sharing with non-neighbors. To test the specific hypothesis that adjacent neighbors share more songs than they do with nearby non-neighbors, we performed a paired *t*-test comparing the average song sharing index with an adjacent neighbor to the average sharing with a non-neighbor (at the same site and year). We performed a third analysis, comparing the amount of sharing between a subject and his nearest neighbor (shortest direct-line distance between territory centers) versus sharing with other birds in the sample. Although all adjacent neighbors share a territory boundary and interact directly with each other, nearest neighbors share a larger portion of their boundaries, and may therefore interact more frequently.

## Results

### Extent of sharing between neighbors

Levels of song sharing for the Gold Creek sparrows and the two Discovery Park samples are shown in Table 1, along with migratory habit, territory size, and density. Average sharing did not differ significantly between sites and years (ANOVA  $F_{2,30}=0.87$ ,  $P > 0.4$ ).

### Spatial pattern of sharing

Gold Creek birds shared more songs with adjacent neighbors than with the other birds in the sample (37% vs 18%,  $t_{11}=1.71$ ,  $P < 0.05$ ). Discovery Park birds also shared more songs with adjacent neighbors (24% vs 9%,  $t_{15}=3.63$ ,  $P < 0.0001$ ). In the patchy habitat of Gold Creek, sparrows had fewer adjacent neighbors than did sparrows at Discovery Park (medians two vs four, ranges one to two vs two to six). Because of this we did a

**Table 1** Percent of song repertoire shared with each neighbor, and ecological variables for two populations of song sparrows in Washington State

	Discovery Park 1992	Discovery Park 1995	Gold Creek 1996
Average sharing (%)	26	24	34
Migratory?	Resident	Resident	Migratory
Territory size (ha)	0.3	0.3	1.0
Territory density (/10 ha)	30–40	30–40	2–8
Number of pairwise comparisons	158	34	16
Number of subject birds	36	15	11

**Fig. 1** Sonograms of song sparrow songs from Gold Creek, Washington. Each song in the *left column* is compared with the most similar song from a neighboring bird, in the *right column*. This figure is designed to show the full range of similarity that we considered as shared songs, from excellent matches (pair *A*) to intermediate matches (pairs *B* and *C*), to minimum matches (*D* and *E*). Song pair *F*, below the horizontal line, while having some similarities (e.g., first phrase, final note) were not considered shared songs. About 70% of matching song pairs were as similar as pair *A* or *B*

second analysis, comparing the level of sharing between a bird and his single closest neighbor versus average sharing with all other birds in the sample. In both populations, birds shared more songs with their nearest neighbor than with the other birds in the sample (Gold Creek: 37% vs 19%,  $t_{11}=1.73$ ,  $P < 0.05$ ; Discovery Park: 37% vs 9%,  $t_{15}=5.49$ ,  $P < 0.0001$ ). Note that when only the nearest neighbor is counted, sharing rises to 37% in the Discovery Park sample, indistinguishable from the Gold Creek sample. This is because Discovery Park birds generally shared most with one or two adjacent neighbors, usually the nearest ones, and less with remaining adjacent neighbors (if they had more).

Considering all birds in each sample, sharing declined significantly with distance at both sites (Mantel's test; Discovery Park,  $P=0.004$ , Gold Creek 1995,  $P=0.011$ ).

### Repertoire size

Repertoire size at Gold Creek was  $8.0 \pm 0.5$  songs. In the 1995 Discovery Park sample it was  $8.2 \pm 0.4$ , and in the 1992 Discovery Park sample it was  $8.2 \pm 0.2$ . There were no significant differences between sites or years (ANOVA  $F_{2,69}=0.31$ ,  $P > 0.7$ ).

## Discussion

Despite migrating like eastern sparrows, Gold Creek song sparrows shared songs with their neighbors, like non-migratory sparrows in Discovery Park. While the small Gold Creek sample provides only an approximate measurement of song sharing, it is clear that the level of sharing is substantial, and more similar to the Discovery Park sparrows or to British Columbian song sparrows (Cassidy 1993) than to migratory eastern song sparrows (see Table 2). Whole-song sharing at Gold Creek, as at Discovery Park, is highest between adjacent neighbors and declines with distance. From this we can conclude that migration and population density have little proximate affect on song sharing in song sparrows.

### Altitudinal migration?

In view of the sedentary habits of other song sparrows of the subspecies *M. m. morphna*, (Arcese et al. 1992; Beecher et al. 1994b), it is quite possible that Gold Creek sparrows are altitudinal migrants, moving only tens rather than hundreds or thousands of kilometers. Before applying the lessons of Gold Creek to eastern song sparrows, we should perhaps consider whether the two types of migration should be expected to affect song sharing in the same way. Key variables in song learning, according to laboratory and field studies, include the timing and extent of exposure to a tutor (Marler and Peters 1987; Beecher et al. 1994b; Nordby et al. 1999;

**Table 2** Levels of song type sharing between neighbors in three western and three eastern song sparrow populations. Average song sharing was calculated from published data as follows: Cassidy provided complete sharing data for 21 subject birds and neighbors, 56 pairwise comparisons in all. We simply calculated the average sharing as we did for Gold Creek and Discovery Park. For Kramer

and Lemon, 6 subject birds had an average repertoire size of 9 songs, and the number of songs shared between neighbors was "most commonly one." For Bower, 12 subject birds had an average repertoire size of 9.6 songs, and average number of songs shared between neighbors was 1

State/province (east/west)	Migratory?	Song sharing (%)	Reference
British Columbia (west)	Resident	32	Cassidy 1993
Washington (west)	Resident	21, 26	This study (Discovery Park)
Washington (west)	Migratory	34	This study (Gold Creek)
Ontario (east)	Migratory	~11	Kramer and Lemon 1983
Pennsylvania (east)	Migratory?	3	Hughes et al. 1998
Ithaca, NY (east)	Migratory	~10	J.L. Bower, personal communication

J.C. Nordby, S.E. Campbell, M.D. Beecher, unpublished data). Song sparrows arrive at Gold Creek in April with the melting of the heavy snows, and while the exact departure dates are unknown, they probably do not linger long after snow returns in October. If so, their stay on the breeding grounds is roughly equivalent to that of migratory eastern sparrows, and quite different from Discovery Park and Mandarte Island, British Columbia, sparrows, which reside on the same territories year round (Arcese et al. 1992; Beecher et al. 1994b). Unless Gold Creek sparrows preserve the social and spatial structure of their breeding neighborhood on the wintering grounds, which seems unlikely, the timing of contact with neighbors as song tutors would resemble that of eastern birds, not Discovery Park birds. Short-distance migration might make natal homing easier, and thus increase sharing by enabling young birds to settle next to their surviving song tutors. However, Nice (1943) noted high levels of philopatry in long-distance migrant song sparrows in Ohio. Thus, even if Gold Creek song sparrows migrate only altitudinally, the timing and place of their song learning should still be very similar to that of migratory eastern sparrows, and different from resident western sparrows.

#### If not migration, then what?

If migration per se does not affect song sharing, the question remains: why do eastern song sparrows share so much less than northwestern ones (Table 2)? It is quite possible that this east-west difference is caused by some unmeasured life history or ecological variable, such as winter mortality or specific patterns of philopatry (see Weatherhead and Boak 1986 on an extreme lack of breeding philopatry at one eastern site). Nonetheless, it is also intriguing to speculate that the reason Gold Creek birds resemble Discovery Park birds in their singing behavior is due not to some common environmental factor but to a genetic similarity in song-learning tendencies that overrides what appear to be quite different life histories. Song-learning experiments using song sparrows from both low-sharing and high-sharing populations would be a good approach to investigate this possibility.

#### Measuring song sharing between neighbors

Accurate estimation of the level of song sharing between neighbors in a repertoire species requires many conditions: (1) fairly complete recording (2) from a large sample (3) of known, marked individuals (4) whose territories have been mapped. It also requires (5) a reasonable criterion for what constitutes a shared song, and (6) reasonable treatment of individual variation in song types. Failure to meet these requirements will result in an imprecise or a biased estimate of song sharing. Taking each point in turn, while neither incomplete recording nor small samples would be expected to bias song-sharing estimates in a consistent direction, complete recording and large sample sizes assure a more precise estimate of song sharing rates. (Note also that the relevant sample size is not simply the number of birds recorded, but the number of pairs of neighbors compared.) Recording birds that are not individually marked and whose territories are not carefully mapped, however, is a more serious problem, and can lead to systematic underestimation of neighbor sharing rates, with the researcher comparing non-neighboring pairs of birds instead of neighbors. Finally, the researcher's criteria for a shared song can strongly influence the level of song sharing reported. That many species of birds vary their songs is well known, and within-type variation in song sparrows, for example, is sufficient to occasionally raise the question: is between-type variation really more important than within-type variation? (to which the answer seems to be a resounding "yes;" see Podos et al. 1992; Stoddard et al. 1992b; Horning et al. 1993; Searcy et al., in press). Whether or not all song variants are considered as possible matches will thus influence estimates of song sharing, as will the criterion used to decide exactly how similar two songs must be to be considered shared. While the exact dividing line may be arbitrary, the "best" criterion will be the birds' own: what the researcher identifies as a shared type should be what the birds themselves perceive as a shared type.

Any song-sharing criterion is necessarily arbitrary, because (1) song similarity is probably perceived by the birds not categorically (same or different) but as continuously varying and, in any case, (2) we have only a partial grasp of the key song features by which birds

evaluate song similarity. Thus it is not surprising that different investigators have come up with somewhat different sharing criteria, implying that the criteria are imperfect, but not that they are invalid. One validates a sharing criterion by seeing if it accurately predicts birds' judgements of song similarity: the bird should behave as if the songs the investigators have classified as "shared" are indeed similar, and as if the ones classified as "unshared" are indeed dissimilar. We have validated our sharing criterion for song sparrows in both field and laboratory studies. In field playback experiments, we have shown that song sparrows type match both strangers' song and, under certain conditions, neighbors' song at about the same high rate as they do self song, 50% (Stoddard et al. 1992a; Beecher et al., in press; the chance rate is around 10%). This finding implies that we are correct in classifying stimulus and reply songs as similar (or the same type, or shared). In laboratory perception experiments, we have shown that song sparrows do indeed confuse songs from different singers that we classify as the same song type (Beecher et al. 1994a); most of these have been neighbor-shared songs we recorded in the field. Moreover, we have shown in both the laboratory and field that hybrid song types, synthesized from the halves of two types, are confused, or replied to, with the "parental" types (Horning et al. 1993). Note that these hybrid songs are half matches to the parental types, and although they would not be classified as matches by our sharing criterion, the birds still perceive the resemblance to the song they partly match. We would add that many studies have validated the song-sharing criteria of other investigators of other songbird species, perhaps the best examples being song-matching studies (e.g., Krebs et al. 1981; Falls 1985).

#### Sharing in song sparrows – what do other studies say?

Comparisons between sites or years within this paper are straightforward. However, to compare these results quantitatively with other studies of song sparrows requires some assurance that the data in the other studies are reliable, and that the methods of assessing song sharing are comparable. Hughes et al. (1998) recently contrasted the levels of sharing found in Discovery Park with their own data from Pennsylvania and with published reports from elsewhere, concluding that neighbor sharing is uniquely high in Washington and "minimal" in Pennsylvania, Ontario, Maine, and California. Our interpretation of the published studies is different. We see a pattern, as shown in Table 2, where the difference Hughes et al. (1998) noted is real, but not of the magnitude they suggest. Song sparrows from Washington and British Columbia share about 25–35% of their repertoire (or two to three songs) with an average neighbor, while birds from the eastern half of the song sparrow's range share 3–11% of their repertoire (about one song in Ontario and New York state, less in Penn-

sylvania). As yet, none of the data from California seem adequate to quantitatively assess sharing.

We believe we reach different conclusions from Hughes et al. (1998) for four reasons. First, the present study – our first attempt to provide a precise, quantitative estimate of song sharing in our Discovery Park population – revises downward our previous rough estimate of 40% (Beecher et al. 1994b), to about 25%.

Second, Hughes et al. (1998) used a sharing criterion for whole-song sharing which appears to be more conservative than ours, assigning many songs to categories like "first trill shared" and "internal trill shared," some of which we would probably classify as fully shared songs (e.g., song pair B in Fig. 1). With our own data set we found that the three following sharing criteria produced roughly equivalent estimates (i.e., switching among these criteria would affect only a few marginal songs and would not change sharing estimates by more than a few percent): "share 1/2 by length," "share 2/3 by length," "share 2/3 of phrases." But Hughes et al.'s (1998) whole-song sharing criterion, matching both "first trill" and "internal trill" would probably result in a sharing estimate 1/2 to 2/3 as high as ours. Cassidy's (1993) system for recognizing shared songs appears comparable to ours. Other than Cassidy (1993) and Hughes et al. (1998), few studies have provided explicit sharing criteria.

Third, Hughes et al. (1998) did not include Cassidy's (1993) careful and detailed study from British Columbia, which shows levels of song sharing similar to those we find in Washington.

Fourth, Hughes et al. (1998) cite low sharing from Maine and California based on three studies (Borror 1965; Mulligan 1966; Baker 1983) whose data appear to us to be unreliable for quantitatively estimating sharing. Mulligan (1966), for example, working largely with unmarked birds and using amplitude profiles instead of sonograms to classify songs, reported moderate numbers of shared songs: about one type per pair of neighbors. However, song sharing as a percentage of repertoires was low in his study because of the anomalously large repertoire sizes (up to 24 song types per male) that he reported. In addition to reporting repertoires twice the size of those found in other studies of song sparrows, he also reported many songs in each bird's repertoire that were rarely used (in contrast to other studies that have found that songs are used at more or less equal frequency; Nice 1943; C.R. Wilkerson, J.C. Nordby, M.D. Beecher, unpublished data). This suggests that Mulligan may have treated as full song types what other investigators treat as variants within types, rendering problematic an interpretation of his conclusions on sharing. Borror (1965) noted shared songs within his study area in Maine (25 instances where a song was shared out of 544 song types recorded from 120 birds), but recorded widely in the state and did not separate neighbor-neighbor comparisons from other within- and between-site comparisons. Likewise, Baker (1983), in California, opportunistically recorded unmarked males at four sites. While Baker (1983) reported low or no whole-song sharing within each of his

four sites, he did not mention taking any special care to include adjacent neighbors, and may thus have been comparing non-neighbors within each site, which would result in an overly low estimate.

In summary, the data suggest that song sparrows in several eastern populations share songs with neighbors at perhaps one-third the rate found in Washington and British Columbia sparrows, still a substantial difference, but not of the order of magnitude suggested by Hughes et al. (1998). The situation in California and other parts of the song sparrow's range is still unclear.

### Function of song sharing

There remains the question of how differences in song sharing might help us better understand the function of song in song sparrows, and what the fitness advantage of song sharing might be, if any. Males in Discovery Park who share a high proportion of songs with their neighbors do so because they were able to establish a territory within their juvenile floater range – birds that share little have moved between the completion of song learning and territory establishment (Beecher et al. 1994b; Nordby et al. 1999), which may indicate that low-sharing sparrows lost in the competition for a limited number of territories in the area where they learned. If low sharing is correlated with moving as a young bird, then high song sharing could act as an audible badge of prior success in competing for a territory, and a female sparrow might use such a cue to choose a mate. Or perhaps a male who shares songs is better able to defend his territory, by type and repertoire matching his neighbors during disputes. To determine the significance of song sharing, it would be desirable, first, to measure any correlation between song sharing and lifetime fitness and, second, to determine whether such an effect was due to mate attraction and stimulation or to territory defense. If there are advantages to song sharing, then does the low song sharing between neighbors in the east mean that the advantages are less there? It would be interesting to learn if patterns of song use such as repertoire and type matching, which are common in at least one high-sharing population (Beecher et al. 1996), also exist in low-sharing populations. Sharing even one song with a neighbor allows a male song sparrow to repertoire match and, to a limited extent, to type match. And sharing “no” songs does not necessarily preclude repertoire and type matching. That is, birds do not have to default to random song usage if they do not share by the standards of a human observer. Birds that appear to share no songs could still match by either (1) relaxing the standards they use to class songs as shared, or (2) arbitrarily treating certain songs in their repertoire as shared songs. These patterns should be detectable by playback experiments (e.g., Stoddard et al. 1992a; Beecher et al. 1996), and further investigation of song use in low-sharing populations (which was an original goal of our studies at Gold Creek) should help clarify these issues.

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