



Song type sharing and territory tenure in eastern song sparrows: implications for the evolution of song repertoires

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Song repertoires are thought to have evolved by sexual selection, with larger repertoires being advantageous in both female choice and territory defence. While most hypotheses of repertoire evolution treat different song types as functionally equal, an alternative hypothesis is that song repertoires evolved to allow song sharing with multiple neighbours. In support of this hypothesis, song sparrows, *Melospiza melodia*, share high proportions of their repertoires with territorial neighbours in at least three west coast populations in North America, and song sharing is correlated with a territorial advantage in at least two of these. We studied song sharing and territory tenure in an east coast population of song sparrows in North America in which song sharing is significantly less common. We found no evidence for a territorial advantage of whole song sharing in our population. We also found no evidence for a territorial advantage for partial song sharing, even though partial song sharing is as common in our population as whole song sharing is in the west coast populations. Population demographics (such as annual survival and territory density) do not seem sufficient to explain different levels of sharing between populations. Thus, we found no evidence in our population to support song sharing as a target of selection in the evolution of song repertoires.

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The evolution of song repertoires has been widely attributed to sexual selection acting through female choice (Catchpole 1980; Searcy & Andersson 1986; Catchpole & Slater 1995). However, Beecher et al. (1994, 2000a) suggested that the primary function of song repertoires is to allow a male to share songs with more than one territorial neighbour. Sharing of songs, in which two or more males have the same or a similar song type in their repertoires, allows males to interact vocally in ways that are impossible without sharing, for example, by 'song type matching',

in which one male replies to another with the same song type (Lemon 1968; Krebs et al. 1981), and by 'repertoire matching', in which one male replies to another with a different shared song type (Beecher et al. 1996). If such vocal interactions are important to maintaining a territory, then sharing might enhance male fitness by prolonging territory tenure. In support of this hypothesis, a study of song sharing in a population of song sparrows, *Melospiza melodia*, in Washington, U.S.A., found that the number of song types that a male shared with his neighbours during his first year of territory tenure was positively correlated with the total number of years that the male maintained his territory (Beecher et al. 2000a). In further support of this hypothesis, Wilson et al. (2000) found that a male song sparrow's probability of retaining his territory into a second year in a California population increased with the average proportion of the male's repertoire that was shared with his immediate neighbours. Here

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we tested whether the predicted relationship between territory tenure and song type sharing also exists for a population of song sparrows in Pennsylvania, U.S.A.

Examining the relationship between territory tenure and sharing in this Pennsylvania population is of particular interest because the level of song sharing is notably low, with pairs of adjacent males sharing on average only 3% of their repertoires (Hughes et al. 1998). In contrast, Hill et al. (1999) found that adjacent neighbours in the Washington population studied by Beecher et al. (2000a) shared on average about 25% of their repertoires, and Wilson et al. (2000) found that adjacent neighbours in their California population shared on average about 17% of their repertoires. Reported variation in sharing may partly be a methodological artefact, caused by differences in the criteria used to judge sharing. Thus, our present study assessed song sharing using the same criteria as that of Beecher et al. (2000a), allowing us to further test for population differences in levels of sharing, as well as to test for a relationship between sharing and territory tenure in the Pennsylvania population.

If geographical variation in song type sharing is real, an adaptive explanation for this variation is that selection favours sharing more strongly in some populations than in others; by this reasoning, we would predict that the relationship between song sharing and territory tenure would be weaker in our Pennsylvania population than in the Washington and California populations. Alternatively, sharing could be favoured equally across populations, but maintained at different levels for other (perhaps proximate) reasons. If so, even when sharing is low on average, males that share more songs would be predicted to hold territories longer (Beecher et al. 1996). To determine whether population differences in song sharing reflect differences in selective advantage, it is necessary to determine the relationship between song type sharing and territory tenure in a population with a low level of song sharing.

A potential proximate explanation for population differences in song sharing is that differences in male turnover rates result in differences in sharing, with rapid turnover (low territory tenure) promoting low sharing. Song sparrows learn their songs during their first year of life (Marler & Peters 1987) and do not subsequently alter their repertoires as adults (Nordby et al. 2002). In Washington, young males learn their songs in the neighbourhood in which they will attempt to establish a territory as 1-year-olds, with the result that former song tutors are often among a male's territorial neighbours (Beecher et al. 1994; Nordby et al. 1999). Furthermore, young birds in Washington preferentially learn songs shared among their tutors, and tend to copy these songs completely, rather than combining phrases learned from different songs (Beecher et al. 1994; Nordby et al. 2000). As long as adult males survive and retain their territories from one year to the next, these learning strategies result in high levels of sharing. If adult mortality is high or territory fidelity is low, however, these same learning strategies might result in low levels of sharing, because few of a bird's former tutors will be present when he establishes his territory. To test whether low territory tenure can

explain low song sharing in our study population, we compared territory tenure in our low-sharing Pennsylvania population to that of Beecher et al.'s (2000a) high-sharing Washington population.

Although whole song sharing is low in our study population, sharing of parts of songs, such as initial trills, is much more common (Hughes et al. 1998). Burt et al. (2002) suggested that song sparrows may not have to share whole songs in order to interact via matching, because males in their study population matched songs that were similar only in general features of song introduction. Anderson et al. (2005) subsequently found that males in our Pennsylvania population were just as likely to match songs that shared only an introductory trill as they were to match wholly shared songs. Thus, sharing of parts of songs may be just as effective in allowing complex signalling interactions with neighbours as is sharing of whole songs, and therefore just as effective in promoting territory tenure. To test this possibility, we examined the relationship of territory tenure with sharing of introductory trills as well as with whole song sharing.

METHODS

Study Sites and Subjects

The study site was an approximately 11-ha section of state game land in Crawford County, Pennsylvania, bounded on the north and south sides entirely by water, and attached to land on the east and west sides only by narrow isthmuses. Thus, while this was not an island population per se, the birds within the study site were separated from song sparrows outside the study site, with the exception of the outermost territories on the isthmuses, and almost all territorial interactions were with other males within the study population.

Males were captured using mist nets or seed-baited traps, and banded with a U.S. Fish and Wildlife Service aluminium band and a unique combination of three colour bands. To study the relationship between territory tenure and song sharing, it is obviously necessary to know the full territory tenure of birds in the study. This study began in 1998, at which time all male song sparrows in approximately one-half of the site were banded and recorded; the study site was expanded to include the full area described above in 1999. In 1999, we were able to identify males that were new (in their first year of territory tenure) in the area that had been fully studied in 1998; in 2000 and subsequent years, we were able to identify all new males within the study site. One male was known to have begun his territory tenure in 1998, because he replaced a previously banded male that disappeared from the study site early in the breeding season.

We measured territory tenure in terms of the number of breeding seasons because song sparrows in this region are partially migratory, with some males migrating at least as far as North Carolina, U.S.A., during the winter and others remaining in the general vicinity of their territories (based on recovery of two U.S. Fish and Wildlife bands). The earliest nests at the study site typically hatch in mid-May;

some males are on territory in early March, but others are not present until early or mid-April (M. Hughes, unpublished data). Although some pairs continue to nest until mid-July, others cease nesting in late June. Thus, we considered males that held territories during May–June as holding territory for one breeding season. Males that either disappeared or lost their territory, or that successfully invaded and established territories during this time (either by replacing an existing male or by establishing a territory between two males) were counted as holding territory for half a breeding season. Beecher et al. (2000a) measured territory tenure in their year-round resident population by counting a bird as being on territory for 1 year if the bird survived at least until 1 June. We opted to give males ‘credit’ for 0.5 years on territory if they were present in May but not in June, because it is possible for a male to breed successfully during this time. This minor difference in assessing tenure between our study and that of Beecher et al. (2000a) is unlikely to affect the results, because we credited only seven (13%) of the individuals in this study with 0.5 years on territory during their tenure.

Our analyses include 55 focal males for whom the first year on territory was known, including all birds that began their territory tenure during 1998–2002 (1998: $N = 1$; 1999: $N = 8$; 2000: $N = 14$; 2001: $N = 15$; 2002: $N = 17$), with the exception of three males whose songs were not recorded before they disappeared from the study site. For comparison, Beecher et al. (2000a) included 45 focal males who entered their study during 1990–1993. We followed territory tenure for all focal males in our study site through 2005. At the end of the 2005 breeding season, six of these males were still on territory, and had territory tenures of 3.5 years ($N = 1$), 4 years ($N = 2$), 5 years ($N = 2$) and 7 years ($N = 1$), respectively.

Song Sharing

We recorded songs of males using Sony TCB5000 EV mono recorders with either Shure omnidirectional dynamic microphones in Sony PBR 330 parabolic reflectors or ATR Telemike shotgun microphones. In addition to recording songs of the focal males, we also recorded songs of all other males in the population (i.e. those that were already present in the population when the study began), because these males were neighbours to focal males. Our goal was to record at least 300 songs from each male; previous work has shown that new song types are only rarely recorded after 200 songs (Searcy et al. 1985; Podos et al. 1992; Nowicki et al. 1994; Hughes et al. 1998). We were able to meet the 300-song criterion for 63 (81%) of the males (including both focal males and neighbours) in this analysis. We recorded 153–299 songs from each of 13 males; for these males, at least 89 songs (mean = 182) from each male were recorded after the male’s last new song type had been sung, so it is unlikely that we missed a rare song type (82% of males with >300 songs recorded had sung their last new song type before the 150th song was recorded). One male, however, had only 99 songs recorded, so we excluded this male from

the analyses of repertoire size, because we were not confident that we had his full repertoire. In addition, to determine whether our analyses of song sharing were affected by inclusion of this male and his neighbours or by inclusion of the neighbours of the three unsampled focal males, we reran the song-sharing analyses without these males; none of the results changed.

Recordings were low-pass filtered at 10 kHz and digitized at 25 000 points/s. Sonograms were made using Avisoft (Avisoft Bioacoustics, Berlin; 1998 and 1999 recordings), Signal/RTSD v. 3.1 (Engineering Design, Belmont, Massachusetts, U.S.A.; 2000 recordings) or Signal v. 4.0 (all later recordings); although the sonograms resulting from these programs differ somewhat in aspect ratio, all sonograms were printed with the same resolution (256-point fast Fourier transform, FFT) and with labelled axes, facilitating comparisons between them. Sonograms of all song types (and all major variations within song types; see below) were printed for song-sharing comparisons. Song sparrow song is typically composed of alternating phrases of trills (one or more repeated notes) and note complexes (sequences of unrepeated notes) (Mulligan 1966). In addition to singing multiple song types, song sparrows often vary their songs within type; the differences between such variants (often only 1–2 notes) are much smaller than differences between song types (Podos et al. 1992). Major song variants printed for song-sharing comparisons included all insertions or deletions of trills or note clusters; variants that differed in the number of repetitions of syllables within trills or that differed by one or two notes within a note cluster were not printed, because such minor variations would not affect our assessment of song sharing.

To assess song sharing, we followed the criteria used in Beecher et al. (2000a): two songs were considered shared if at least one-half of their phrases were shared (see Fig. 1). We did not consider the number of repetitions within a trill when assessing sharing; nor did we consider the order of notes within note complexes, in part because additions and subtractions of notes are common in note complexes (Podos et al. 1992), and in part to ensure that our assessments of song sharing would not be overly conservative (see below). If any variants of the song types met this criterion, we considered the song types to be shared, even if other variants of the song types did not meet this criterion. As it is possible that the low levels of sharing previously reported for the Pennsylvania population resulted from more conservative assessments of what is shared (Hill et al. 1999), we attempted to be as liberal as possible in assessing sharing while still following the one-half match criterion. We also assessed sharing of the first trill only. Sharing was independently assessed by two of us (M.H. and R.C.A.) with very high agreement (see Results).

Following Beecher et al. (2000a), we calculated the measure of sharing for each focal bird as the sum of the number of songs shared (or, for first trill sharing, the number of first trills shared) with each of his neighbours, including immediate territorial neighbours as well as neighbours one territory away; if the two observers differed in their assessment of the total number of songs or first trills shared,

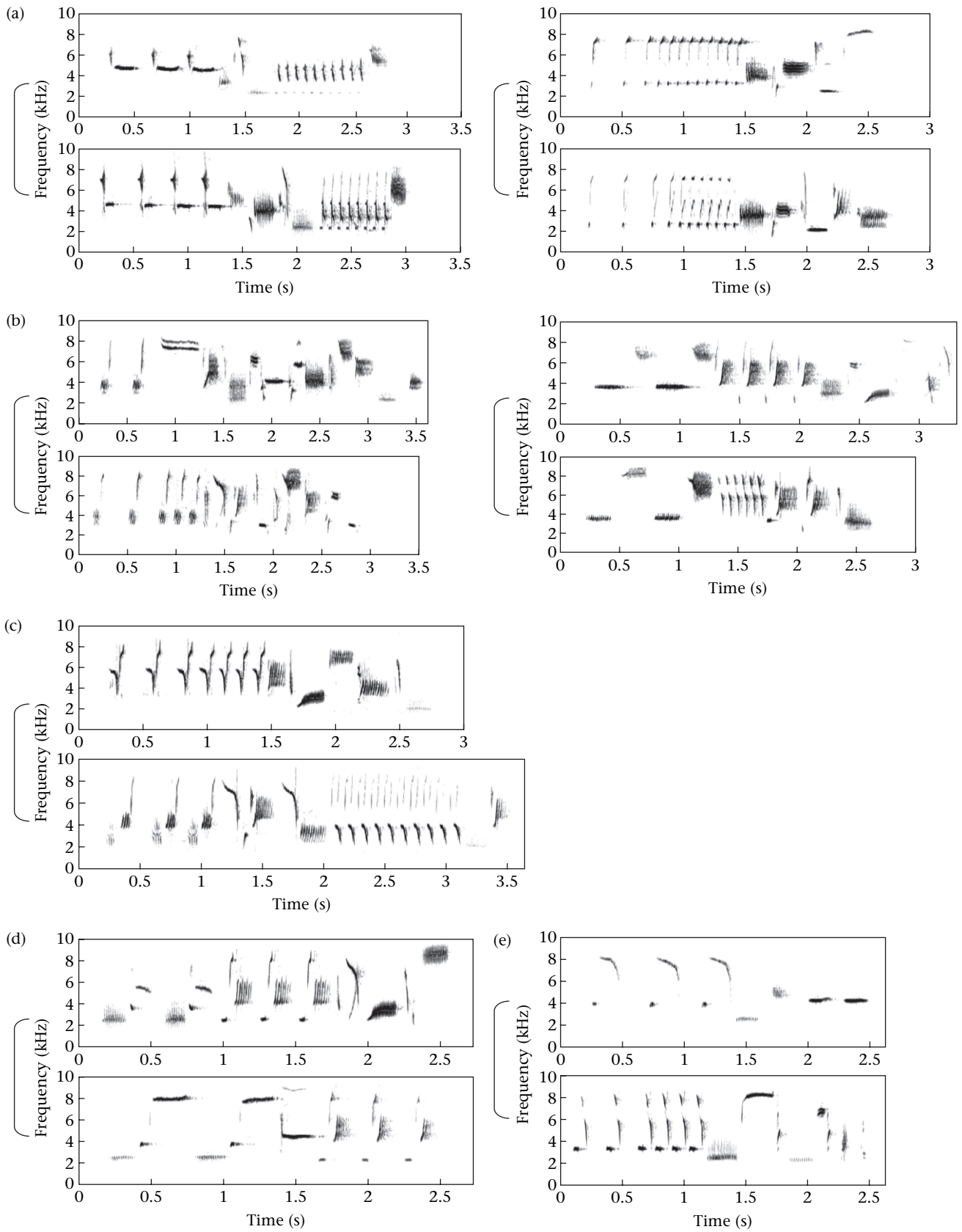


Figure 1. Examples of first trill and whole song sharing in song sparrows. (a) Whole song sharing. (These songs also share first trills.) (b) First trill sharing (but not whole song). (c) Unshared songs. (d) Whole songs classified as shared by only one observer. (e) First trills classified as shared by only one observer.

we used the average. Each focal male had 4–14 neighbours (mean = 7.4; median = 7), depending primarily on the structure of the habitat.

Statistical Analyses

We tested for correlations between repertoire size, song sharing, first trill sharing and the number of neighbours for each focal male using Pearson product–moment correlation coefficients. In addition, to compare levels of song sharing between Washington and Pennsylvania song sparrows, we binned song-sharing frequencies into categories (Beecher et al. 2000a) and analysed the data using chi-square tests.

Following Beecher et al. (2000a), we tested for a relationship between sharing and tenure in two ways. First, we tested for a correlation between sharing (either whole songs or first trills) and territory tenure using Pearson product–moment correlation coefficients. Second, we performed an ANOVA of tenure between bins of sharing. Using the same bin sizes as in Beecher et al. (2000a) for whole song sharing would result in half of the bins having few to no birds (see Fig. 3a); although the distributions of whole song sharing in Washington and first trill sharing in Pennsylvania were similar, 75% of the birds in our analysis fell into three of the bins used by Beecher et al. (2000a). Thus, we used smaller bin sizes to create sample sizes across bins that were as similar as possible. For whole song sharing, sharing was binned into seven categories, as follows: 0–1.5 songs ($N = 8$ birds), 2–3.5 songs ($N = 8$), 4–5.5 songs ($N = 12$), 6–7.5 songs ($N = 10$), 8–9.5 songs ($N = 5$), 10–11.5 songs ($N = 6$) and >12 songs ($N = 6$; the highest sharing in this bin was 26.5, average = 21.5). For first trill sharing, sharing was binned into eight categories, as follows: 0–2.5 first trills ($N = 2$), 3–5.5 first trills ($N = 6$), 6–8.5 first trills ($N = 11$), 9–11.5 first trills ($N = 9$), 12–14.5 first trills ($N = 8$), 15–17.5 first trills ($N = 8$), 18–20.5 first trills ($N = 4$) and >21 first trills ($N = 7$; the highest sharing in this bin was 37, average = 29.86).

Similarly, we tested for a relationship between repertoire size and tenure using both the Pearson product–moment correlation coefficient and an ANOVA of tenure between bins of repertoire size, as follows: 5–6 song types ($N = 10$ birds), 7 song types ($N = 12$), 8 song types ($N = 15$), 9 song types ($N = 10$) and 10–12 song types ($N = 7$).

We were unable to transform the tenure data from our study and that from Beecher et al. (2000a) to meet the assumptions of a parametric test; therefore, we compared territory tenure between populations using a Mann–Whitney U test. We also tested for differences in the distribution of tenure times using a chi-square test.

RESULTS

The median territory tenure for birds in this study and for birds in Washington (as calculated from data presented in Beecher et al. 2000a) was 2 years. The two populations did not differ in median tenure (Mann–Whitney U test: $U = 1408$, $N_1 = 55$, $N_2 = 45$, $P = 0.225$), or in the

distribution of birds across territory tenures (chi-square test: $\chi^2_7 = 10.257$, $P = 0.174$; Fig. 2). The Pennsylvania population appeared to be growing at the time of this study; there was a tendency for population size to increase over the years (1998–2002) when birds in this study joined the population (Pearson product–moment correlation: $r_2 = 0.944$, $P = 0.056$). Territory densities ranged from 27 to 36 territories/10 ha.

Focal males had 5–12 song types (median = 8) in their repertoires. The two independent assessments of song sharing agreed for over 98% of the song comparisons in both the ‘whole song’ and ‘first trill’ analyses (whole song agreement = 98.9%; first trill agreement = 98.1%). Following this assessment, we reviewed all disagreements between the two assessments to remove typographical errors (such as transposing the song types shared by two males; e.g. male 1 type A shared with male 2 type B versus male 1 type B shared with male 2 type A) and to ensure that we did not become more or less conservative across the comparisons; following these corrections, the final agreement was over 99% for both analyses (whole song agreement = 99.8%; first trill agreement = 99.2%).

The distribution of sharing of whole songs in the Pennsylvania population was significantly lower than that of the Washington population (chi-square test: $\chi^2_5 = 34.58$, $P < 0.001$; Fig. 3a), with more than two-thirds of the Pennsylvania birds falling into the lowest two categories of sharing. However, the distribution of sharing of first trills in Pennsylvania did not differ significantly from the sharing of whole songs in Washington (chi-square test: $\chi^2_5 = 6.81$, $P = 0.235$; Fig. 3b).

Whole song and first trill sharing were significantly correlated (Pearson product–moment correlation: $r_{53} = 0.899$, $P < 0.001$), and both whole song and first trill sharing were significantly correlated with repertoire size (whole song: $r_{52} = 0.332$, $P = 0.014$; first trill: $r_{52} = 0.361$, $P = 0.007$). In contrast to what Beecher et al. (2000a) found in Washington, we found that song sharing in our population (both whole song and first trill) was significantly correlated with the number of neighbours (whole song: $r_{53} = 0.565$, $P < 0.001$; first trill: $r_{53} = 0.651$, $P < 0.001$). To take this difference into consideration, we performed the song-sharing analyses in four ways: (1) to

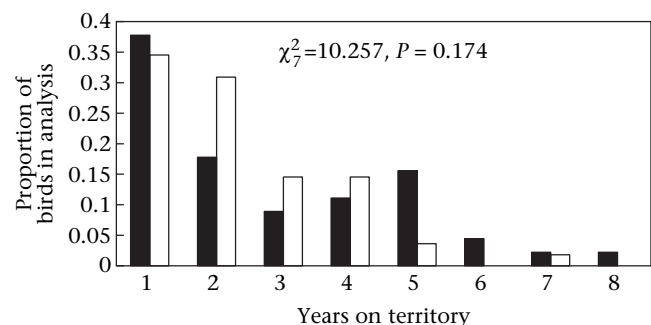


Figure 2. Comparison of territory tenure between populations of song sparrows. ■: Washington population, $N = 45$ (data from Beecher et al. 2000a); □: Pennsylvania population, $N = 55$ (this study).

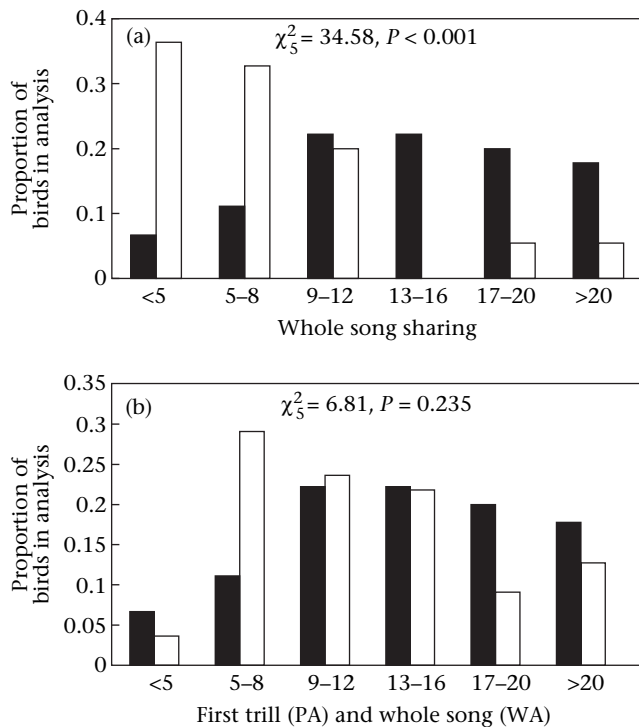


Figure 3. Distribution of (a) whole song sharing and (b) first trill sharing in Pennsylvania (PA) and whole song sharing in Washington (WA) in song sparrows. ■: Washington, $N = 45$ (data from Beecher et al. 2000a); □: Pennsylvania, $N = 55$ (this study). Sharing categories are the number of shared songs binned, as defined in Beecher et al. (2000a); see text for details.

replicate the analysis of Beecher et al. (2000a), we used the sum of songs shared across all neighbours as a measure of song sharing; (2) because song sharing was correlated with the number of neighbours in our population, we repeated this analysis using the same measure of song sharing, but divided by the number of neighbours for each individual (i.e. song sharing/neighbour); (3) we also performed the analyses using only the number of songs shared with immediate neighbours (i.e. those sharing a territorial boundary with the focal male) and (4) finally, we performed the analyses using the number of songs shared with immediate neighbours divided by the number of immediate neighbours, because the number of immediate neighbours was correlated with both whole song sharing ($r_{53} = 0.458$, $P < 0.001$) and first trill sharing ($r_{53} = 0.509$, $P < 0.001$).

Song sharing was not correlated with territory tenure (whole song: $r_{53} = 0.030$, $P = 0.828$; Fig. 4a; first trill: $r_{53} = 0.027$, $P = 0.847$; Fig. 5a). This result did not change when we adjusted the measure of sharing based on the number of neighbours (whole song sharing/neighbours: $r_{53} = 0.061$, $P = 0.657$; first trill sharing/neighbours: $r_{53} = 0.056$, $P = 0.682$), or when we restricted the neighbour group to immediate neighbours sharing a territorial boundary (whole song: $r_{53} = -0.014$, $P = 0.920$; first trill: $r_{53} = 0.029$, $P = 0.831$; whole song sharing/immediate neighbours: $r_{53} = 0.051$, $P = 0.710$; first trill sharing/immediate neighbours: $r_{53} = 0.124$, $P = 0.367$).

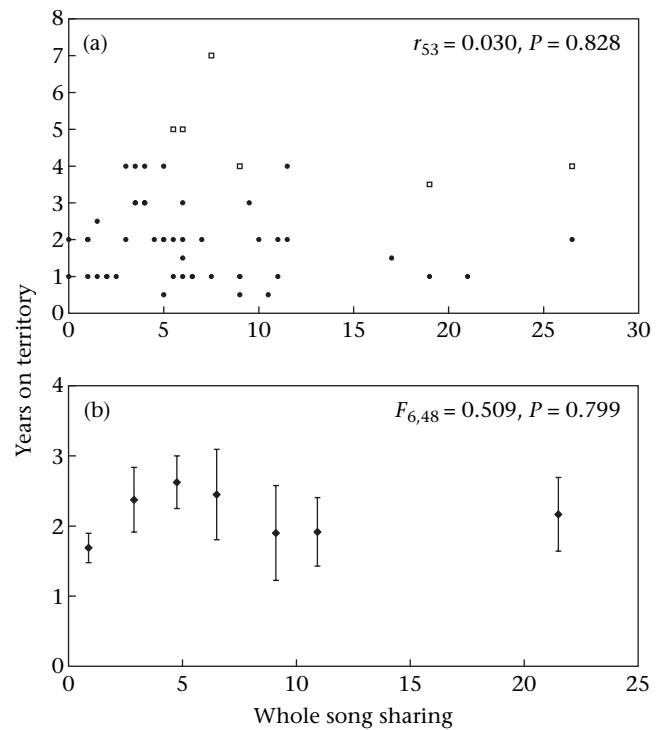


Figure 4. Relationship between whole song sharing and territory tenure in song sparrows. (a) Levels of song sharing in birds whose full territory tenure was known (●) and in birds that were still present on their territory at the conclusion of this study (□). (b) Mean \pm SE level of song sharing for each bin (0–1.5 songs, $N = 8$ birds; 2–3.5 songs, $N = 8$ birds; 4–5.5 songs, $N = 12$ birds; 6–7.5 songs, $N = 10$ birds; 8–9.5 songs, $N = 5$ birds; 10–11.5 songs, $N = 6$ birds; >12 songs, $N = 6$ birds; highest sharing = 26.5 songs).

Our song-sharing results were unchanged when we excluded birds that were still on territory at the end of the study (i.e. birds for which territory tenure may have been underestimated) (whole song: $r_{47} = -0.161$, $P = 0.270$; whole song sharing/neighbour: $r_{47} = -0.116$, $P = 0.426$; whole song sharing with immediate neighbours only: $r_{47} = -0.175$, $P = 0.229$; whole song sharing with immediate neighbours/immediate neighbour: $r_{47} = -0.117$, $P = 0.423$; first trill: $r_{47} = -0.140$, $P = 0.336$; first trill/neighbour: $r_{47} = -0.074$, $P = 0.614$; first trill sharing with immediate neighbours only: $r_{47} = -0.138$, $P = 0.345$; first trill sharing with immediate neighbours/immediate neighbour: $r_{47} = -0.072$, $P = 0.622$).

Following Beecher et al. (2000a), we also performed an analysis using binned data. We found no difference in territory tenure between song-sharing bins (ANOVA: whole song: $F_{6,48} = 0.509$, $R^2 = 0.06$, $P = 0.799$; Fig. 4b; first trill: $F_{7,47} = 0.621$, $R^2 = 0.085$, $P = 0.736$; Fig. 5b). (Note that the degrees of freedom in these analyses differed because the number of bins differed; see Methods for details.)

Territory tenure was also not correlated with repertoire size (Pearson product–moment correlation: $r_{52} = 0.083$, $P = 0.552$; Fig. 6a); however, in the binned analysis, there were significant differences in territory tenure between bins of repertoire size (ANOVA: $F_{4,49} = 4.960$, $R^2 = 0.288$, $P = 0.002$; Fig. 6b).

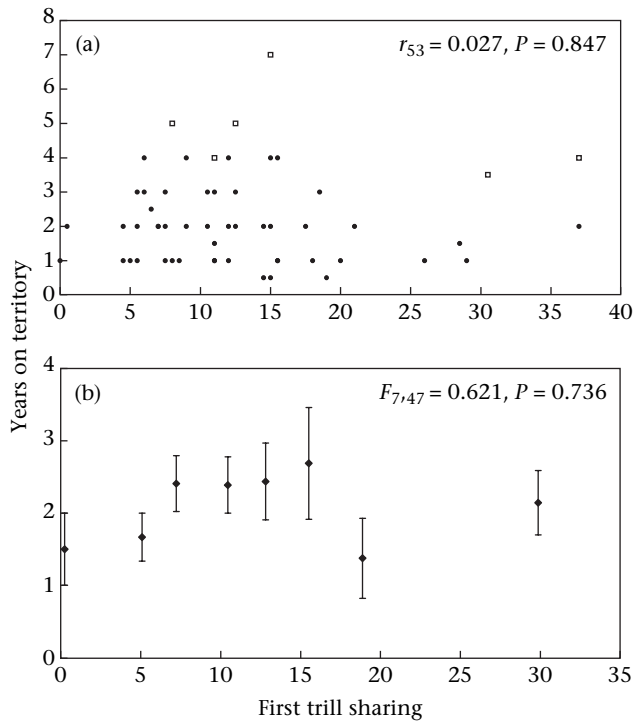


Figure 5. Relationship between first trill sharing and territory tenure in song sparrows. (a) Levels of first trill sharing in birds whose full territory tenure was known (●) and in birds that were still present on their territory at the conclusion of this study (□). (b) Mean \pm SE level of first trill sharing for each bin (0–2.5 first trills, $N = 2$ birds; 3–5.5 first trills, $N = 6$ birds; 6–8.5 first trills, $N = 11$ birds; 9–11.5 first trills, $N = 9$ birds; 12–14.5 first trills, $N = 8$ birds; 15–17.5 first trills, $N = 8$ birds; 18–20.5 first trills, $N = 4$ birds; >21 first trills, $N = 7$ birds; highest sharing = 37 first trills).

DISCUSSION

Song sparrows in at least two populations from Washington share large proportions of their song repertoires with neighbouring males (Beecher et al. 1994; Hill et al. 1999), and in at least one of these populations, males with higher levels of song sharing hold territories longer than do males with lower levels of sharing (Beecher et al. 2000a). Similarly, in a California population with high levels of sharing, return rates are significantly higher for males that share songs (Wilson et al. 2000). Thus, song sharing is correlated with territory tenure in at least two populations in which sharing of songs is common. In the Pennsylvania population, average whole song sharing is low but partial song sharing is high (Hughes et al. 1998). However, we found no evidence for a relationship between either whole or partial song sharing and territory tenure in this population. Thus, the selective advantage of song sharing appears to differ between populations.

Song Sharing

Using the criterion that at least one-half of the song is shared (Beecher et al. 2000a), we found that the frequency of whole song sharing in our Pennsylvania population of

song sparrows was significantly lower than that of the Washington population studied by Beecher et al. (2000a) (Fig. 3a), confirming our previous report that whole song sharing is lower in Pennsylvania (Hughes et al. 1998) than it is in at least some western populations (Hill et al. 1999; Wilson et al. 2000). Whole song sharing has also been reported to be low in other eastern populations (Maine: Borror 1965; Ontario: Harris & Lemon 1972), but quantitative data are lacking. Whether there is a consistent east/west difference in levels of whole song sharing remains to be determined.

Levels of song sharing may be affected by rates of territory turnover. Even if males learn songs from older males that hold territories in the areas where they will later establish territories, as occurs in Washington (Beecher et al. 1994; Nordby et al. 2002), sharing can still be low if territory turnover is rapid enough. Demographic differences, however, do not seem to explain the difference in whole song sharing between Pennsylvania and Washington. We found no difference in median tenure time between the populations, nor did we find a difference in the distribution of tenure times (Fig. 2). Beecher (1996) reported an annual survival rate for males of 60–70% in the Washington population, while in our Pennsylvania population, the median annual survival rate for males during this study was 60% (range 52–68%). Thus, while survival may be somewhat lower for males in Pennsylvania than in Washington in some years, in other years survival is comparable.

More subtle differences in territorial systems also might explain differences in sharing. Sharing should be reduced if some males survive as territory holders but shift the location of their territories from one year to the next. In Pennsylvania, 28% (median over the course of this study) of the males that return each year have territorial boundaries that are nonoverlapping with their boundaries the previous year (M. Hughes, unpublished data). Most of these territorial relocations are within one to two territories of their previous territory. Comparable data have not been published for other song sparrow populations in which sharing has been measured, so we cannot say whether this level of territory movement is high or low. The fact that 72% of returning males in our population held territories that overlapped with their previous year's territory, however, argues that territory movement ought not to lower sharing levels radically.

Territorial density may also affect song sharing; perhaps in less dense populations, young birds are less able to assess what songs are shared among neighbour groups or are less able to establish territories between former tutors (if low density reflects lower levels of resources, for example). The density of territories in our Pennsylvania population (27–36 birds/10 ha) was somewhat lower than that of the Washington population (30–40 birds/10 ha; Hill et al. 1999) studied by Beecher et al. (2000a), and birds in our population also had smaller neighbour groups (4–14, mean = 7.4; median = 7) than the Washington population (7–18, mean and median = 12; Beecher et al. 2000a). However, Hill et al. (1999) found no difference in song sharing between the Washington population studied by Beecher et al. (2000a) and a migratory population

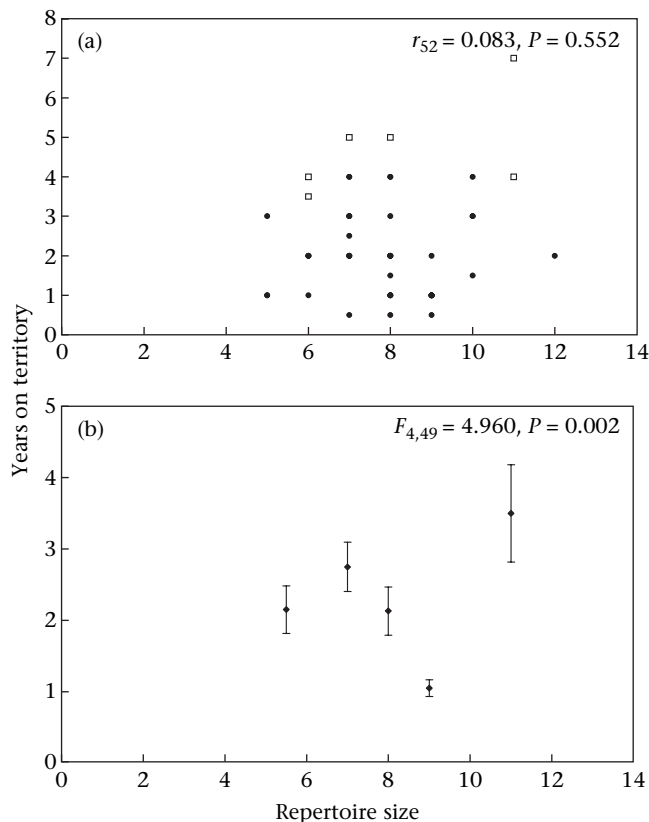


Figure 6. Relationship between repertoire size and territory tenure in song sparrows. (a) Repertoire sizes of birds whose full territory tenure was known (●) and of birds that were still present on their territory at the conclusion of this study (□). (b) Mean \pm SE repertoire size for each bin (5–6 song types, $N = 10$ birds; 7 song types, $N = 12$ birds; 8 song types, $N = 15$ birds; 9 song types, $N = 10$ birds; 10–12 song types, $N = 7$ birds).

elsewhere in the state that had a density considerably lower than that of our population (2–8 birds/10 ha).

Thus, there appears to be no evidence for demographic or ecological differences between these populations sufficient to account for the observed differences in song sharing, suggesting that song sparrows in Pennsylvania may follow a different song-learning strategy. This difference could reflect when songs are learned: rather than learning songs after dispersal, song sparrows in Pennsylvania could learn songs before or during dispersal, ultimately establishing territories at some distance from their former song tutors. A difference in song learning could also reflect how songs are learned: if song sparrows in Pennsylvania are less likely to learn whole songs and more likely to recombine song phrases learned from different tutors, then even if they settle adjacent to their former tutors, they may only share song phrases with them, not whole songs. As predicted by such a strategy, in Pennsylvania, sharing of song phrases is significantly more common than is sharing of whole songs (Hughes et al. 1998; this study; Fig. 3). Geographical variation in song learning has been documented in white-crowned sparrows, *Zonotrichia leucophrys* (Nelson et al. 1995, 1996); whether Washington and Pennsylvania

song sparrows differ in song-learning strategies remains to be tested.

Another possibility is that song sparrows show phenotypic plasticity in song learning: how a male learns song may depend on what he hears during song development. When exposed to song tutors singing many shared songs, males may maximize sharing by preferentially learning shared songs and copying them completely, as has been observed in Washington (Beecher et al. 1994; Nordby et al. 1999, 2000). Under conditions of low song sharing, by contrast, males may maximize song diversity by copying and recombining song phrases from many tutors. Common garden experiments with different levels of sharing among tutors are needed to distinguish between these possibilities.

Song Sharing and Territory Tenure

Although the average level of whole song sharing was low in our study population, the range of sharing (0–26.5 shared songs/male, summed across all neighbours) was comparable to that found in Washington (1–31, Beecher et al. 2000a). Thus, despite the low levels of song sharing on average in this population, some individual males nevertheless had high levels of song sharing, raising the possibility that variation in whole song sharing could function similarly in populations with high and low sharing. We found no evidence that whole song sharing was associated with success in holding a territory, however (Fig. 4). Whole song sharing was not correlated with territory tenure, nor were there any significant differences between binned categories of sharing and territory tenure. The results were similar when we restricted our analysis to immediate neighbours or when we included all neighbours, or when we corrected for the number of shared songs based on the number of neighbours. In short, the sharing of whole songs was not related to territory tenure in this population of song sparrows.

As reported previously (Hughes et al. 1998), we found that sharing of first trills in the Pennsylvania population was considerably more common than was the sharing of whole songs. In fact, the frequency distribution of first trill sharing in Pennsylvania did not differ significantly from the frequency distribution of whole song sharing in Washington (Fig. 3b). Furthermore, Anderson et al. (2005) showed that Pennsylvania males are just as willing to match songs that share only the first trill as they are to match wholly shared songs. This evidence suggests that partial song sharing may substitute for whole song sharing in the Pennsylvania population, and that territory tenure may be associated with the level of partial song sharing rather than the level of whole song sharing. However, we also found no evidence for a territorial advantage to sharing first trills (Fig. 5). First trill sharing was not correlated with territory tenure in the full analysis, the binned analysis, the analysis restricted to immediate territory neighbours, or the analysis of first trill sharing/neighbour. Thus, even though levels of first trill sharing were high (this study), and males match songs that share first trills (Anderson et al. 2005), we conclude that sharing of first trills is not related to territory tenure in this population.

Repertoire size and territory tenure in song sparrows are strongly correlated in a population on Mandarte Island, British Columbia (Hiebert et al. 1989; Reid et al. 2005a), but not in a population in Washington (Beecher et al. 2000a); in the Pennsylvania population studied here, the relationship was unclear. Although we found significant differences in territory tenure between binned categories of repertoire size, this was largely the result of the long tenure times for males in the highest repertoire size category (10–12 song types) compared to those in the next highest repertoire size (9 song types); among focal males in this study, males with nine song types had unusually short territory tenures (Fig. 6b). The overall correlation coefficient between repertoire size and territory tenure was near zero. Thus, among focal males in our study, territory tenure was not related to song sharing or repertoire size. One possible explanation for the observed population differences in the relationship between repertoire size and tenure is that the Mandarte population, in which repertoire size is correlated with tenure, is unusual in being an isolated island population with high levels of inbreeding (Keller & Arcese 1998). How isolation, inbreeding, or selection for inbreeding avoidance would lead to a relationship between territory tenure and repertoire size, however, is not clear.

The Evolution of Song Repertoires

Beecher et al. (1994, 2000a) suggested that song repertoires have evolved in large part to allow song sharing with multiple neighbours. Support for this hypothesis includes evidence that male song sparrows use their shared song types when interacting with territorial neighbours in Washington (Beecher et al. 2000b; Burt et al. 2001) and in California (Nielsen & Vehrencamp 1995), and that the number of shared songs is a better predictor of territory tenure than is repertoire size in Washington (Beecher et al. 2000a). Song sharing is also correlated with return rates in California (Wilson et al. 2000). Although territory tenure of song sparrows on Mandarte Island is correlated with repertoire size (Hiebert et al. 1989; Reid et al. 2005a), song sharing has not been measured in this population, so it is not known whether sharing is a better or worse correlate. In our Pennsylvania population, we found no correlation between territory tenure and song sharing, either at the whole song or partial song level.

An alternative view of the evolution of song repertoires is that song repertoires in song sparrows have evolved because of female preferences for large repertoires (Searcy & Andersson 1986; Searcy & Yasukawa 1996). Although Searcy (1984) found no relationship between repertoire size and female choice for pairmates, a more recent study by Reid et al. (2004), taking advantage of the long-term Mandarte Island data set, found that first-year males were more likely to acquire a mate, and acquired a mate earlier in the season, if they had a larger song repertoire. Reid et al.'s (2004) study was better positioned to detect patterns in female choice than was Searcy's (1984) study, both because of a larger sample size and because other variables that may affect female choice (e.g. age, density,

population sex ratio, etc.) could be controlled for in the statistical analysis (Reid et al. 2004). Males with large repertoires are superior in fitness in this population, in part because of increased longevity and territory tenure (Hiebert et al. 1989; Reid et al. 2005a); in addition, song repertoire size is negatively correlated with inbreeding, which is also associated with depressed cell-mediated immune responses (Reid et al. 2003, 2005b). Female preferences for males with large repertoires, then, would probably be adaptive. The effect of early developmental stress on song characteristics, including repertoire size, has been proposed as a mechanism enforcing the reliability of song as a signal of male quality in songbirds (Nowicki et al. 1998; Nowicki & Searcy 2005; Searcy & Nowicki 2005). In addition to the correlative evidence from Mandarte Island, there is experimental evidence that female song sparrows respond preferentially to large repertoires during courtship (Searcy & Marler 1981; Searcy 1984). Analogous experimental evidence showing that higher levels of song sharing lead to improved territory defence or increased territory tenure is lacking.

The two hypotheses proposed above for the evolution of song repertoires (i.e. that they have evolved in response to the advantages of song sharing between males or have evolved because of female preferences) are not mutually exclusive. Nor do these two hypotheses exhaust the list of possible explanations for the evolution and maintenance of song repertoires. Thus, evidence in favour of one hypothesis is not evidence against the other, nor does evidence against one hypothesis constitute evidence in support of the other. In our Pennsylvania study population, however, we found no evidence that song sharing is associated with territory tenure, and thus no evidence for the hypothesis that repertoires are adaptive because they promote song sharing between males.

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