The Auk 124(1):53–62, 2007

HIGH LEVEL OF SONG SHARING IN AN EASTERN POPULATION OF SONG SPARROW (*MELOSPIZA MELODIA*)

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Abstract.—Using shared songs is believed to be an integral part of neighbor communication and territory establishment strategies among many avian species with repertoires. Previous studies of two western subspecies of Song Sparrows (*Melospiza melodia*) reported a high level of song sharing among neighboring males, whereas studies of an eastern subspecies have reported a very low level. The purpose of our study was to investigate another population of the eastern subspecies to determine whether higher song-sharing levels existed within its range. Every song in the repertoire of 29 males was compared with the songs of all other males to assess the number of shared songs. For each male, we calculated the mean song-sharing level with neighbors and non-neighbors. Males shared, on average, 33% of their repertoire with neighbors, significantly more than they shared with non-neighbors (27% of their repertoire). Two first-year males learned whole song types from several individuals and preferentially learned the song types shared among those individuals. Our results suggest that the eastern and western subspecies may not differ genetically in the way they learn songs, because song-sharing levels and song learning in our population were more similar to those of the western subspecies than to those of other populations within its own subspecies. Song-sharing differences among eastern populations may be explained instead by factors acting at the level of individual populations. *Received 19 January 2005, accepted 5 January 2006.*

Key words: *Melospiza melodia*, neighbors, site fidelity, song learning, song sharing, Song Sparrow.

Niveau Élevé de Chants Partagés chez une Population de l'Est de *Melospiza melodia*

Résumé.—L'utilisation de chants partagés est considérée comme faisant partie intégrante de la communication entre voisins et des stratégies d'établissement des territoires chez plusieurs espèces aviaires possédant des répertoires. Des études antérieures portant sur deux sous-espèces de l'Ouest de Bruant chanteur (*Melospiza melodia*) ont rapporté un niveau élevé de chants partagés entre les mâles voisins, alors que les études d'une sous-espèce de l'Est ont rapporté un niveau très faible. Le but de notre étude était d'examiner une autre population de la sous-espèce de l'Est afin de déterminer si des niveaux plus élevés existaient dans son aire de répartition. Chaque chant du répertoire de 29 mâles a été comparé à ceux de tous les autres mâles pour évaluer le nombre de chants partagés. Pour chaque mâle, nous avons calculé le niveau moyen de chants partagés avec les voisins et les non voisins. Les mâles partageaient, en moyenne, 33% de leur répertoire avec leurs voisins, soit

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significativement plus que ce qu'ils partageaient avec leurs non voisins (27% de leur répertoire). Deux mâles de première année ont appris des chants entiers de plusieurs individus et ont appris de façon préférentielle les chants partagés entre ces individus. Nos résultats suggèrent que les sous-espèces de l'Ouest et de l'Est ne soient pas différentes génétiquement dans leur façon d'apprendre des chants, car les niveaux de chants partagés et l'apprentissage des chants dans notre population étaient davantage similaires à ceux des sous-espèces de l'Ouest qu'à ceux des autres populations de sa propre sous-espèce. Les différences dans les chants partagés parmi les populations de l'Est peuvent être plutôt expliquées par des facteurs agissant au niveau des populations individuelles.

MALES OF MANY species with repertoires, such as American Redstarts (*Setophaga ruticilla*; Lemon et al. 1985), Great Tits (*Parus major*; McGregor and Krebs 1982), and Carolina Wrens (*Thyrothorus ludovicianus*; Morton 1987), share songs with neighboring males. Studies suggest that the use of shared song types is important in neighbor communication (Krebs et al. 1981, Falls et al. 1982, Falls 1985, Weary et al. 1990, Vehrencamp 2001). Males that share songs may either type-match (sing the same song type) with their neighbor, which is believed to be an aggressive signal (Burt et al. 2001) or, if less aggressive, repertoire-match (sing another shared song type), thereby honestly relaying their intentions (Burt et al. 2001, Vehrencamp 2001). Burt et al. (2001) found that aggressive responses by Song Sparrows (*Melospiza melodia*) were significantly greater to type-matching neighbor-song playback than to repertoire-matching neighbor-song playback. Additionally, male Song Sparrows type-matched their neighbor's song only early in the breeding season, when territory boundaries were unstable (Beecher et al. 2000a). In two western subspecies, territory tenure (subspecies *morphna*; Beecher et al. 2000b) and survival (subspecies *cooperi*; Wilson et al. 2000) were positively related to song-sharing levels. In both subspecies, the frequency of song sharing declined with distance between individuals (Hill et al. 1999, Wilson et al. 2000), which suggests that the Song Sparrow's strategy is to settle on the territory that maximizes the number of songs shared with neighbors.

Song Sparrows are socially monogamous, territorial passerines that nest throughout temperate North America (Rising 1996). There are 24 subspecies (Arcese et al. 2002), which are highly variable in both size and body proportions across their range (Aldrich 1984). They have a repertoire size of 5–14 song types (Borror 1965), which does not change in size or composition after the first year (Nordby et al. 2002). Males sing with eventual versatility, singing one song type several times before switching to the next type (Kramer and Lemon 1983). They continue to sing throughout the breeding season, albeit at a lower rate than when unpaired (Turner and Barber 2004). Males share song types with other males in the local population but do not share an entire repertoire with any one male (Hill et al. 1999). Hatch-year males learn song types in their natal summer from territorial males (tutors), preferentially learning song types that are shared among their tutors; they then attempt to settle on a territory near these tutors in subsequent breeding seasons (Beecher et al. 1994, Nordby et al. 1999).

Differences in song-sharing levels (percentage of repertoire shared) have been observed among the subspecies. Both migratory and nonmigratory western Song Sparrows in Washington (*morphna*) share 24–34% of their repertoire with neighbors (Hill et al. 1999); in San Diego (*cooperi*), nonmigratory males share 22% of their songs with neighbors (Wilson et al. 2000). Sedentary Song Sparrows in North Carolina (likely *euphonia*) also share songs (Peters et al. 2000). However, the partially migratory eastern Song Sparrows in Pennsylvania (*melodia*) share only 3% of their songs with neighbors (Hughes et al. 1998), whereas those in Ontario (*melodia*) share ~11% of their songs with neighbors (Kramer and Lemon 1983, Hill et al. 1999).

Differences in migratory tendency (Hughes et al. 1998), methodology of song-sharing analysis (Hill et al. 1999), or genetics of song learning (Hughes et al. 1998) may explain variations in song-sharing levels among subspecies or populations. However, it is important to examine first

several populations of a subspecies to determine whether the differences lie, in fact, along subspecific lines or whether they are unique to particular populations within a subspecies (see Hill et al. 1999). First, we quantify the repertoire size and number of songs shared between neighbors and non-neighbors in an eastern population of Song Sparrows (subspecies *melodia*) in Nova Scotia, Canada. Second, we compare the percentage of a male's repertoire that is shared with neighboring males to that shared with non-neighbors to determine whether eastern males have a higher song-sharing level with neighbors than non-neighbors, as was found in western males. Finally, we identify the potential tutors of two first-year males to examine song learning in this subspecies.

Methods

Field site and techniques.—Our study was conducted at Bowlin's Hobby Horse Farm, located in Lower Sackville, Nova Scotia, Canada (44°45′N, 63°41′W). The farm consisted of 12 ha of fields divided by areas of mixed forest, brush, or both.

We captured males using mist nets and banded them with a unique combination of three color bands and a numbered aluminum Canadian Wildlife Service band. To quantify repertoire size, we recorded males only when they were singing, over several days, until we had 90 min of continuous singing for each male using a Marantz PMD 222 cassette recorder and a Sennheiser directional microphone. Total sample size consisted of 29 different males: 22 males in 2002 and 7 males in 2003.

Repertoire size and song-sharing level.—All songs recorded were digitized at 22,050 kHz, 16-bit, mono (43 kb s^{-1}) with WINDOWS Sound Recorder. Sonograms were viewed using SYRINX-PC, version 2.2b (J. M. Burt, Seattle, Washington). For each male, all variants of song types were printed for analysis. At least 20 song-type switches, as well as a minimum of 200 songs, were viewed before the repertoire of a male was considered fully documented (Searcy et al. 1985, Hill et al. 1999). For the first eight repertoires examined, we made plots of repertoire size versus number of songs examined. Using 200 songs was adequate for repertoire estimation in this population; the curve for each male reached an asymptote well before 200 songs. For males whose final song type was observed after 100 but before 200 songs, we went on to look at 300 song types without discovering any new song types. Two independent observers assessed the repertoire size of each male by viewing all its sonograms and determining the number of different song types present. To determine male territory boundaries, we mapped all territories through observations of male singing and perching locations and sites of neighbor boundary disputes as well as by using brief playbacks soon after territory establishment. Males holding adjoining territories were considered neighbors, whereas males with non-adjoining territories were considered non-neighbors.

Song-sharing levels among neighboring and non-neighboring males were determined using the method described by Hill et al. (1999) for 22 males in 2002 and 20 males in 2003. Thirteen males were present in both years on the study site. For each of these 13 males, we used their mean level of song sharing with (A) all neighbors and (B) all non-neighbors over both years, so that they were included only once in the paired analysis. To summarize Hill et al.'s (1999) methodology, two independent observers visually compared sonograms of each song type of one male to all song types in its neighbors' repertoires, as well as to the songs of all other males in the population. Figure 1 shows an example of shared and unshared songs of two neighboring males. A song type is shared when two-thirds or more of the song phrases are identical. The sharing index, $2(N_s)/(R_1 + R_2)$, was used to calculate the proportion of the repertoire shared between two males, where N_s is the number of songs shared, R_1 is the number of songs in the first male's repertoire, and R_2 is the number of songs in the second male's repertoire (McGregor and Krebs 1982). For each of the 29 males, we calculated the mean sharing index with neighbors and with non-neighbors.

Assigning potential tutors.—The repertoires of two first-year males banded as juveniles in 2002 and holding breeding territories in 2003 were compared with those of all males present during 2002. We considered males with the closest match to the song-type variants of the subject to be potential tutors. Males were assigned a tutor score of 1 if they had the closest match to the juvenile male's song type. When ties occurred (two or more males who had songs equally similar to the first-year male's songs), each male

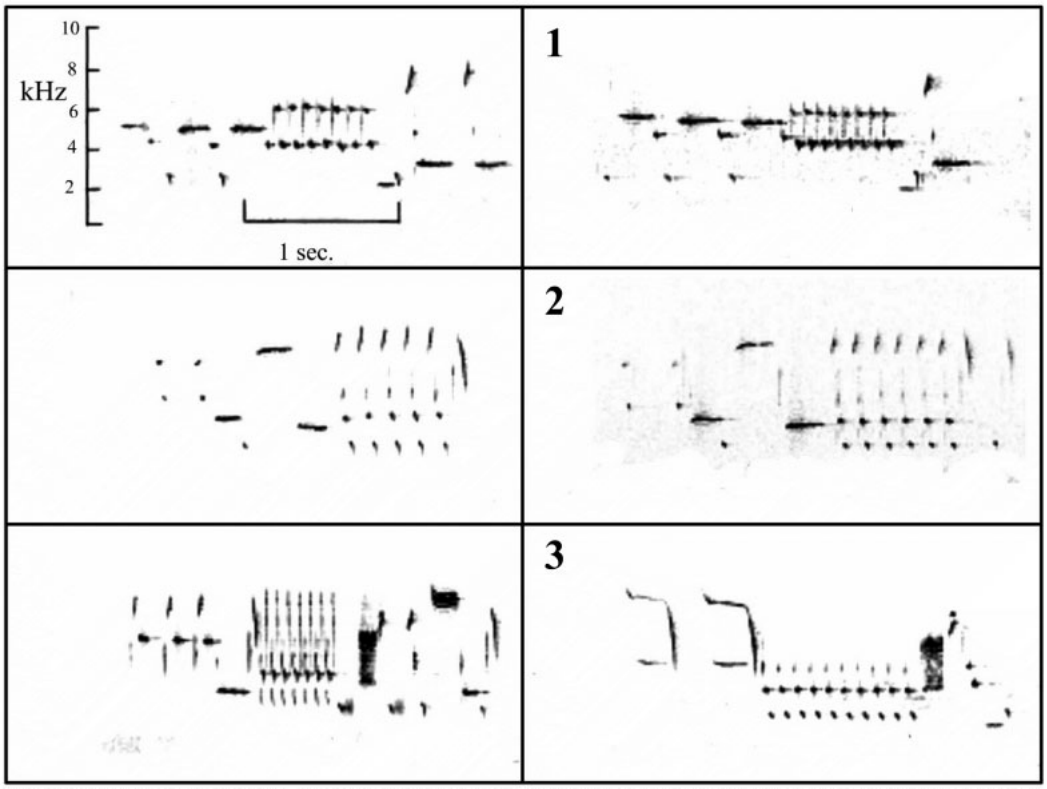

FIG. 1. Comparison of three song types from the repertoires of two neighboring male Song Sparrows. These neighbors share types 1 and 2; type 3 is not shared.

was assigned a partial tutor score for that song (e.g., if two males were potential tutors for a song type, they would each be given a tutor score of 0.5). Tutor scores were then totaled for each potential tutor of the first-year males (Nordby et al. 1999). For all songs of the two first-year males, potential tutor songs matched ≥90% of the subject's song type. Potential song tutors were identified using both the inclusive and exclusive methods of tutor assignment, as described by Nordby et al. (1999). Inclusive analysis assigned all possible tutors for all song types, whereas exclusive analysis identified the smallest number of potential tutors that could be responsible for tutoring the subject's repertoire. For example, in inclusive analysis, if for a song type there were four possible tutors and one of those males tutored other songs in the repertoire, whereas the other three did not, in exclusive analysis that male would be considered the potential tutor for that song, whereas the other three would not.

Statistical analyses.—We used Shapiro-Wilk normality tests on data for repertoire size and song-sharing levels of males with their neighbors and non-neighbors. Because there were no significant differences between 2002 (22 males) and 2003 (20 males) in song-sharing levels (mean ± SE) of neighbors (35.3% ± 3.4% vs. 30.5% ± 1.7%; unpaired $t = 1.242$, df = 40, $P = 0.22$) or non-neighbors (28.9% ± 2.1% vs. 24.8% ± 1.6%; unpaired $t = 1.501$, df = 40, $P = 0.14$), years were pooled for analysis. We used a paired *t*-test to determine whether song-sharing levels differed between neighbors and non-neighbors. All tests are two-tailed. Means ± SE are presented. Results are considered significant when $P < 0.05$.

RESULTS

Males had a mean repertoire size of 9.21 ± 0.28 song types; repertoire size ranged from 6 to 12 song types ($n = 29$ males). A high proportion of

neighboring males shared between two and four song types (69.5%; Fig. 2A), whereas a somewhat lower proportion of non-neighboring males shared this range of song types (54.1%; Fig. 2B); more than half (56.6%) of non-neighboring males shared between zero and two song types, whereas 32.2% of neighbors shared this range of song types. Interestingly, one male shared eight song types with a non-neighbor (Fig. 2B), and not with a neighbor. Many song types were common in the population; six of the most common song types were sung by a large percentage of males (76%, 59%, 55%, 55%, 52%, and 45% of the 29 males recorded over the two years).

Males shared 33.1 ± 2.5% (means ± SE) of their repertoire with neighboring males (range: 7.0–71.4%), which is significantly greater than the 26.9% ± 1.7% of their repertoire they shared with non-neighbors (range: 9.1–43.0%) (paired t = 3.476, df = 28, P = 0.0017). When considering years separately, males still shared a significantly greater percentage of their repertoire with neighbors than with non-neighbors (2002: 35.3% ± 3.4% vs. 28.9% ± 2.1%; paired t = 2.168, df = 21, P = 0.042) and (2003: 30.5% ± 1.7% vs. 24.8% ± 1.6%; paired t = 4.721, df = 19, P = 0.0001).

Subject G was banded as a nestling in 2002. Following natal dispersal that summer, it was recaptured as a fledgling near its future (2003) breeding territory (located four territories away from its natal territory). All of G's 11 songs were found in the repertoires of males breeding in 2002. Using the inclusive tutor assignment, this male had six potential tutors (Table 1). Exclusive analysis identified three of these potential tutors (Table 1); each of these three potential tutors survived to breed in 2003. Of the three potential tutors from 2002 remaining in the inclusive analysis, male N did not survive and the remaining two did not hold territories adjacent to G in 2003 (Table 1; Fig. 3A). In 2003, male G held the territory of his secondary potential tutor (second highest score, male #9, Table 1); male #9 moved into an adjacent vacant territory between males G and D (Fig. 3A). The third

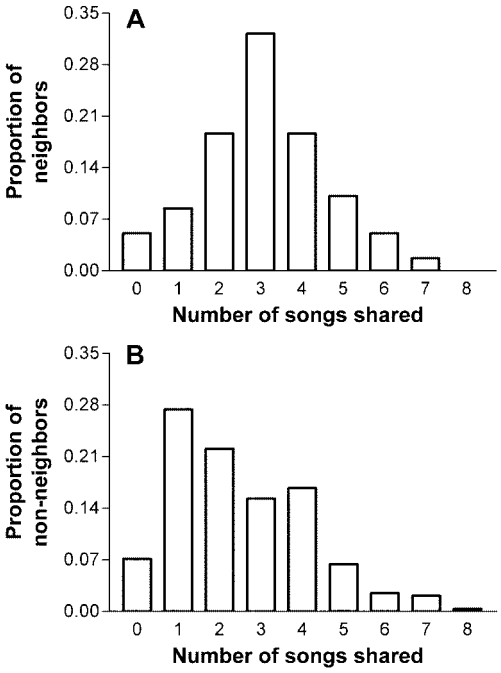

FIG. 2. Proportion of (A) neighboring (n = 59) and (B) non-neighboring (n = 281) male Song Sparrows that share between zero and eight song types.

TABLE 1. Inclusive and exclusive tutor scores of all potential tutors of first-year male G in 2002, with the potential tutor's proximity to G's territory in 2003 and whether the potential tutor survived to the following year.

Potential tutor	Inclusive tutor score	Exclusive tutor score	Proximity to subject in 2003 [a]	Survival to 2003
D	6.0	7.0	Gap [b]	Yes
#9	2.5	2.5	Contiguous	Yes
BP	1.0	1.5	Contiguous	Yes
N	0.5	0	–	No
Q	0.5	0	Gap	Yes
UR	0.5	0	Farther	Yes

[a] Proximity to subject was defined as in Nordby et al. (1999): contiguous = adjacent territory, gap = another male's territory or large open space, farther = farther than one gap, and — = not present in 2003.

[b] Male D was separated from G's territory by one male; but in 2002, these two territories were contiguous.

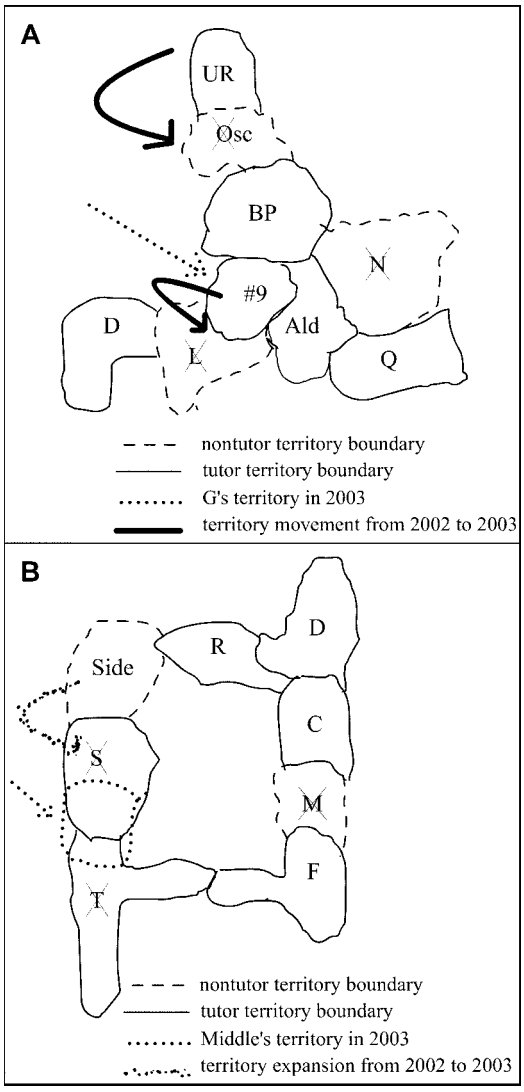

FIG. 3. Territories of potential tutors and nontutors present in 2002 for males (A) G and (B) Middle. Territories of males G and Middle in 2003 are indicated, as well as the territories of surviving potential tutors. Males that did not survive to 2003 are indicated by an X.

potential tutor (BP) was a neighbor to male #9 in 2002 and to G in 2003.

The second male, Middle, was banded as a fledgling in July 2002 on its future (2003) breeding territory (natal territory unknown, but likely just off the study site). Three of Middle's nine songs could not be assigned to potential tutors. However, in 2003, it resided near the edge of our study site where contiguous Song Sparrow habitat existed, so it is possible the potential tutor(s) lived just outside of our study site. One of the three song types was also recorded from another new male in 2003 whose age was unknown. All three types were similar in pattern to others found in the population but were not matches and did not appear to be hybrids. The inclusive method assigned 10 potential tutors, whereas the exclusive method assigned 4 (Table 2). This large difference was attributable to one song type that could have been learned from any of six males (two of whom resided in the same field and were more likely to be potential tutors: males S and F). Removing the other four possible tutors for this song from the inclusive analysis leaves six potential tutors (Table 2). The four exclusive and remaining two inclusive potential tutors were all residents of the same field (Fig. 3B). Two of these potential tutors, males S and T, did not survive. In 2003, Middle held a piece of each of these two males' territories (Fig. 3B). Of the other two surviving exclusive potential tutors (R and C), both were separated from Middle by a gap (Table 2; Fig. 3B). Of the two remaining inclusive potential tutors (D and F), one was separated from Middle by a gap and the other was farther away (Table 2; Fig. 3B).

Males preferentially learned songs shared between at least two potential tutors (shared tutor songs). From its six potential tutors, male G had the possibility of learning 16 shared tutor songs and 14 unique tutor songs. It chose all of its 11 songs from those shared among its potential tutors. Likewise, from its six potential tutors, male Middle had 17 shared tutor songs and 15 unique tutor songs from which to learn. It chose five of its six songs from those shared among potential tutors (three more of its songs could not be assigned). The sixth song was unique to one of its potential tutors, but was also sung by male Side who was not a tutor, but who was Middle's neighbor in 2003. For both G and Middle, most song types learned from potential tutors were also sung by one of the potential tutor's neighbors (who were or were not potential tutors).

DISCUSSION

Male Song Sparrows in our eastern population had an average repertoire size of 9.2 song

TABLE 2. Inclusive and exclusive tutor scores of all potential tutors of first-year male Middle in 2002, with the potential tutor's proximity to Middle's territory in 2003 and whether the potential tutor survived to the following year.

Potential tutor	Inclusive tutor score	Exclusive tutor score	Proximity to subject in 2003 [a]	Survival to 2003
R	2.0	2	Gap	Yes
S	0.67 (1) [b]	2	–	No
C	1.0	1	Gap	Yes
T	1.0	1	–	No
F	0.17 (0.5) [b]	0	Gap	Yes
D	0.5	0	Farther	Yes
Alder	0.17 (0) [b]	0	Farther	Yes
O	0.17 (0) [b]	0	Farther	Yes
#2	0.17 (0) [b]	0	Farther	Yes
HM	0.17 (0) [b]	0	–	No

[a] Proximity to subject was defined as in Nordby et al. (1999): contiguous = adjacent territory, gap = another male's territory or large open space, farther = farther than one gap, and — = not present in 2003.

[b] Potential tutor score in parentheses represents the score if the song type with six possible tutors was learned from only the two males in the same field.

types, which is comparable to that found in other eastern and western Song Sparrow populations (range: 7.9–9.6 song types; Borror 1965, Searcy 1984, Beecher et al. 1996, Hughes et al. 1998, Hill et al. 1999, Wilson et al. 2000). This finding allows us to compare levels of song sharing among the different subspecies of Song Sparrow.

We found that males of *melodia* shared, on average, 33.1% of their repertoire with neighboring males, which is comparable to western *morphna* and *cooperi* populations (Hill et al. 1999, Wilson et al. 2000, respectively). Nice (1937, 1943) documented song sharing among males of *euphonia* in Ohio but did not quantify it. Males in our study shared a significantly greater percentage of their repertoire with neighbors than they did with non-neighbors, as was also found for western Song Sparrows (Hill et al. 1999). However, one male shared the most number of song types with a non-neighbor rather than a neighbor, illustrating that despite significant differences in song-sharing levels, variation among individuals within a population still exists. Commonly recorded song types in our population were likely responsible for the relatively high level of song sharing found between some non-neighboring individuals (six song types were very common; 45–76% of the recorded males sang them). Our study area was relatively small, such that many of a male's non-neighbors were not too far away, and some were within hearing distance.

In contrast to our finding of high song-sharing levels, males in Pennsylvania (also *melodia*) shared only 3% of their repertoires with a randomly chosen neighbor (Hughes et al. 1998). Those authors found that song sharing between neighbors varied from 0 to 40%, with two-thirds of males sharing no song types with any neighbors. Similarly, Song Sparrows in Ontario (subspecies *melodia*) shared either no songs (Harris and Lemon 1972) or typically shared only one song type with neighbors (Kramer and Lemon 1983). Hill et al. (1999) estimated that males in Kramer and Lemon's (1983) Ontario population shared ~11% of their repertoire with neighbors.

Why do song-sharing levels vary so much in Song Sparrows and particularly within *melodia*? Migratory tendency is one potential explanation. Males in resident populations likely have a greater probability of breeding close to their potential tutors and of sharing more songs than males in migratory populations. Evidence for migratory tendency effects on song-sharing levels exists in some avian species (e.g., Ewert and Kroodsma 1994, Kroodsma et al. 1999a). Although the extent or distance of migration in our Song Sparrow population is unknown, males returned over a period of several weeks in April, which indicates that this population is at least partially migratory, like those studied in Ohio and Pennsylvania (Nice 1937, Hughes et al. 1998). Similarly, winters are no milder at our study site in Nova Scotia than at sites in Ontario

and Pennsylvania (Meteorological Service of Canada, National Climatic Data Center).

Beecher et al. (1994) suggest that migration is not necessarily a factor, because if males in migratory populations return to the area where they learned their songs, then sharing should be as high as in resident populations. Migratory tendency did not affect song-sharing levels in the western Song Sparrow subspecies *morphna* (Hill et al. 1999). Also, males of *euphonia* (partially migratory) obtained breeding territories, on average, 280 m from their natal territories, which indicates that they returned to the area where they likely learned their songs (Nice 1937). Males in our eastern population return year after year to their breeding territory (59% of males returned in 2003). Given that yearly survival of adult Song Sparrows is estimated to be between 45% and 64% (Halliburton and Mewaldt 1976, Arcese et al. 1992, Sandercock and Jaramillo 2002), all males that survived to the following breeding season likely returned. Thus, our study population appears to have high site fidelity (as also seen by Nice 1937; Beecher et al. 1994, 2000b; Wilson et al. 2000) and is stable. Low site fidelity has been reported for eastern Song Sparrows (*melodia*) in Ontario (Weatherhead and Boak 1986), as have low song-sharing levels (Harris and Lemon 1972, Kramer and Lemon 1983). No banded nestlings were resighted as adults, and 83% of banded adult males were never resighted (even within a breeding season; Weatherhead and Boak 1986). Similarly, male North American Sedge Wrens (*Cistothorus platensis*) were unpredictable breeders (arriving and departing at unusual times during the breeding season) and did not share songs, whereas males in the sedentary Neotropical populations with high site fidelity had high song-sharing levels (Kroodsma et al. 1999b). Although the degree of within-season territory fidelity is not reported for Song Sparrows in Pennsylvania, 61% of males return each year (Hyman et al. 2004), which indicates that population stability and site fidelity cannot be the only explanations for observed song-sharing differences among populations.

The observed differences in song-sharing levels may simply be an artifact of using different methodologies of song-sharing analysis (Hill et al. 1999). However, many (>85%) of the songs we considered shared were very similar, with only slight variation in the end portions of songs. Hughes et al. (1998) might also have considered these songs as shared and detected a similar level of song sharing if it existed in their population (see Fig. 1).

Differences in song-sharing levels between eastern and western Song Sparrows could be genetically based and attributable to differences in song-learning strategies (Hughes et al. 1998). Western Song Sparrows copy whole song types from tutors (Beecher et al. 1994). A field-based study by Nordby et al. (1999) on western *morphna* identified the probable song tutors of first-year males. Males had three to four song tutors that were neighbors during the natal summer; these males subsequently obtained territories next to at least one of their tutors or, if the tutor was dead, settled on the tutor's vacant territory. Also, males preferentially learned songs that were shared by the tutor and the tutor's neighbors (Beecher et al. 1994, Nordby et al. 1999). In our population, we found that two hatch-year males that returned to their natal site learned their songs from other males in the population in the same way as described for western Song Sparrows. Genetics of song learning at the population level could still potentially explain why Song Sparrows in Pennsylvania and Ontario have a low level of song sharing, but lab-based studies would be required to test this possibility.

To conclude, Song Sparrows in our eastern population share songs at a level similar to that found for *morphna*, *cooperi*, and likely *euphonia* (Hill et al. 1999, Wilson et. al. 2000, Nice 1943, respectively), but our results contrast with those from another study on *melodia* (Hughes et al. 1998). Further investigation is necessary to discover the relationship between site fidelity and song-sharing levels to determine why some populations of this subspecies share a large percentage of their repertoire, whereas others do not. Our results suggest that the difference in levels of song sharing is likely not attributable to genetic differences in song-learning strategy among subspecies but may result from different life histories of populations within *melodia*.

Acknowledgments

We thank A. Bowlin and G. Bowlin for allowing us the opportunity to study Song Sparrows on their miniature horse farm. J. Benjamin, M.

Markabi, K. Murphy, and C. Nordlund provided excellent field assistance. K. Murphy was the second independent observer, determining repertoire size and song-sharing levels. We thank M. Beecher and three anonymous reviewers for their helpful comments on a previous version of this manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada through a graduate research scholarship to J.R.F. and a Discovery grant to C.A.B., and by Saint Mary's University through grants to C.A.B. from the Faculty of Graduate Studies and Research. This research complied with the laws of Canada and all proper permits were obtained.

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Associate Editor: K. Yasukawa