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Melissa Hughes · Stephen Nowicki
William A. Searcy · Susan Peters

Song-type sharing in song sparrows: implications for repertoire function and song learning

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Abstract One hypothesis for the function of song repertoires is that males learn multiple song types so that they may share songs with neighbors, allowing them to match during territorial interactions. In at least one song sparrow population, in Washington, territorial males share a high proportion of song types with their neighbors and use these shared songs in matching. We recorded song sparrows in Pennsylvania and quantified sharing of whole songs and song segments. We found that song sharing is an order of magnitude less common in the Pennsylvania population. We found sharing of song segments to be significantly more common than the sharing of whole songs in three of the five fields we examined, while we found no significant differences between whole and partial song sharing in the remaining two fields. Finally, we found no evidence that sharing is greater between birds in the same field compared to birds in different fields. Taken with the data from Washington song sparrows, these results provide evidence for intraspecific geographic variation in the organization of song repertoires, and suggest that song sharing has not been a strong selective force in the evolution of song repertoires in song sparrows as a species. Furthermore, Washington and Pennsylvania song sparrows differ in how they learn song, in that Washington birds copy whole songs, while Pennsylvania birds appear to copy and recombine song segments, as has been found in laboratory studies of song learning. Thus both song learning and the function of song repertoires differ between populations of song sparrows. Such intraspecific geographic variation offers a unique opportunity to explore the ecological and historical factors which have influenced the evolution of song.

Key words Birdsong · Repertoires · Song sharing · Song learning · Geographic variation

Introduction

Males of many species of songbirds sing more than one version of song. In a few cases, notably among North American warblers, males produce different song types in specific contexts, suggesting that each song conveys a separate message (Spector 1992). In most species, however, the different song types sung by an individual all appear to have the same message and function, and are therefore said to be redundant. One explanation for the occurrence of repertoires of redundant song types is that such repertoires evolved through sexual selection (Catchpole 1982; Searcy and Andersson 1986). This hypothesis is supported by observational studies showing correlations between repertoire size and male mating success (Catchpole 1980; Hasselquist et al. 1996), by laboratory playback studies showing that larger repertoires function better in stimulating female courtship (Catchpole et al. 1984; Searcy 1984), and by field playback experiments showing that rival males are more intimidated by larger repertoires (Krebs et al. 1978; Yasukawa 1981). An alternative hypothesis is that repertoires have evolved to allow song matching between males. Song matching occurs when a male replies to a rival's song with the same song type, and is thought to be a method of directing an aggressive signal to a specific opponent (Brémond 1968; Armstrong 1973), or a form

M. Hughes[1]
Institut für Verhaltensbiologie, Haderslebenerstrasse 9,
Free Universität-Berlin, D-12163 Berlin, Germany

S. Nowicki (✉) · S. Peters
Evolution, Ecology and Oranismal Biology Group,
Department of Zoology, Duke University,
Box 90325, Durham, NC 27708-0325, USA
e-mail: snowicki@acpub.duke.edu, Fax: +1-919-6846168,

W.A. Searcy
Department of Biology, University of Miami,
Coral Gables, FL 33124-0421, USA

Present address:
[1]M. Hughes, Department of Ecology
and Evolutionary Biology, Princeton University,
Princeton, NJ 08544-1003, USA

of graded signaling, such that matching songs are more aggressive than nonmatching songs (Krebs et al. 1981). In either case, possession of a repertoire increases the number of rivals that can be matched.

Recent work on song sparrows (*Melospiza melodia*) in Washington state suggests a function of vocal repertoires related to this latter hypothesis (Beecher et al. 1994, 1996; Beecher 1996). Males typically sing 7–11 distinctive song types and share a large proportion of their repertoires (about 40% on average) with each of their territorial neighbors. The similarity of these shared songs is often exact and detailed (see Fig. 1 in Beecher et al. 1996). This extensive song sharing is thought to be a consequence of a song-learning strategy in which a young male copies whole songs from older males, choosing as tutors males that hold territories near where he will later establish his own territory, and learning preferentially those songs sung by more than one of the older males (Beecher et al. 1994; Beecher 1996).

However, song sparrows in this Washington population show only chance levels of song type matching to neighbor songs, (Stoddard et al. 1992). Instead, playback experiments reveal that males in this population respond to a neighbor's song with another song type shared with that neighbor, rather than with the particular song type just heard, a response that has been termed "repertoire matching" (Beecher et al. 1996). Beecher et al. (1996) point out that repertoire matching may be more efficient and more effective than song type matching – more efficient because repertoire matching is possible when the neighbor sings one of his unshared songs as well as when he sings a shared song type, and more effective because the signal demonstrates that the responding male has identified the particular singer as an individual. The pattern of song type sharing thus has important implications for the function of song repertoires as well as for theories of song development.

Repertoire size in song sparrows has been shown to correlate in the field with male reproductive success (Hiebert et al. 1989), and large repertoires have been shown in the laboratory to be more effective in sexually stimulating females (Searcy and Marler 1981; Searcy 1984). These results are consistent with the hypothesis that repertoires have evolved in this species because of sexual selection favoring larger numbers of song types. Nevertheless, given the extensive song sharing observed in Washington song sparrows, the use of song sharing in repertoire matching, and a strategy of song learning that maximizes song sharing, Beecher et al. (1994) suggest

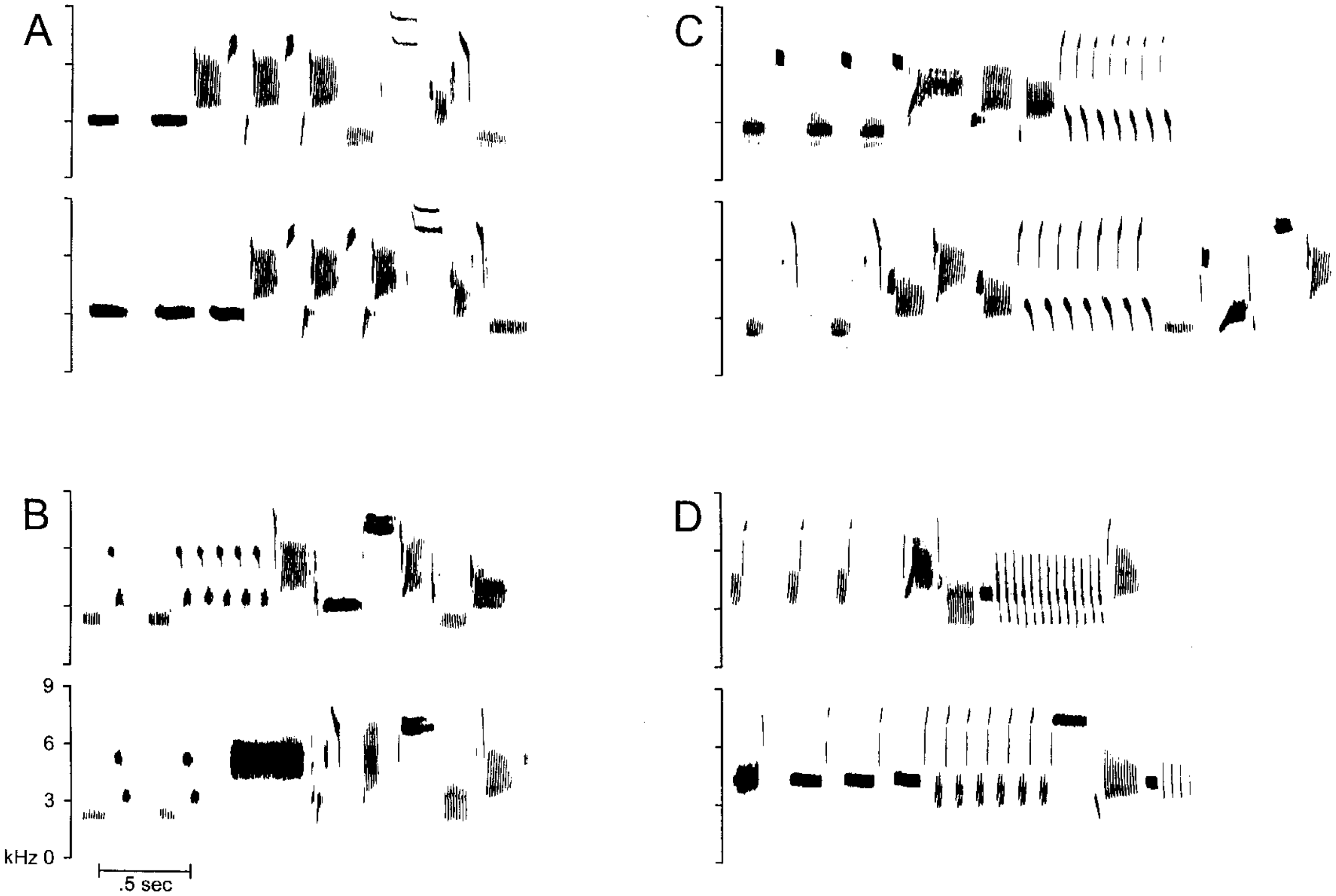

Fig. 1A–D Examples of the four categories of song sharing. **A** Whole-song sharing. **B** First-trill sharing. **C** Internal-trill sharing. **D** Other sharing (in this case, the first trill of one song and the internal trill of the other are shared) that "it may be sharing of song types with several neighbors, rather than the number of song types per se, that is the target of selection" in the evolution of repertoires. In other words, the primary function of song repertoires may be to allow males to share song types with several neighbors simultaneously.

The pattern of song learning observed in the field for Washington song sparrows (Beecher et al. 1994) also appears to contradict some conclusions that have emerged from the extensive laboratory studies of song development in this species (Marler and Peters 1977, 1987, 1988; Beecher 1996). Most importantly, young males in the laboratory typically copy only parts of songs, such as syllables, rather than whole songs, as found in the Washington field study. The implication is that this particular aspect of learning is distorted by the laboratory learning environment. In addition, the laboratory studies gave no hint that males preferentially learn songs shared by more than one of their tutors. Beecher (1996) notes that the design of most laboratory experiments, especially those using tape tutoring, precludes such a discovery.

Although Beecher and colleagues have suggested that song sharing is important to understanding both the function of repertoires and strategies of song learning in song sparrows, it is not clear that sharing is widespread in the species as a whole. Based on their study of song sparrows in Ontario, Harris and Lemon (1972) concluded that "entire songs were rarely shared among two or more birds." Borror (1965) came to a similar conclusion concerning song sharing in Maine, as did Mulligan (1966) and Baker (1983) in California. Moreover, Harris and Lemon (1972) found that sharing of parts of songs was much more common than sharing of whole songs in Ontario. While the details of how song sharing was assessed differ somewhat among these studies, it seems unlikely that the large differences reported between populations in terms of song sharing are due solely to differences in methodology. Patterns of song sharing and learning thus appear to vary geographically. Accordingly, we have investigated song sharing in another song sparrow population, in Pennsylvania, recording song repertoires and quantifying sharing in order to compare this population to the Washington population. Our study of song sharing had two objectives: (1) to test the generality of the hypothesis that song sharing and repertoire matching represent the primary function of song repertoires in song sparrows, and (2) to test the generality of conclusions regarding the song-learning strategy of song sparrows with regards to the copying of whole songs rather than parts of songs in the field, and the validity of the resulting criticisms of laboratory song-learning results.

Methods

Song sparrows were recorded during 1995 and 1996 in the vicinity of Hartstown, Crawford County, Pennsylvania. The study sites were on a state gameland, and consisted of grassy fields of varying sizes bordered by woods. The fields are regularly mowed by the Pennsylvania Game Commission and so persist from year to year. Male song sparrows defend territories around the perimeter of the fields, singing almost exclusively from trees and shrubs along the border, and interacting mainly with their neighbors on either side in the hedgerow. A field is thus both a geographic area and a social neighborhood for song sparrows.

We recorded birds in two fields in 1995 (Parking and Isthmus) and in three fields in 1996 (Eagle, Pony, and Apple). All birds were color-banded for individual identification. Recordings were made in May and June, well after the establishment of territories. We recorded using either a Marantz PMD 221 or a Sony TCM 5000EV tape recorder with either a Sennheiser ME88 shotgun microphone or a Sony ECM-170 microphone in a Sony PBR-330 parabola. We considered a bird's repertoire fully recorded when we had at least 200 songs; Searcy et al. (1985) found that novel song types only rarely occurred after the 200th recorded song. In the present study, in all but one case in which more than 200 songs were recorded, no new song types were recorded after the 200th song. We included in our statistical analysis only birds which met the 200-song criterion, with the exception of bird 2 in Isthmus Field, which was included with 194 songs.

Song sharing was assessed visually from sonagrams produced on a Kay Elemetric sonagraph (1–9 kHz, 300-Hz frequency resolution, 50-ms time resolution). In general, we were liberal in our assessment of whether songs or parts of songs were shared, in order to be conservative about accepting differences in the extent of sharing between Pennsylvania and Washington. We examined sonagrams of all songs recorded for each bird, and printed exemplars of each song type that we found, and of all variants with unique notes or note sequences. We compared every song type of each bird to all other song types of birds recorded in the same year, and classified each match to one of four categories of song sharing, based on the sharing of trills (repeated sequences of one or more notes) and note complexes (unrepeated sequences of notes) (Mulligan 1966). We considered two trills to be shared if they contained the same notes at the same acoustic frequencies. The number of repetitions in the trill was not a criterion in deciding whether two trills were shared. We considered two note complexes to be shared if at least half of the notes were the same in both. In all cases where the sharing of a trill or note complex was ambiguous based on these criteria, we classified the trill or note complex as shared. For example, there were a small number of cases in which trills were identical except for minor differences such as the presence in only one trill of an additional note, or slight differences in the acoustic structure of one note; these trills were all classified as shared.

Most song sparrow songs begin with a trill, and thereafter trills alternate with note complexes (e.g., trill – note complex – trill – note complex). Songs may occasionally include only a single phrase, but more usually include three, four, or more phrases (Podos et al. 1992). We defined four categories of song sharing, as follows (see also Fig. 1).

1. "Whole-song sharing" requires that the songs share the first trill. In addition, if the songs contain an internal trill, the internal trill must also be shared. Any note complexes in these songs may also be shared, but note complex sharing is not necessary if both the first and internal trills are shared. If the songs contain no internal trill, however, then the songs must share the first trill and the following note complex. Note that this definition of whole-song sharing does not require songs to be completely identical, but only identical in their trill portions, maximizing our likelihood of finding whole-song sharing between individuals' repertoires. Beecher et al. (1996) give three examples of pairs of songs which they consider to be representative of song sharing in their population, including one song pair which shares only the introductory and internal trill. By our criteria, all three would be classified as whole-song sharing. Thus our category of whole-song sharing corresponds to song sharing as seen in the Washington population.
2. "First-trill sharing" requires that the songs share at least the first trill. In some cases, the subsequent note complex is also shared, but note complex sharing is not necessary.

3. "Internal-trill sharing" requires that the songs share at least one internal trill. In some cases, songs also share the note complex preceding and/or following the internal trill, but again note complex sharing is not necessary.
4. "Other sharing" includes songs that do not meet the above criteria but that share some note sequences. The most common kinds of sharing in this category are (a) songs that share a trill, but in one song the trill is the first trill and in the other it is an internal trill, (b) one song has notes in a note complex which another song repeats as a trill, and (c) songs share only a note complex.

A given pair of songs was only assigned to one category, that of the highest category of sharing whose criteria were met. For example, two songs showing whole-song sharing by definition must share the first trill, but they would only be counted as showing whole-song sharing, not first-trill sharing. Thus these categories of sharing allow us to assess the degree of whole-song sharing versus the degree of sharing only specific parts of songs. This comparison is important because Beecher et al. (1994, 1996) found that birds in the Washington population rarely share only parts of songs, a result which is inconsistent with laboratory song-learning experiments (Marler and Peters 1987, 1988), in which birds usually copy parts of songs, not whole songs.

One observer (M.H.) performed all song comparisons. To confirm the reliability of our method, a second observer (S.P.) independently compared all song types within one field. These two observers exhibited 100% agreement on which whole songs were and were not shared among the eight males and 56 song types recorded in this field. For all categories of sharing combined and all possible comparisons, the observers agreed for 1541 of 1552 comparisons (99.3% agreement). Of the 115 comparisons for which at least one observer found sharing in any category, the observers agreed for 104 comparisons (90.4% agreement).

Whereas only birds we considered fully recorded were included in the statistical analyses, we compared the songs of these birds to those of all birds for which we had recorded any songs (Table 1), to maximize the potential for finding shared songs. Beecher et al. (1994, 1996) found that birds in Washington share on average 40% of their repertoire with any given neighbor. To test whether whole-song sharing differs between Pennsylvania and Washington, we randomly selected a fully recorded immediate neighbor for each of our fully recorded males, and used a χ^2 test to compare the observed level of whole-song sharing in our neighbor pairs to an expected level of 40%. As stated above, our category of whole-song sharing agrees with the examples of song sharing given by Beecher et al. (1996).

To determine whether birds were more likely to share whole songs or parts of songs only, we calculated for each male the proportion of his songs that were shared with other birds in the same field for each of the four categories of sharing: whole song, first trill only, internal trill only, other. We then tested for differences in the frequency of the four categories of sharing, using Friedmann's nonparametric repeated-measures ANOVA, with individual males as sample points.

If song sharing functions in territorial interactions, for example by allowing matching during territorial disputes, then song sharing may be greatest with territorial neighbors. Indeed, Beecher et al. (1994, 1996) found song sharing primarily between territorial neighbors. We therefore repeated the above analysis, counting only songs shared with immediate territorial neighbors, to ask whether birds share a greater proportion of their repertoire with neighbors as whole songs, first trills, internal trills, or other song components. Immediate territorial neighbors were defined as those birds within the field with whom the focal bird shared a boundary along the hedgerow.

Finally, we also tested whether birds share more songs, in any sharing category, with birds in the same field than with birds in other fields recorded in the same year (see Table 1). In 1995, we recorded males in only two fields, and so we compared the proportion of a bird's repertoire that was shared with birds within its own field versus the proportion shared with birds in the other field. Because we recorded males in three fields in 1996, we compared sharing in each field with the average sharing with birds in the other two fields. Each field and category of sharing were tested separately, using Wilcoxon signed-ranks tests.

Results

Among the 31 males that we considered to be fully recorded, repertoire sizes ranged from 4 to 12, with a mean of 7.9 (Table 1). We found no correlation between number of song types and number of songs recorded ($r = -0.166$, $P > 0.05$), which supports our conclusion that we obtained the full repertoires of these males. Among the five additional males that we considered not to be fully recorded, mean repertoire size was 6.4, so we probably missed on average about 1.5 song types per male in this group.

For the sharing of whole songs, the fully recorded males in our sample shared on average 2.1 of their 7.9 songs, or a mean of 24% of their repertoires, with another male in the same field (Table 1). Because most interactions are with immediate neighbors, it is perhaps more relevant that these males shared on average only 0.6 whole-song types, or an average of 6% of their repertoires, with any immediate neighbor, and that 18 of 27 males for which we recorded immediate neighbors shared no songs with their neighbors (Table 1). We also calculated the proportion of whole-song sharing between each fully recorded male and one, randomly chosen, fully recorded immediate neighbor. This analysis is relevant to the likelihood that a territory owner will be able to interact with a particular neighbor through matching, and is also the measure reported for the Washington population (Beecher et al. 1994, 1996). Focal males in our population shared on average 0.3 song types with their randomly chosen neighbor, or a mean of 3% of their repertoires. The number of song types shared by pairs of neighbors was significantly lower than the number predicted based on the Washington population ($\chi^2 = 115.3$, $df = 25$, $P < 0.001$). Of the 27 focal males, 22 (81%) shared no song types with their randomly chosen neighbor, whereas only 5 (19%) shared one or more song types.

In three of our five fields, birds shared overall a significantly greater proportion of their repertoires as parts of songs (first trills, internal trills, or other components) than as whole songs (Apple Field: Friedman statistic = 12.1, $P = 0.007$, Fig. 2A; Eagle Field: Friedman statistic = 14.2, $P = 0.003$, Fig. 2C; Isthmus Field: Friedman statistic = 8.3, $P = 0.04$, Fig. 2E). In the remaining two fields, there was no significant difference between sharing of whole songs, first trills, internal trills, or other (Pony Field: Friedman statistic = 0.3, $P = 0.88$, Fig. 2B; Parking Field: Friedman statistic = 3.8, $P = 0.29$, Fig. 2D). In general, birds tend to be at least as likely or significantly more likely to share parts of songs rather than whole songs.

Table 1 Whole-song sharing in Pennsylvania song sparrows. Included are numbers of song types shared with any bird in the same field, with any immediate neighbor, and with one randomly chosen neighbor. Isthmus Field was not included in neighbor analyses, as too few immediate neighbors were recorded in this field. *Asterisked* birds were not included in statistical analyses, as fewer than 200 songs were recorded; matches with their song types were included for other birds, however. See text for further details

Year	Field	Bird	Songs recorded	Song types	Shared in field	Shared with any neighbor	Shared with random neighbor
1995	Isthmus	1	356	8	0	–	–
		2	194	9	0	–	–
		3	253	8	0	–	–
		4	228	9	0	–	–
	Parking	1	264	10	5	0	0
		2	252	7	6	0	0
		3	274	4	0	0	0
		4	209	7	0	0	0
		5	221	9	4	4	4
		6	325	11	7	4	0
		7*	29	7			
1996	Apple	1	315	6	1	0	0
		2	390	9	0	0	0
		3	308	8	2	0	0
		4	342	7	1	0	0
		5	375	6	1	0	0
		6	285	10	2	1	0
		7	342	10	2	1	0
	Pony	1	366	8	7	0	0
		2	264	8	3	0	0
		3	483	6	0	0	0
		4	342	6	0	0	0
		5	306	12	8	1	1
		6	259	6	3	1	1
		7*	151	10			
		8*	33	4			
	Eagle	1	281	7	1	0	0
		2	273	5	0	0	0
		3	266	9	4	1	1
		4	334	9	2	1	1
		5	363	7	1	0	0
		6	481	7	1	0	0
		7	231	9	3	1	0
		8	364	8	0	0	0
		9*	37	5			
		10*	20	6			

We find the same pattern if the analysis of song sharing is restricted to immediate territorial neighbors. In two of our fields, birds were significantly more likely to share parts of songs with their neighbors than whole songs (for Apple Field, Friedman statistic = 16.6, $P = 0.001$, Fig. 3A; for Pony Field, Friedman statistic = 7.6, $P = 0.023$, Fig. 3B). There was a nearly significant trend in the same direction in Eagle Field (Friedman statistic = 7.4, $P = 0.061$, Fig. 3C). In the Parking Field, there were no significant differences between the proportions of whole- or partial-song sharing with neighbors (Friedman statistic = 2.6, $P = 0.46$, Fig. 3D). The Isthmus Field was not included in this analysis, because we did not record enough immediate neighbors there. In general, sharing of parts of songs, especially trills, is at least as common or more common than sharing whole songs with neighbors.

For most categories of sharing in most fields, sharing with birds in the same field did not differ significantly from sharing with birds in other fields ($P > 0.05$ by Wilcoxon signed-ranks tests; Fig. 4A–E). Exceptions are that Apple Field birds shared a significantly greater proportion of internal trills with birds in other fields than with birds in their own field ($Z = 2.20$, $P = 0.028$), and Pony Field birds shared significantly more internal trills with birds in other fields than with birds in their own field ($Z = 1.99$, $P = 0.046$). Eagle Field birds shared significantly more other song components with birds in the same field than with birds in other fields ($Z = 2.24$, $P = 0.025$). We conclude overall that birds are not more likely to share songs or parts of songs with birds in their own field than with birds in other fields.

Discussion

The extensive whole-song sharing observed in Washington song sparrows has suggested that a primary

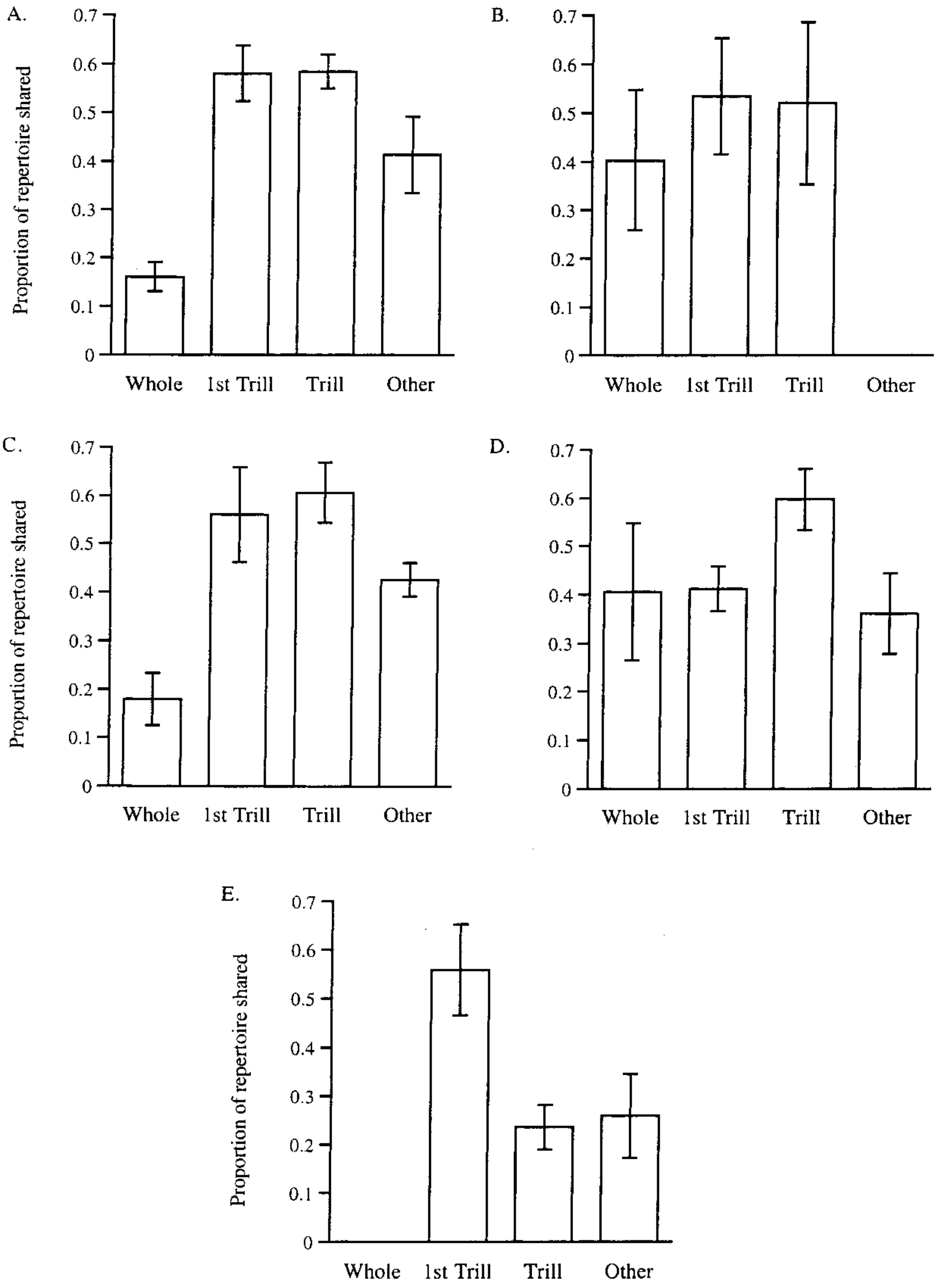

Fig. 2A–E Mean (±SE) proportion of song sparrow repertoires which are shared with at least one other bird in the same field, as whole-song sharing, sharing of first trill only, sharing of an internal trill only, or sharing of other song components. Within three of the fields, sharing of parts of songs is significantly more common than whole-song sharing (Apple, Eagle, Isthmus). **A** Apple. **B** Pony. **C** Eagle. **D** Parking. **E** Isthmus

function of song repertoires in this population may be to allow sharing with more than one territorial neighbor, enhancing an individual's ability to repertoire match with his neighbors (Beecher et al. 1994; Beecher 1996). Consistent with this view, all of the sampled males in the Washington population shared at least one song type with a randomly chosen neighbor, and on average 42% of song types were shared between pairs of neighbors (Beecher et al. 1996). By contrast, sharing in our Pennsylvania population was an order of magnitude lower; our subjects shared on average only 3% of their repertoire with a randomly selected neighbor, and most pairs of neighbors (81%) shared no songs. Neither whole-song sharing nor sharing of any song segment was consistently more common among birds in the same field than among birds in different fields, another indication that sharing is not greater between neighbors than to other birds in the population at large (Fig. 4).

The minimal amount of song sharing we observed in Pennsylvania, along with earlier reports of minimal song sharing in populations in Ontario (Harris and Lemon 1972), Maine (Borror 1965), and California (Mulligan 1966; Baker 1983), suggests that the functional interpretation of song repertoires as a mechanism to permit song sharing and repertoire matching cannot be applied to all song sparrow populations, let alone to songbirds in

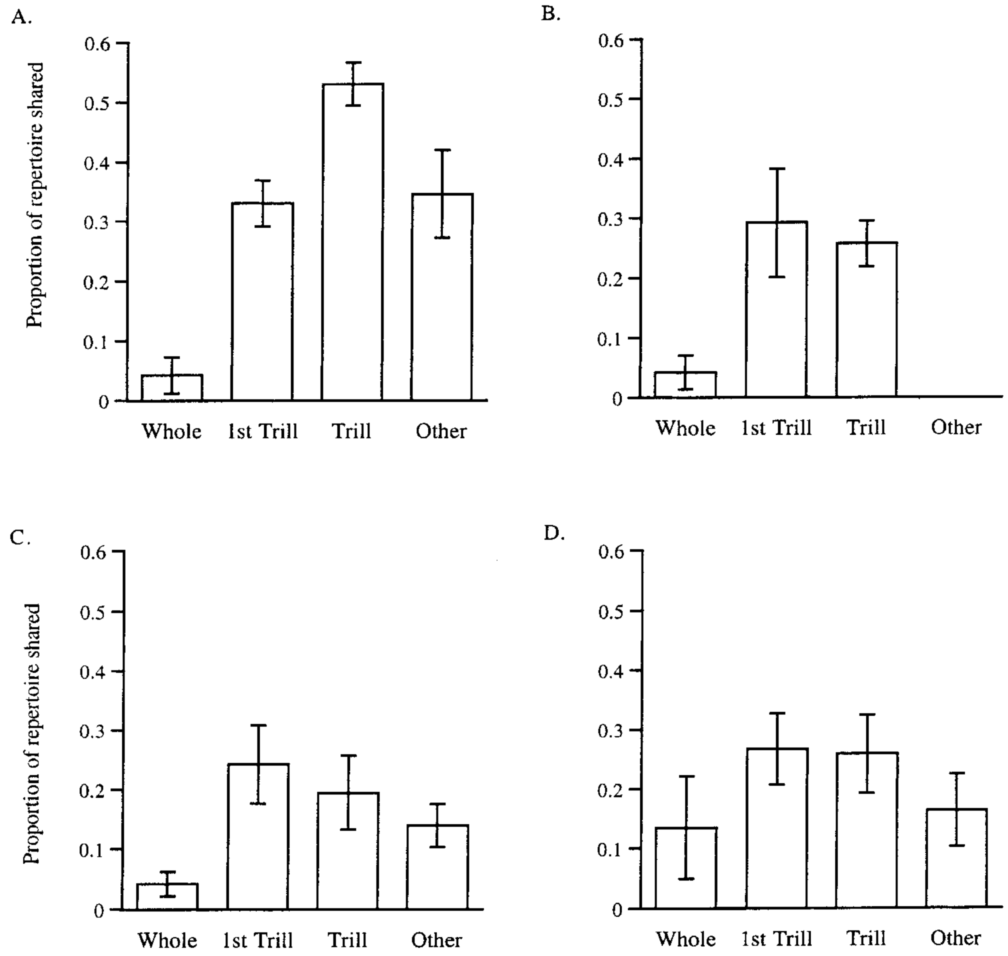

Fig. 3A–D Mean (±SE) proportion of song sparrow repertoires which are shared with at least one immediate territorial neighbor, as whole-song sharing, sharing of first trill only, sharing of an internal trill only, or sharing of other song components. Sharing of parts of songs with at least one neighbor is significantly more common than sharing of whole songs in Apple and Pony. **A** Apple. **B** Pony. **C** Eagle. **D** Parking

general. Pennsylvania song sparrows have repertoires comparable in size to Washington birds, and yet song sharing is so uncommon in our population that matching with whole songs, as seen in the Washington population, is precluded in most cases. We have not investigated repertoire matching directly, but clearly matching is impossible when two neighbors share no song types, as is the case for the majority of birds in Pennsylvania. As repertoires exist in so many populations lacking song type sharing, sharing seems unlikely to explain the evolution of repertoires. Furthermore, no one to our knowledge has yet demonstrated for any species that the ability to match song types actually is advantageous to males in territorial interactions, i.e., that matching leads to greater success in gaining or holding a territory. By contrast, there is direct experimental evidence that song repertoires are of advantage to males in stimulating females to court and copulate, in song sparrows (Searcy and Marler 1981; Searcy 1984) and many other species (Searcy and Andersson 1986; Catchpole and Slater 1995).

The pattern of song sharing observed in Washington song sparrows, with young birds preferentially copying whole songs from males who will be their future neighbors, suggests that song learning in song sparrows is a process shaped to maximize sharing of whole songs between territorial neighbors, perhaps due to a selective advantage of repertoire matching in territorial interactions (Beecher et al. 1994; Beecher 1996).

The song-learning strategy of Pennsylvania song sparrows must differ from that in Washington, however. Contrary to what would be expected if birds copied whole songs from future neighbors, whole-song sharing is rare between immediate neighbors (Fig. 3) and within fields (Fig. 2), and no form of sharing is greater within a field than between fields (Fig. 4). Whole-song sharing has been reported to be rare in two other eastern populations, one in Ontario (Harris and Lemon 1972) and one in Maine (Borror 1965), and also in populations in central California (Mulligan 1966; Baker 1983). Males in many song sparrow populations thus appear to follow a different song-learning strategy from that followed by Washington males. Our song-sharing data are consistent with the view that young birds copy parts of songs which they combine to produce their own adult song types, and that these parts are not more likely to be learned from, and thus shared with, future territorial neighbors. Thus song learning, like song sharing, appears to differ between populations of song sparrows.

Geographic variation in song learning has been documented previously (Nelson et al. 1995, 1996) for a related species, the white-crowned sparrow (*Zonotrichia*

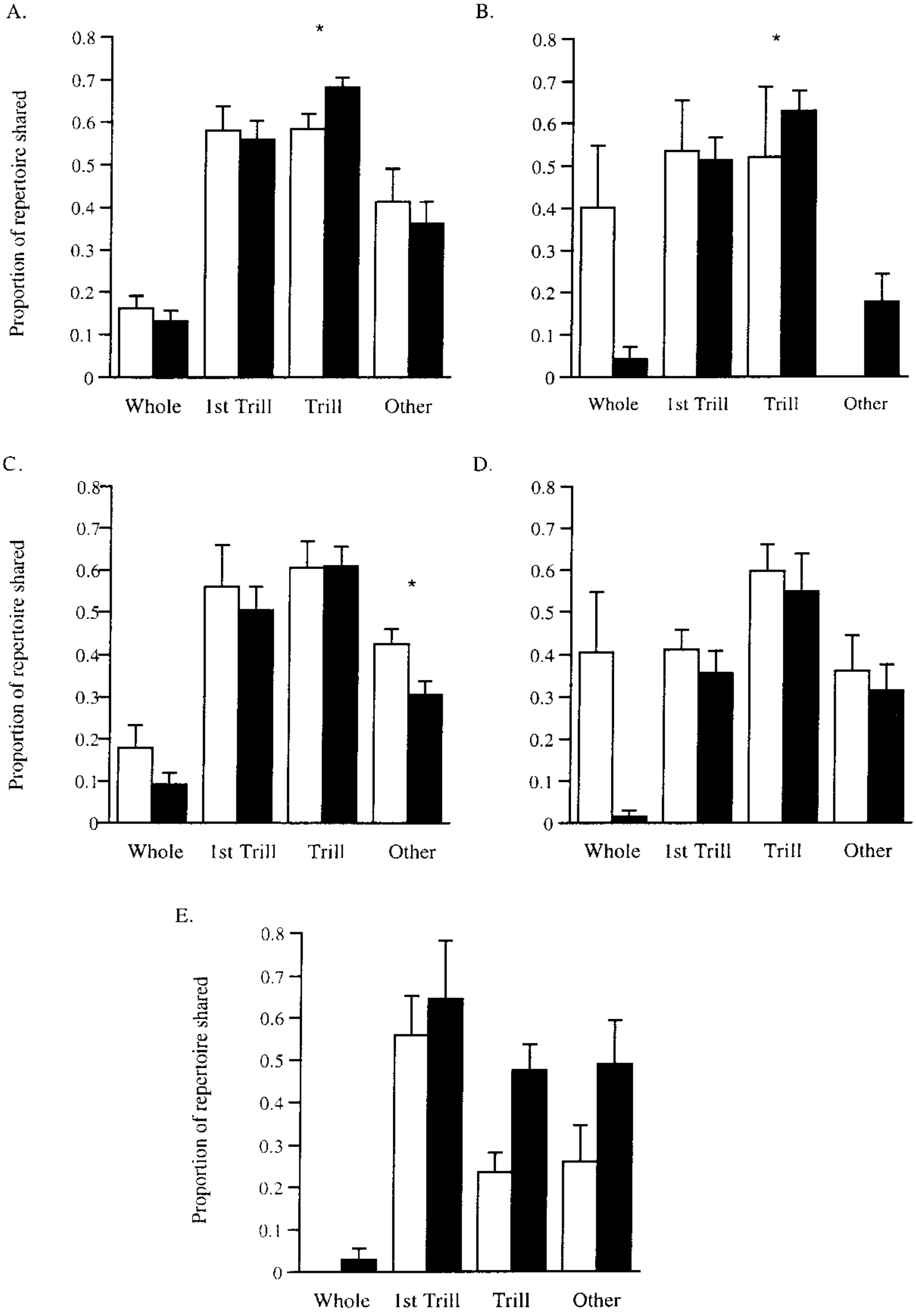

Fig. 4A–D Mean (±SE) proportion of song sparrow repertoires which are shared with at least one other bird in the same field (*open bars*) compared to the proportion shared with at least one bird in other fields recorded in the same year (*shaded bars*). An *asterisk* indicates a significant difference ($P < 0.05$). Overall, there is no evidence that sharing in any category is greater within than between fields. **A** Apple. **B** Pony. **C** Eagle. **D** Parking. **E** Isthmus

leucophrys). The between-population differences in song learning in this species were attributed to differences in migratory behavior; under identical laboratory conditions, males from a population of year-round residents copied songs at a later age and sang fewer song types during plastic song than did males from a migratory population. Males from a resident population were also significantly more likely to crystallize songs that were combinations of different tutor songs.

Geographic variation in song sharing has also been documented in several species. For example, population differences in song sharing have been reported between California populations of dark-eyed juncos (*Junco hyemalis*; Williams and MacRoberts 1977), and between east- and west-coast populations of house finches (*Carpodacus mexicanus*; Bitterbaum and Baptista 1979). Using a measure of song variation that incorporates both sharing and the similarity of unshared song sections, Wiens (1982) found that Oregon and Nevada populations of sage sparrows (*Amphispiza belli*) differ in between-individual song variation, such that populations with lower turnover had more similar songs. In some species, differences in song sharing may be associated with the extent to which populations are migratory or resident. DeWolfe et al. (1974) reported greater between-individual variability in the warble song sections of migratory Gambel's white-crowned sparrows (*Z. l. gambelii*) than is found in the song of resident Nuttall's white-crowned sparrows (*Z. l. nuttalli*). Similarly, migratory populations of rufous-sided towhees (*Pipilo erythrophthalmus*) in the northeastern United States show less song sharing than resident populations in Florida (Ewert and Kroodsma 1994).

Given evidence in other species for differences in song learning and song sharing between resident and migratory populations, it is tempting to ascribe the differences between Washington and Pennsylvania song sparrows to differences in tendency to migrate, as the Washington population consists of year-round residents, and our Pennsylvania population is almost certainly at least partially migratory. Nice (1943) found that in an Ohio population approximately 300 km distant from ours, about half of the male territory owners remained on her study site during winter while the other half apparently migrated. Nevertheless, song sparrows in California are year-round residents (Johnston 1956) but show low song sharing (Mulligan 1966; Baker 1983). Clearly, more work needs to be done to investigate the apparent differences in song learning between song sparrow populations, with the first step being to determine whether real genetic differences exist in learning strategies, as opposed to identical learning mechanisms producing different outcomes depending on ecological circumstances.

As noted by Beecher (1996), song sparrows in laboratory song-learning experiments learn only parts of songs (e.g., Marler and Peters 1987, 1988), whereas males in the field in Washington learn whole songs (e.g., Beecher et al. 1994). This difference could be attributed to the greater saliency of songs produced by freely interacting adult territory owners in the field rather than by tape recorders or caged tutors in the laboratory. However, our field results from Pennsylvania suggest that free-living song sparrows there also learn discrete parts of songs rather than whole songs, thus more closely resembling captive males in laboratory studies. In three of our five fields, birds shared a significantly greater proportion of their repertoires as parts of songs than as whole songs (Fig. 2). Sharing parts of song was also reported to be more common than whole song sharing in Ontario (Harris and Lemon 1972). The males studied in captivity by Marler and Peters (1977, 1987, 1988) were obtained from another eastern population, in New York, relatively near the Pennsylvania and Ontario populations. The difference in the results of Beecher et al. (1994) and Marler and Peters (1987, 1988) on the learning of whole versus partial songs could represent another instance of geographic variation in learning strategies, rather than a difference in learning between the laboratory and field. It is possible, of course, that some birds learn differently in the laboratory and in the field, as has been suggested for birds in the Washington population (Beecher 1996). It is interesting to note that under circumstances of high song sharing among song tutors, such as in the Washington population, song sparrows copy whole songs, while under conditions of low song sharing among song tutors, such as in the Pennsylvania population and in most laboratory studies, song sparrows copy and recombine parts of songs. The degree of whole-song sharing that young males hear during development may affect the degree to which they copy whole songs.

The differences in song sharing between song sparrow populations suggest differences in how these populations use their songs in territorial interactions and in how they learn to sing. These dramatic within-species differences offer a significant opportunity for furthering our understanding of song function and song learning, and the ecological and historical factors which have shaped their evolution.

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