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Ecological correlates of song learning in song sparrows

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Most studies of song learning have been conducted in the laboratory, and thus little is known about how song learning is affected by ecological variables in nature. Taking an ecological perspective, we studied song learning and territory establishment in a sedentary population of song sparrows (*Melospiza melodia*). We examined the song repertoires of an entire cohort of males (41 subjects) hatched in 1992 and compared them to those of potential song tutors (adults who were present in the young birds' first year). We found that a young bird learns songs from multiple tutors who were neighbors in his first year and usually establishes a territory among or near these tutors. The degree to which tutors influenced the repertoires of the young birds varied greatly. Adult males who survived into 1993 tutored more songs than those who did not survive, supporting the hypothesis that a young male's repertoire is influenced by social interactions with adults continuing beyond the classical sensitive period of the natal summer. The final repertoire of a young bird in most cases was weighted toward one of his tutors with whom he continued to interact, as an immediate neighbor, into his first spring. We found no correlations between potential measures of male quality or vigor and degree of tutor influence. *Key words:* bird song, male quality, *Melospiza melodia,* song learning, song repertoire, song sparrow, territory establishment. *[Behav Ecol 10:287–297 (1999)]*

The use of songs in territorial defense and mate attraction is common in a wide variety of animal groups (Searcy and Andersson, 1986). In the oscines (songbirds), song has one additional, intriguing aspect: it is learned, with much, and in some cases all, of that learning occurring very early in life. Song learning in oscines has been extensively analyzed in the laboratory and has become a leading model system for studying the neurobiology of learning (e.g., Konishi, 1985; Marler, 1990; Nottebohm, 1991). In contrast, we know little about the process of song learning in nature, or about the relationship of song learning to key aspects of a bird's natural life, such as territory establishment.

In the present study we took an ecological perspective on song learning in the song sparrow (*Melospiza melodia*), a species in which males have song repertoires of 6–12 distinct song types. Our study takes off from field studies of a sedentary insular song sparrow population by Arcese (1987, 1989a,b). Arcese showed that at about 1 month of age, young male song sparrows disperse from their natal area into the area where they will set up their adult breeding territory. Young birds (''floaters'') spend the next few months moving about the territories of 4–6 adult males (the ''floater range''), ultimately setting up territories within this floater range, generally in the following spring. We know that song sparrows learn all their songs in their first year, for as is the case in many songbird species, they do not change their repertoire or add any new song types after their first year (Cassidy, 1993; Smith et al., 1997); thus the processes of song learning and territory establishment occur concurrently.

Examining song learning in the field rather than in the laboratory does sacrifice some experimental control. However, if all the songs of all the birds in the local study population are recorded, and if the young bird has learned his songs from birds in this population, then his ''song tutors'' can be identified just as in a laboratory experiment on the basis of the similarity between the song types of student and potential tutor (Beecher, 1996). Although in the laboratory one knows with more certainty which songs the bird has heard (at least when tape-recorded song is used), tutor identification can be easier in some respects in the field if song copying is more faithful and precise in the field than in the laboratory (Beecher et al., 1994).

In a preliminary investigation of song learning in our population, we found that young song sparrows learned songs from several older birds who were adjacent neighbors in the bird's first year (Beecher et al., 1994). The young birds typically copied complete song types from tutors rather than improvising new song types from learned syllables. We found that the young birds typically set up their territories the following spring next to or among these tutor-neighbors, in some cases occupying the territory of one of the tutors who had died. The Beecher et al. (1994) study should be regarded as preliminary, however, because it was based on a sample of only 14 birds drawn from 5 different hatch years. In the present study we monitored an entire cohort (all first-year males within our study area in 1 year) to evaluate whether most males followed the same patterns of song learning and territory establishment suggested by our earlier study. Specifically, we wanted to know whether males in the cohort learn songs from three to four adult tutors who are contiguous neighbors and establish territories near these tutor-neighbors. In addition, we examined whether birds learned more songs from adult males who survived into the next spring, when the young birds were becoming fully territorial (i.e., whether song learning extended into the young bird's first spring).

A laboratory study using tape-recorded song as tutor song (Marler and Peters, 1987) showed that song sparrows learn most of their songs during a sensitive period which occurs roughly during the second and third months of life. For our study population this period would start as early as May and end as late as August (given hatchings from late March through June). Evidence from field and laboratory studies of other species, however, indicates that social interactions in the young bird's first spring following the natal year may affect a

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bird's final song repertoire (Baptista and Morton, 1988; Byers and Kroodsma, 1992; DeWolfe et al., 1989; Kroodsma and Pickert, 1984; Marler and Peters, 1982; Nelson, 1992; Nelson and Marler, 1994; O'Loghlen and Rothstein, 1993; Payne and Payne, 1997; Slater and Ince, 1982). There are two models for how this modification of song during a bird's first spring can occur, and both models identify social interactions with close neighbors as shaping the final song repertoire. According to Nelson and Marler (1994), the bird selectively retains the song or songs from the pool of songs memorized in the earlier sensitive period that best match his neighbor's songs. Alternatively, the bird may learn his song or songs de novo from his neighbors in his first spring, as Payne and Payne (1997) have shown in a migratory population of indigo buntings (*Passerina cyanea*). In either case, a young bird in a resident population should learn more songs, on average, from birds present in the natal summer and following spring than from adults who fail to survive from the natal summer to the next spring.

A late influence/learning phase has not yet been demonstrated in song sparrows, and data on this point in the Beecher et al. (1994) study were limited but consistent with the alternative hypothesis that song learning in song sparrows is confined to the bird's natal year. In the present study we tested the late influence hypothesis by comparing the number of songs taught by adult males (potential song tutors) who survived versus those who did not survive past January 1. We chose January 1 as the cutoff date because most young birds in our study population ''crystallize'' their songs and establish their breeding territories in the period January to March.

Examining the song learning strategy of all males in one cohort permitted us to ask a second class of questions concerning which adult males the young males selected as their song tutors. Specifically, we tested the hypothesis that young males select song tutors on the basis of male quality. We examined four possible correlates of the degree of influence exerted by a tutor: the song repertoire size of the tutor, the age of the tutor in the young bird's natal summer, the number of years a tutor survived past the young bird's natal summer, and the total number of years a tutor survived. Years on territory is the major component of male lifetime reproductive success in song sparrows (Smith, 1988). Repertoire size has been reported to predict territory tenure and other measures of male reproductive success in one population of song sparrows (Hiebert et al., 1989). In addition, considerable theory and evidence suggest that repertoire size may be a predictor of male quality in a number of songbird species (Catchpole, 1980; Hasselquist et al., 1996; McGregor et al., 1981; Mountjoy and Lemon, 1996; Searcy and Andersson, 1986).

There are many more adult males in our study population than first-year males in a given year, and, moreover, a given adult can tutor many young birds, so it is possible that not every adult will be selected as a tutor. Because we identified all tutors of all first-year males who established breeding territories in our study area, we were able to compare adults that were chosen as song tutors to those who were not using the same four measures of quality as above.

METHODS

Study population

Our study site is a 200-ha area within an undeveloped park along Puget Sound in Seattle, Washington, USA. The song sparrow habitat consists of mixed deciduous and coniferous woodland (including big leaf maple, *Acer macrophyllum*; red alder, *Alnus rubra;* Douglas fir, *Pseudotsuga menziesii*; and western red cedar, *Thuja plicata*) with a dense understory (including blackberry and salmonberry, *Rubus* spp.; ferns, *Polypodium* sp.; and nettle, *Urtica dioica*). There are also a few interspersed open grass fields ranging in size from 100 m^2 to 7500 m^2.

In 1992, 122 color-banded, sedentary, adult male song sparrows were on territories. This site has been part of a long-term study started in 1986. During the years of the present study, nearly all the adult males were banded and their song repertoires recorded. Because this population is sedentary, turnover in the male population only occurs through death of adult males and recruitment of first-year males (i.e., rarely do males immigrate and establish territories after their first year). Thus, except for birds in their first spring, all adult birds holding breeding territories in 1993 were also present in 1992.

Subjects

Subjects were 41 males hatched in 1992 and banded in their first year. We gave each subject a unique combination of one U.S. Fish and Wildlife aluminum band and three plastic color bands. We identified subjects as first-year birds either by their juvenile plumage (in summer 1992) or by the undeveloped and variable (plastic) quality of their song (before March 1993). Using the occurrence of plastic song to identify first-year males is reliable because song sparrows do not change their song repertoires between years and they do not go through an additional plastic song phase during their second year as may occur in other species (Beecher et al., unpublished data; Cassidy, 1993). We attempted to identify and band every first-year male in our study area, and these 41 subjects represent all but 3 yearling males who set up breeding territories in spring 1993. We were unable to record the crystallized repertoires of the three additional first-year males, so they were not included in this study. Besides these 44 males, we banded 30 additional yearling males in 1992 who we either never saw again after banding (possibly because they were predispersal) or who disappeared before spring without establishing breeding territories in our study area.

We banded 34 of the 41 males in the final sample between June and November 1992. The earliest hatch dates for our population occur in March and the latest in June; thus we banded all subjects at 1 month of age or older. We banded six males in January, February, or March 1993, and recorded the plastic song repertoire of one additional male in February 1993, but did not band him until May 1993. This last male's crystallized repertoire matched the plastic song repertoire recorded earlier in February on the same territory and thus we identified him as a first-year male despite the late banding date. It is possible that the seven males banded in 1993 did not disperse into our study site until early 1993, in which case we might expect differing results for them. Therefore, data from these seven males are included in the analysis but are also separately identified throughout.

Song analysis and identification of tutors

A male song sparrow typically has 6–12 distinct song types. A bird sings bouts of one song type, varying each successive rendition slightly, before beginning a bout of another song type (i.e.; AAA . . . , BBB . . .). Song sparrows sing throughout the breeding season and, to a lesser extent, during other times of the year.

We recorded each subject's crystallized repertoire in the field after 15 March 1993 using Sony TC-D5M stereo recorders and Sennheiser ME-88 condenser microphones. A bird was considered fully recorded after at least 16 consecutive song types or after about 2 h of continuous singing (method and rationale described in Cassidy, 1993; Kroodsma, 1982). All songs were analyzed on a Kay DSP-5500 Sonagraph. Sonagrams of each song type, including variations, were visually matched, based on the consensus of three judges, to those of the adult males who were alive at least through May 1992 (1 month after the earliest hatch month for our population). For this analysis we assumed that the only possible tutors were birds that were a year or more older than the subjects (i.e., we excluded birds born in the same cohort).

We identified the adult bird with the most similar rendition of a young bird's type as the tutor for that type. Other birds who had less similar versions of that type were not counted as tutors. In cases where two or more older birds had equally similar versions of the same type, we counted all birds in the tie as tutors (if there were two such tutors, each was credited with tutoring 0.5 of that song type, if there were three, 0.33 of that song type, etc.). Credit for tutoring was also shared if two adults had slightly different versions of a type and the young bird sang both versions or blended them. For every subject, each tutor was assigned a score based on the number of song types he matched to the subject, devalued by the number of other tutors identified for those song types. For example, if he was the sole identified tutor for three song types (3.0 credits), shared credit with one other tutor for another type (0.5 credits), and shared credit with two other tutors for a third type (0.33 credits), he would receive a score of 3.83. Thus, with this ''inclusive'' analysis we attempted to include any adult male who could have influenced the subject's repertoire as evidenced by having a closely matching song type.

We also analyzed the data using a contrasting procedure, an ''exclusive'' analysis, which attempted to identify the fewest number of tutors that could account for all of a subject's song types. Working from the tutor list generated using the inclusive method, we first selected those birds who had the sole match for a song type or distinct variation. Following that, we selectively retained the tutors who had the highest number of matches until we had accounted for all song types. Thus, a bird would not be counted as a tutor if, for example, he only had one matching song type which he shared with another tutor who had two or more matching types. The reality of who tutored whom probably lies somewhere between these two analyses. So, by using these two different contrasting methods, we hoped to identify robust relationships—i.e., ones that were common to both analyses and thus did not depend on minor details of the method of tutor identification.

Contiguity of tutor territories

After we identified each subject's putative tutors, we mapped the tutors' territories in 1992 (the subjects' hatch year) and evaluated their contiguity. Territory boundaries were estimated following observations of perch use and interactions between neighbors throughout spring 1992. Territories that shared a common border were considered contiguous. Spaces between territories, either an uninhabited area (e.g., an open field) or a nontutor bird's territory, were designated as gaps. The entire tutor range (includes all tutor territories) was considered contiguous if there were no gaps.

Proximity of subject territories to tutor territories

We evaluated the territories that the subjects eventually established in 1993 for their proximity to the territory of the closest identified tutor. Again, we considered territories contiguous if they shared a common border; if not, we counted nontutor territories or uninhabited areas as gaps. If the subject occupied the territory of a tutor who was no longer present, he was considered to have replaced that tutor.

RESULTS

Subject repertoires

The size of subjects' repertoires ranged from 6 to 11 song types, with a median of 8 (mean = 8.15). Of the 334 song types analyzed, we were able to identify tutors for all but 29 (8.7%). As an example, Figure 1 shows the partial repertoire of subject RAOM with the matching song types of his tutors. We identified tutors for all song types for 24 subjects, for all but 1 song type for 10 subjects, and for all but 2 song types for 5 subjects. The two remaining subjects had four (out of eight) and five (out of nine) song types, respectively, for which we were unable to identify a tutor. It is possible that these two males improvised these new songs (as could have the other 15 males who had unidentifiable songs). Another explanation, however, is that we missed recording the major tutors for these two birds. One of the two males had a territory that was on the edge of our study site, adjacent to another area that also supports song sparrows. The second male's territory was in an area within our site where we possibly missed recording an adult. Because we were unable to identify tutors for more than half of these two males' songs, they were included only in analyses that examined individual tutor influence (to give credit to those tutors we could identify), and not in analyses that examined subjects' song-learning strategy (as we most likely missed one or more of their tutors).

Number of tutors and tutor scores

Nearly all subjects learned songs from more than one tutor (38/39 subjects in the inclusive analysis and 33/39 in the exclusive analysis). The mean number of tutors identified per subject was 4.92 (range 1–10) in the inclusive analysis and 2.55 (range 1–5) in the exclusive analysis (Figure 2). Tutor scores (number of songs credited to each tutor for a subject) ranged from 0.20 to 8.00 using the inclusive method of tutor analysis (Table 1) and from 0.33 to 10.00 using the exclusive method. We designated the tutor who had the highest tutor score for a subject as the primary tutor; the tutor with the second highest score as the secondary tutor; and so on. If two tutors had the same inclusive score for a subject, the higher ranking was given to the tutor who had the higher exclusive score.

On average, subjects learned about half their repertoire from their primary tutor, as shown in Table 1. There was, however, considerable variance in primary tutor scores, which is discussed below. There was a general trend toward subjects having more tutors if their primary tutors had low scores. This is a logical result if all subjects have a similar number of song types. It is possible that this pattern might occur if some neighborhoods had higher amounts of song sharing than other neighborhoods (i.e., males in a neighborhood with high sharing would all be identified as tutors and have low scores because they would share credit for many songs). This is not so, however, because the Pearson correlation coefficient between the inclusive and exclusive tutor scores is 0.95, and the exclusive analysis controls for the effect of song sharing.

Contiguity of tutor territories

A bird's tutors were usually contiguous neighbors in his hatch year (1992). The tutor range (inclusive analysis) of one subject and the territory he eventually established is represented in Figure 3. This subject had five tutors whose territories were contiguous in 1992, but only one of these tutors was still present in spring 1993. This subject settled in a portion of the area vacated by three of his tutors, adjacent to his only surviving tutor. Results were similar for other subjects (Figure 4). Twenty-eight of 39 subjects had tutors whose territories were

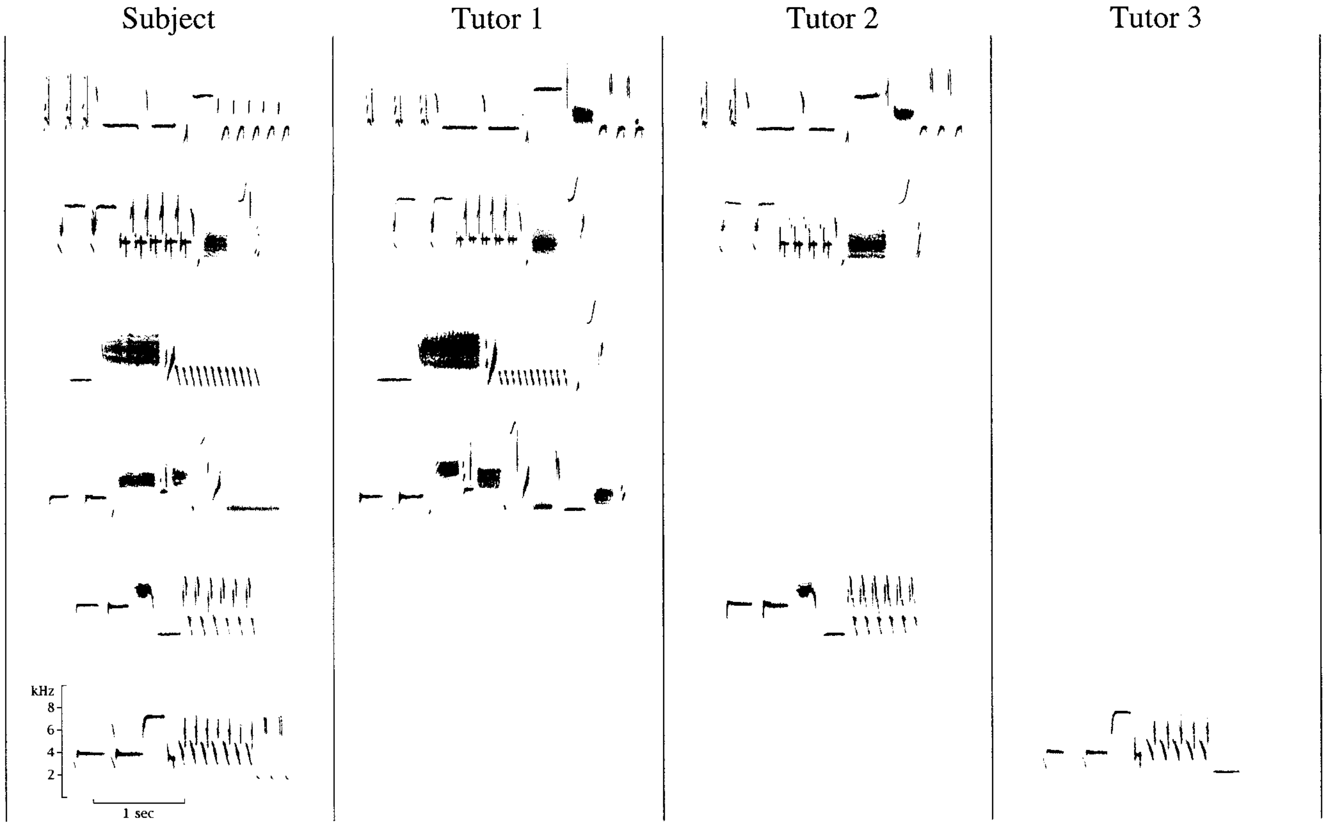

Figure 1
Partial repertoire (6 of 10 song types) of subject RAOM showing matching song types from 3 of his 6 identified tutors. Blank spaces indicate that a tutor did not have a match for that particular song type.

completely contiguous or had only one or two gaps. Eleven subjects had tutor ranges with three or more gaps. The contiguity of tutors was not an artifact of the inclusive method of tutor identification, for the exclusive tutor groups actually contained fewer gaps (only six birds had three or more gaps in their tutor range).

Proximity of subject territories to tutor territories

Overall, subjects tended to replace or settle near their tutors in their first breeding season (1993). Twenty-nine subjects replaced and/or were contiguous to one of their tutors, eight were one gap removed from the nearest tutor, and two were farther removed (Figure 5). Results were similar for the exclusive set of tutors: 26 subjects replaced and/or were contiguous to 1 of their tutors, 9 were 1 gap removed, and 4 were farther removed.

Subjects banded in 1992 versus 1993

Results from the seven subjects who were banded in 1993 were similar to those banded in 1992. The only notable difference between the two groups appears in the inclusive number of tutors per subject (Figure 2). Results from subjects banded in 1993 were slightly weighted toward the higher numbers (2 of the 3 subjects who had 9 or 10 tutors were banded in 1993). However, this difference was reduced when the exclusive method of analysis was used. Furthermore, three of the seven subjects banded in 1993 had tutors who disappeared before 1993. Together, these findings led us to believe that these subjects probably had entered into our study site in 1992, and thus we included them with the rest of the subjects for the remaining results and discussion.

Individual tutors and nontutors

The above analyses have been from the subjects' perspective, and many tutors are represented more than once; the 188 tutors in Table 1 represent 85 birds. Of these 85 birds identified using the inclusive method of analysis, 32 tutored 1 subject, 25 tutored 2 subjects, and 28 tutored 3 or more subjects. Only 7 of the birds who tutored 2 or more males were primary tutors for more than 1 subject (i.e., the 39 primary tutors represent 30 actual birds). Twenty tutors were eliminated using the exclusive method; three were secondary tutors, and the rest were tertiary or lower. Because we analyzed the repertoires of all first-year males in our study site (except the three we were unable to record), we were able to identify those males who presumably did not tutor any of the yearling males who established breeding territories within our study area. Of the 122 adult males who were present in 1992, 37 were identified as not having been tutors using our inclusive method of song analysis. This assessment, and the following tutor-based analyses, include data from the two subjects for whom we could identify tutors for only half their songs.

Survivorship of adults and late influence

We tested the late influence hypothesis that subjects would learn more songs from tutors who survived into 1993 by comparing the number of songs learned from males who were present at least through 1 January 1993 with those who dis-

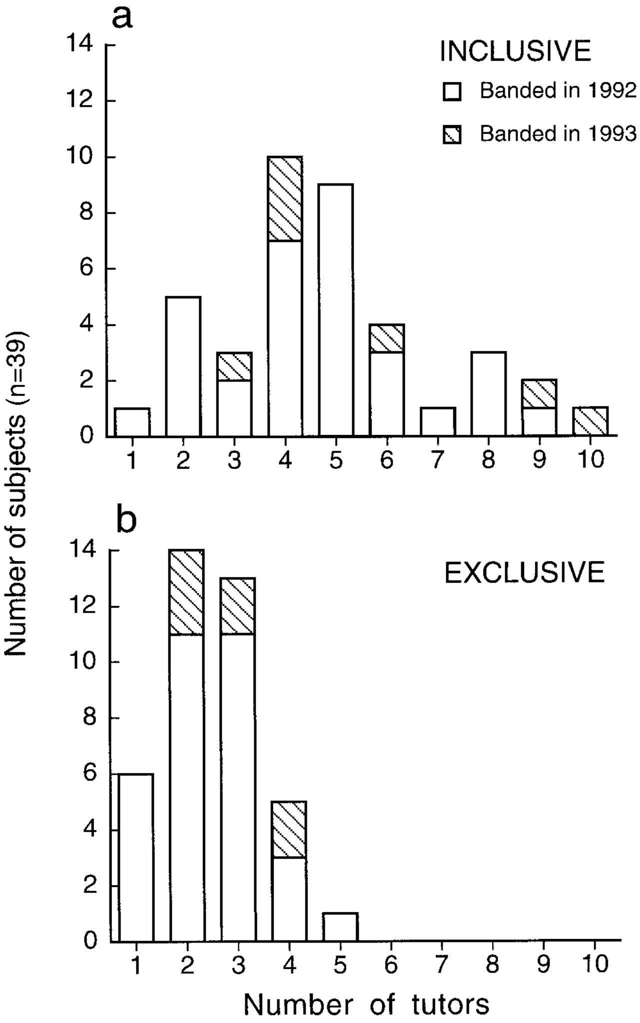

Figure 2
Frequency distribution of the number of tutors identified per subject using (a) the inclusive method of tutor identification and (b) the exclusive method. Results from the seven subjects banded in 1993 (striped bars) are stacked on top of those from subjects banded in 1992 (open bars).

appeared before then. For each adult male, we summed his tutor scores (inclusive) across all subjects to obtain the total number of songs he tutored (grouped by whether or not the male was present after 1 January 1993; Figure 6). The total number of songs tutored ranged from 0.20 to 20.41 for males identified as tutors; nontutors were given a score of 0.00. Eighty-seven of the 122 males survived past January, and even though many of the adults who were alive into 1993 had low tutor scores, males who survived the winter tutored more songs on average than those who did not survive (means = 3.01 versus 1.21 songs, n = 87 versus 35, respectively, t = 3.56, p = .001). This result holds even when we consider only those males identified as tutors (t = 3.05, p = .003) or when we exclude the one outlier male with a score of 20.41 (t = 2.88, p = .005). Furthermore, the highest tutor scores went to tutors who survived into 1993; all 16 males who had total tutor scores greater than 6.00 were alive past January 1.

Degree of influence of surviving adults

We examined four quality traits of surviving tutors that might correlate with their degree of influence: (1) the repertoire size of the tutor, (2) the age of the tutor, (3) the vigor of the tutor as assessed by the number of years survived past 1992, and (4) total years of survival. We considered only tutors surviving into 1993 to avoid confounding with the late influence effect noted in the preceding section (i.e., a tutor dying in the winter of 1992 might have low influence not because he was a low-quality bird but because he was not present during crystallization of the young bird's repertoire in early spring 1993).

We analyzed the total tutor scores (i.e., summed across subjects) of the 65 adult males identified as tutors who survived into 1993. Tutor scores were not predicted by tutor repertoire size (7–11 song types, 2 tutors with 5 and 6 song types excluded, F = 0.53, p = .71), nor by tutor's subsequent survival (measured from the subject's hatch year, 1–4 years, F = 0.41, p = .75, or from the tutor's hatch year, 2–8 years, F = 0.38, p = .89). There was a significant effect of tutor age (1, 2, 3, or 4 or more years old in 1992, F = 3.95, p = .01); however, this effect does not persist when the one outlier male with a score of 20.41 (see Figure 6) is deleted from the sample (F = 2.07, p = .11).

Second, we compared adults identified as tutors (n = 65) with those who were not identified as tutors (n = 22), again using only those males who survived past January 1. There were no significant differences between these two groups on any of the four traits we measured: repertoire size (t = 1.03, p = .30), age in 1992 (t = 0.24, p = .81), years on territory past 1992 (t = 1.56, p = .12), and total years on territory (t = 1.49, p = .14).

Degree of influence of primary tutors

The influence of the primary tutor varied from complete (subject GAIM learned all his songs from his primary tutor) to weak (subject GMYI learned only 1.33 songs from his primary tutor; Table 1). Primary tutors, by definition, had the strongest influence on a particular subject, and this wide range in primary tutor scores prompted us to examine traits that might explain these differences.

As in the analysis of all adult males, there is a late influence effect. Subjects learned more songs, on average, from primary tutors who survived past January than from those who did not (means = 4.14 versus 2.93, n = 35 versus 4 respectively, t = 2.61, p = .026).

We also examined the same four possible predictors of the degree of influence that we did for all surviving adults (again using only those birds who survived into 1993 to avoid confounding with the late influence effect). The results were the same. Primary tutor scores were not predicted by tutor repertoire size (7–11 song types, 1 tutor with 6 song types excluded, F = 0.87, p = .49), tutor age (1–5 years, F = 0.74, p = .57), years on territory past 1992 (1–4 years, F = 0.46, p = .71), or total years on territory (2–7 years, F = 1.08, p = .39).

Switching to the perspective of individual adult males, there were also no significant differences in any of the four quality measures between surviving males that were identified as primary tutors (n = 26) and all other surviving males (n = 61): repertoire size (t = 0.90, p = .37), age in 1992 (t = 1.43, p = .15), years on territory past 1992 (t = 0.43, p = .67), and total years on territory (t = 0.80, p = .43). Because some of the primary tutors had low tutor scores, we compared the total tutor scores of the top 15 primary tutors (those with primary tutor scores of ≥4.0) to all other surviving males. Again, there were no significant differences: repertoire size (t = 1.52, p = .13), age in 1992 (t = 1.16, p = .25), years on territory past 1992 (t = 0.89, p = .38) and total years on territory (t = 0.18, p = .86).

We also examined one other correlate, the proximity of the

Table 1
Tutor scores and proximity of each subject to his primary tutor in spring 1993

Subject	No. of songs[a]	Tutor no.										Proximity to to tutor 1[b]
		1	2	3	4	5	6	7	8	9	10	
GMYI	8, 2	1.33	1.08	1.00	0.58	0.50	0.33	0.33	0.33	0.25	0.25	Farther
GRRM	6, 1	1.33	1.33	1.00	1.00	0.33						1 gap
YARM	7, 1	1.33	1.25[c]	1.08	0.75	0.58	0.50	0.25[c]	0.25[c]			Farther
ARYM	6	1.41	1.08	0.91	0.75[c]	0.66	0.50	0.33	0.33			Farther
YYAM	9	2.20	2.00	1.53	1.00	0.83	0.53[c]	0.50	0.20	0.20[c]		Contiguous
ABGM	8	2.50	2.00	1.75	0.75	0.50[c]	0.50					Farther
AIBM	8	2.50[c]	2.00[c]	1.50	1.50[c]	0.50						—
AIRM	9	2.50[c]	2.00	2.00[c]	1.50[c]	1.00[c]						—
GMOY	6	2.50	1.50	1.00	0.33	0.33	0.33					1 gap
PARM	8	2.50	2.00	2.00	1.50							Farther
WWAM	8, 1	2.58	2.58	0.75	0.75	0.33						1 gap
OPOM	8, 2	2.83	1.00	0.83	0.83	0.50						Farther
RMIO	6	2.83[c]	1.83	1.33[c]								—
AIYM	7, 2	3.00	2.00									1 gap
OIGM	8, 2	3.00	2.00	1.00								Contiguous
RAYM	7	3.08	1.75	1.33	0.58[c]	0.25						Farther
RMRR	7, 1	3.08	0.70	0.58	0.58	0.25	0.20	0.20	0.20	0.20		1 gap
PRAM	8, 1	3.25	1.75	1.00[c]	0.75	0.25[c]						Contiguous
IOOM	10	3.33	2.25	1.25	0.83	0.83	0.75	0.75				Farther
BRAM	11	3.83	3.16	1.83	1.33	0.83						1 gap
ORIM	7	3.91[c]	0.75	0.58[c]	0.50	0.33	0.33[c]	0.33	0.25			—
PPOM	8, 1	4.00	1.50	1.00	0.50							Contiguous
BARM	10	4.16	2.33[c]	2.33	0.83	0.33						Contiguous
RAOM	10	4.20	2.20	2.00	0.70	0.70[c]	0.20[c]					Contiguous
YOAM	8, 2	4.33	0.83	0.50	0.33[c]							1 gap
BAYM	6, 1	4.50	0.50									1 gap
IAYM	10	4.82	3.82[c]	1.00[c]	0.33[c]							1 gap
IIAM	8	4.95	0.95[c]	0.95	0.50	0.45	0.20					Contiguous
YRAM	10	5.50	3.00	1.50								1 gap
YYGM	9	5.50	2.33	0.83	0.33							Contiguous
OOYM	10	5.65	2.15	1.82[c]	0.33							Contiguous
IAIM	8, 1	6.00	1.00									Contiguous
OARM	7	6.25	0.25[c]	0.25	0.25							Contiguous
IMYY	8	6.33	0.83	0.50	0.33[c]							Contiguous
YMRR	8	6.50	0.50	0.50[c]	0.50[c]							1 gap
GARM	8	7.00	1.00[c]									Contiguous
GAYM	9	7.00	1.00	0.50	0.50[c]							Contiguous
IIBM	10, 1	7.00	2.00									Contiguous
GAIM	8	8.00										Contiguous
Mean		4.14	1.63	1.14	0.71	0.49	0.41	0.41	0.26	0.23	0.25	

Subjects are listed in order of primary tutor score. Tutor scores are the number of song types a tutor matches with a subject, devalued by the number of other tutors identified for those song types.

[a] First number indicates subject's repertoire size; second number indicates number of songs for which we could not identify a tutor.

[b] Proximity of each subject to his primary tutor in spring 1993 (contiguous = adjacent territory; gap = large open space or another bird's territory; farther = farther than 1 gap; dash indicates tutor not present in 1993).

[c] Tutors who did not survive past 1 January 1993.

young bird's final territory to the primary tutor's territory. We compared birds who settled next to their primary tutor (n = 16), to those who settled one gap away from him (n = 11) or who settled farther (two or more gaps) away from him (n = 8; Table 1). Subjects who settled next to their primary tutor were more influenced by the primary tutor than those who did not (F = 11.43, p <.001; Tukey post-hoc pairwise comparisons: contiguous versus 1 gap removed, p = .04; contiguous versus farther, p < .001).

Subjects that moved away from their tutors

Two subjects established territories that were far removed from all of their tutors. Both of these subjects, PARM and

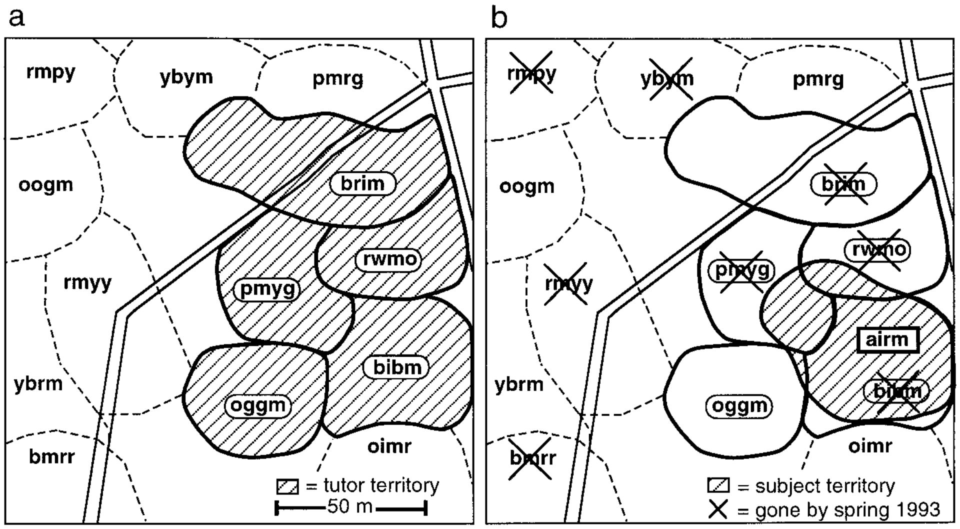

Figure 3
Schematic representation of (a) the contiguous territories of subject AIRM's tutors in 1992 and (b) an overlay of the territory AIRM established in spring 1993. This bird settled in a portion of the area vacated by three of his tutors, who did not survive into 1993 (crossed out), and which was adjacent to his only surviving tutor (OGGM).

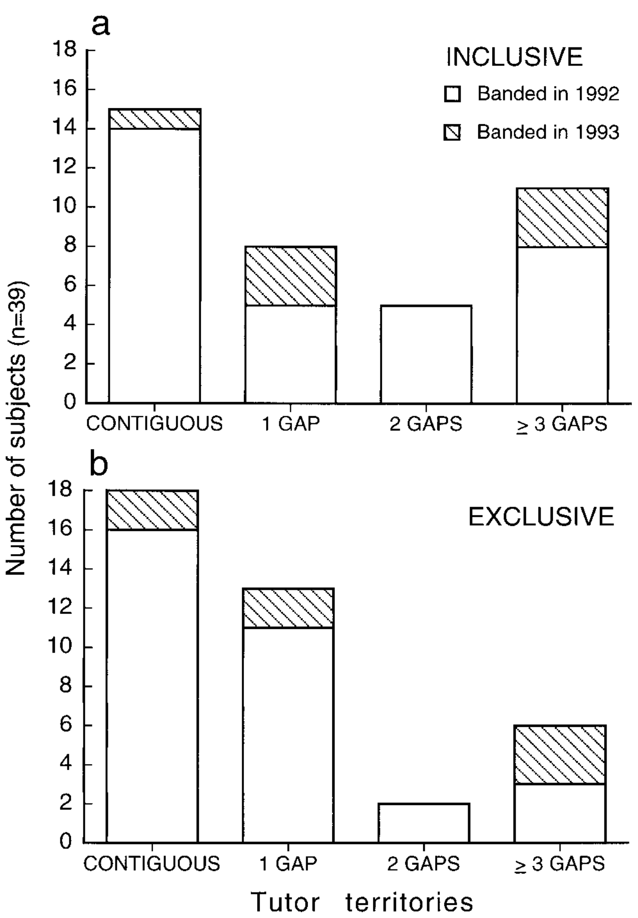

Figure 4
Frequency distribution of the contiguity of each subject's tutor territories in 1992 (subjects' hatch year) using (a) the inclusive method of tutor identification and (b) the exclusive method. Results from the seven subjects banded in 1993 (striped bars) are stacked on top of those from subjects banded in 1992 (open bars). Territories that shared a common border were considered contiguous, and gaps were either uninhabited areas or nontutor bird's territories.

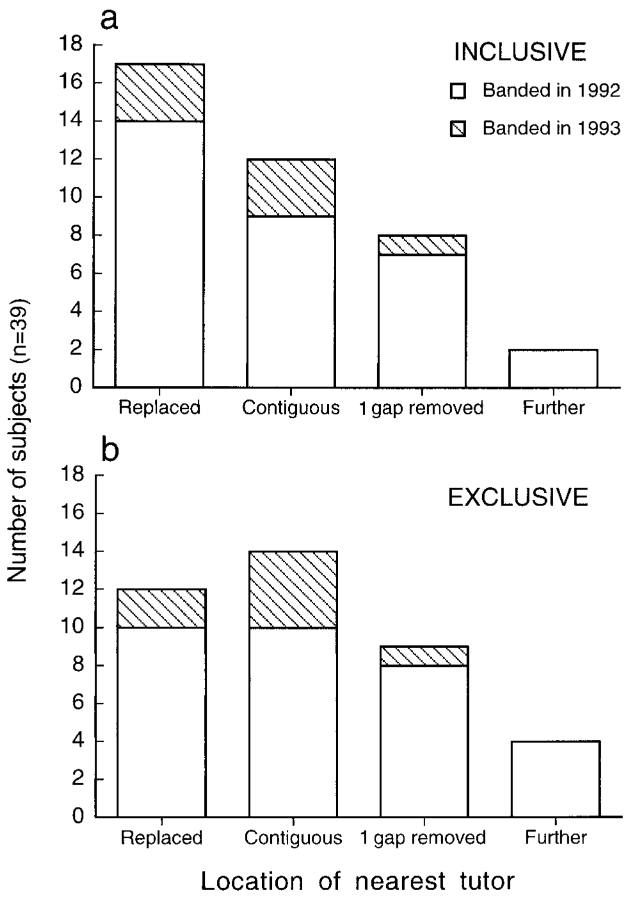

Figure 5
Frequency distribution of the location of each subject's nearest tutor in spring 1993 using (a) the inclusive method of tutor identification and (b) the exclusive method. Results from the seven subjects banded in 1993 (striped bars) are stacked on top of those from subjects banded in 1992 (open bars). Replaced = subject occupied the area of a tutor who was no longer present. Contiguous = subject and tutor share a common border. Gap = uninhabited area or a nontutor bird's territory. Note that subjects who replaced tutors may also have settled in territories contiguous to a surviving tutor, but were only categorized as "replaced."

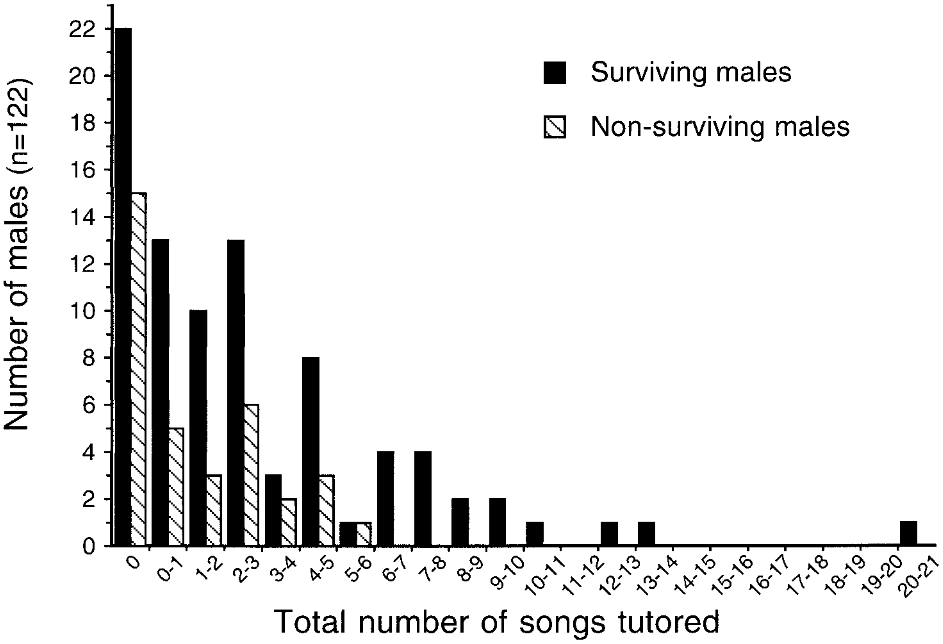

Figure 6
Frequency distribution of the total number of songs (inclusive analysis) tutored by adult males who survived past 1 January 1993 (shaded) and by those who did not (striped).

ARYM, were banded near their identified tutors (in July and October, 1992, respectively) but subsequently established breeding territories that were more than 500 m (approximately 10 territories) away from their tutors. ARYM was last seen near his tutors in November 1992 and was observed on his breeding territory in March 1993. PARM was last seen near his tutors in February 1993 and was observed on his breeding territory in April 1993. Neither of these two subjects had any song types that matched those of their nearest adult neighbors in 1993. It is unclear why these birds moved away from their tutors. One possible reason is that there were few or no territorial openings among their tutors: only one of ARYM's eight tutors died, and none of PARM's four tutors died.

There were also four subjects who had tutors in two discontinuous areas. Each of these four subjects, ABGM, GMYI, GRRM, and RAYM, was banded in the area where they established breeding territories which were also near some of their tutors. Three of these subjects were banded between August and October 1992, and the fourth was banded in February 1993. They all, however, had at least two tutors whose territories were in a separate area of our study site that was more than 600 m (approximately 12 territories) away. Interestingly, three of these subjects established territories adjacent to one another and had many of the same tutors. Two of these three subjects, ABGM and RAYM, had the same primary and secondary tutors who were in the area discontinuous from the subjects. It appears that these subjects may have "moved together" from one area to the other. Again, it is unclear why these subjects moved away from some of their tutors, if they did so. Considering the tutors of the four birds collectively, none of the 11 tutors in the areas the subjects appear to have moved from died, and thus perhaps they had little opportunity to establish territories near these tutors. Considering all 6 subjects together, only 4% of the tutors in the areas they moved from died, compared with 23% of the tutors of the remaining 33 subjects.

DISCUSSION

The results of this study confirm and extend those of our previous study of song learning in this sedentary population of song sparrows (Beecher et al., 1994). As suggested by the earlier study, a bird's song repertoire is based on songs of multiple tutors who were neighbors in the bird's first year, and he generally establishes a territory among or near these tutors. New findings of this study are that the young bird's final repertoire is (1) influenced by social interactions continuing beyond the sensitive period of the natal summer and into the following spring and (2) weighted in most cases toward one of his tutors with whom he continues to interact, as a close neighbor, into the following spring. The primary tutor appears to be "chosen" early, because if the primary tutor does not survive the winter, or if the young bird cannot maintain a territory next to him, the young bird retains only a relatively small number of the primary tutor songs and does not compensate by acquiring many songs from one of his new contiguous neighbors (even a neighbor who was one of his original tutors). These results suggest that a bird learns many songs from a particular tutor only if he (1) is exposed to that adult's songs during the sensitive period and (2) continues to interact with that tutor into the following breeding season.

Finally, we found no correlations between degree of tutor influence and potential measures of male quality or vigor. Our most direct measures of male quality, the number of years a bird survived on territory, measured either from the subject's hatch year or from the tutor's hatch year, failed to predict the degree of a tutor's influence or whether an adult was selected as a tutor. Two other measures that might relate to male quality, age and repertoire size, also failed to predict tutor influence. In the end, the best predictor was geography—young birds who were heavily influenced by a particular tutor had territories adjacent to that tutor. Other factors, which we did not examine, may have contributed to differences in tutor influence. For example; field sparrows retain the song type that matches their adult neighbor who sings more frequently (Nelson, 1992); white-crowned sparrows retain the song type of a neighbor with whom they have engaged in matched countersinging bouts (DeWolfe et al., 1989); and indigo buntings learn more songs from first-year individuals with bluer plumage (Payne and Payne, 1993).

Song learning strategy of the song sparrow

The results of the present field study, in conjunction with those of our earlier study (Beecher et al., 1994), suggest a song-learning strategy with the following characteristics. The young song sparrow constructs his song repertoire by (1) sampling, in his first year, the repertoires of several older tutor-neighbors, (2) attempting subsequently to establish his territory next to these tutor-neighbors, and (3) preferentially retaining song types of those tutors with whom he continues to interact into his first breeding season. One additional feature of this song-learning strategy was revealed in Beecher et al. (1994): the young bird preferentially memorizes or retains song types shared among his tutors (versus song types unique to a particular tutor). This preference for shared songs maximizes the number of songs the bird shares with neighbors in his first breeding season.

We found, however, a few notable exceptions to this general pattern. The first exception was that some subjects had only one tutor (one subject in the inclusive analysis and six subjects in the exclusive analysis). We found no correlates that would explain why these subjects learned songs from only one tutor. Perhaps these birds had particularly strong interactions with their primary tutor and did not, for some reason, interact as much with other neighbors.

The second exception was the four subjects who had tutors in two discontinuous areas. These birds were all banded in the area where they established territories, which was near some of their tutors. We did not observe these subjects in the other discontinuous area, but all of them were banded in August 1992 or later, which was after their presumed sensitive period for song memorization. We do not know whether these birds ranged back and forth between the two areas during their first year and thus acquired songs from adults in both areas or whether they moved from one area to the other.

The third notable exception was the subjects who established territories away from all their tutors. The two subjects who were banded near their tutors but who established territories in a separate area were seen near their tutors as late as November 1992 and February 1993. These birds appear to have moved away from their tutors later in their first year, perhaps, as we suggested, because there were few or no territorial openings near the tutors. The fact that these birds did not share any song types with their adult neighbors suggests that they were unable to acquire new songs after they moved. We do not know if these exceptions perhaps reflect the unusual circumstances of these particular subjects, or if they possibly represent alternative strategies for song learning and territory establishment.

Function of song sharing in song sparrows

The pattern of song learning in this population suggests that it may be advantageous for young male song sparrows to learn song types that they will share with their future neighbors. How does a male song sparrow benefit by sharing songs with his near neighbors? Two lines of evidence bear on this question.

Countersinging with neighbors is one context in which song sharing may be advantageous. In a playback experiment, we have demonstrated that song sparrows selectively use their shared song types in singing interactions with neighbors (Beecher et al., 1996). We found that established neighbors typically replied to playback of neighbor song (shared or unshared) with a song that they shared with that neighbor. If the neighbor stimulus song was one of the song types they shared, the subject usually replied not with that type, but with one of the other song types he shared with that neighbor (''repertoire matching,'' which implies the subject's knowledge of the stimulus bird's repertoire; Beecher et al., 1996). The results of this experiment suggest that song sparrows preferentially use the songs they share with a neighbor when they communicate with that neighbor and that shared songs may play a significant role in the establishment and maintenance of territorial relationships between neighbors.

Second, if sharing songs does afford a song sparrow some advantage, this should be reflected in measures that are likely to relate to fitness, such as years on territory (the major component of male reproductive success; Smith, 1988). In a recently completed longitudinal study, we compared the ability of repertoire size and degree of song sharing to predict the territory tenures of a sample of young song sparrows. We found that song sharing is a better predictor of territory tenure than is repertoire size (Beecher et al., unpublished data). Payne et al. (1988) also found that song sharing relates to fitness in indigo buntings; first-year males who shared a song type with an adult neighbor tended to be more successful in mating and in fledging young than males who did not.

In summary, we have evidence that song sparrows preferentially use the songs they share with particular neighbors when interacting with those neighbors and that birds who share more songs with their neighbors hold their territories longer. These findings suggest that a song-learning strategy that maximizes the number of songs the bird shares with his ultimate neighbors may be advantageous.

Relation to song-learning theories

Our results are consistent with the theory of action-based song learning proposed by Marler and Nelson (Marler, 1990; Nelson and Marler, 1994). Although their theory has been developed on species in which males sing only a single song type (white-crowned sparrows and field sparrows), it is easily generalized to a repertoire species. According to this theory there are two key stages of song learning. First is a sensitive period for song memorization. During this early memorization or ''sensory'' phase, the young bird memorizes multiple songs. Second is the late learning phase which occurs after the memorization phase; for migratory populations this is thought to be the following spring (e.g., field sparrows; Nelson, 1992). For sedentary populations, this phase could begin as early as the late natal summer, perhaps even overlapping the memorization phase. During this later action-based phase the bird retains those songs that best match his neighbors' song through a process of ''selective attrition.''

In our population of song sparrows, we found that at least some songs are memorized early because we identified tutors that were not present after 1 January 1993. However, the adults who disappeared before then had less influence than those who were present into the following spring, suggesting that social interactions later in the first year are important in shaping the repertoires of these first-year males.

In our population we cannot distinguish between the two models of how song modification occurs during the later phase of song learning (either selective retention of earlier memorized songs or de novo late learning) because all adult males that are present during the later phase were also present earlier. Thus, although we have shown that experience with tutors later in the first year is relevant, we do not know when the memorization of all song material is completed. Our two subjects who moved away from their primary tutors and did not learn the songs of their new neighbors provide some indirect support for the idea that new songs are not learned (memorized) during the later phase.

Field studies of song learning in other passerines

Only a few other studies have attempted to trace song learning in the field. Nevertheless, the results of these studies similarly suggest that song-learning strategies provide the young bird with songs he will share with his eventual neighbors. In a sedentary Oregon population of Bewick's wrens (*Thryomanes bewickii*), Kroodsma (1974) showed that after dispersal from the natal area, young males learned the songs of their new neighbors (average repertoire size 16 songs). Jenkins (1978) studied a sedentary population of saddlebacks (*Philesturnus caruncultatus*). He too showed that after dispersal from the natal area, young males learned the songs of their new neighbors (repertoire size one to four songs). O'Loghlen (1995) showed that male brown-headed cowbirds returning for their second breeding season had modified their repertoires (three to eight songs) to match the local dialect.

Turning to species in which a male sings only one song type, Payne's studies (Payne, 1996; Payne and Payne, 1993) of a migratory population of indigo buntings showed that neighbors often sing the same song type, and this pattern of song sharing arises because first-year males tend to copy the song of an adult neighbor. In white-crowned sparrows, males also tend to learn or retain a song type matching their neighbors; this result has been found in both a sedentary population (DeWolfe et al., 1989) and a migratory population (Baptista and Morton, 1988). Nelson (1992) showed that yearling field sparrows return from migration with two song types but retain the one that best matches their neighbors in their first breeding season.

Although closure of song learning in the first year of life occurs in many songbirds besides song sparrows, we now know that males in other species modify their repertoires from year to year by adding or dropping songs. Such annual adjustments of the repertoire apparently occur in several songbirds (saddlebacks, Jenkins, 1978; American redstarts, *Setophaga ruticilla,* Lemon et al., 1994; great tits, *Parus major,* McGregor and Krebs, 1989; European starlings, *Sturnus vulgaris,* Mountjoy and Lemon, 1995). In the cases identified so far, the birds appear to add songs to increase song sharing with new neighbors. Although song sparrows do not add songs past the first breeding season, we have found that birds in our population maintain a high level of sharing in subsequent years, presumably because the young birds entering the neighborhood each year learn the song types prevalent in that neighborhood (Beecher et al., unpublished data). Although the evidence suggests that sharing songs may be an important goal of song-learning strategies, song sharing between neighbors is limited in some populations. Perhaps the best established such case is the western meadowlark (*Sturnella neglecta*). Horn and Falls (1988) reported that western meadowlark males in their population shared no more songs with their close neighbors than they did with birds more than a mile away. Furthermore, the close song sharing among neighbors observed in sedentary populations of song sparrows (this study; see also Cassidy, 1993; Nielsen and Vehrencamp, 1996) is apparently not seen in migratory populations of song sparrows (Hughes et al., 1998; Kramer and Lemon, 1983). It is possible that birds in a migratory population have rather different strategies of song learning (e.g., they do not copy whole song types). It would be interesting to examine this contrast in a comparative study of song learning in migratory versus sedentary populations.

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REFERENCES

Arcese P, 1987. Age, intrusion pressure and defence against floaters by territorial male song sparrows. Anim Behav 35:773–784.

Arcese P, 1989a. Intrasexual competition, mating system and natal dispersal in song sparrows. Anim Behav 38:958–979.

Arcese P, 1989b. Territory acquisition and loss in male song sparrows. Anim Behav 37:45–55.

Baptista LF, Morton ML, 1988. Song learning in montane white-crowned sparrows: from whom and when. Anim Behav 36:1753–1764.

Beecher MD, Campbell SE, Stoddard PK, 1994. Correlation of song learning and territory establishment strategies in the song sparrow. Proc Natl Acad Sci USA 91:1450–1454.

Beecher MD, Stoddard PK, Campbell SE, Horning CL, 1996. Repertoire matching between neighbouring song sparrows. Anim Behav 51:917–923.

Byers BE, Kroodsma DE, 1992. Development of two song categories by chestnut-sided warblers. Anim Behav 44:799–810.

Cassidy ALEV, 1993. Song variation and learning in island populations of song sparrows (PhD dissertation). Victoria, British Columbia: University of British Columbia.

Catchpole CK, 1980. Sexual selection and the evolution of complex songs among warblers of the genus *Acrocephalus.* Behaviour 74:149–166

DeWolfe BB, Baptista LF, Petrinovich L, 1989. Song development and territory establishment in Nuttall's white-crowned sparrows. Condor 91:397–407.

Hasselquist D, Bensch S, von Schantz T, 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature 381:229–232.

Hiebert SM, Stoddard PK, Arcese P, 1989. Repertoire size, territory acquisition and reproductive success in the song sparrow. Anim Behav 37:266–273.

Horn A, Falls JB, 1988. Structure of western meadowlark (*Sturnella neglecta*) song repertoires. Can J Zool 66:284–288.

Hughes M, Nowicki S, Searcy WA, Peters S, 1998. Song type sharing in song sparrows: implications for repertoire function and song learning. Behav Ecol Sociobiol 42:437–446

Jenkins PF, 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. Anim Behav 26:50–78.

Konishi M, 1985. Birdsong: from behavior to neuron. Annu Rev Neurosci 8:125–170.

Kramer HG, Lemon RE, 1983. Dynamics of territorial singing between neighbouring song sparrows (*Melospiza melodia*). Behaviour 85: 198–223.

Kroodsma DE, 1974. Song learning, dialects, and dispersal in the Bewick's wren. Z Tierpsychol 35:352–380.

Kroodsma DE, 1982. Song repertoires: problems in their definition and use. In: Acoustic communication in birds, vol. 2 (Kroodsma DE, Miller EH, eds). New York: Academic Press; 125–146.

Kroodsma DE, Pickert, R, 1984. Sensitive phases for song learning: effects of social interaction and individual variation. Anim Behav 32:389–394.

Lemon RE, Perrault S, Weary DM, 1994. Dual strategies of song development in American redstarts, *Setophaga ruticilla.* Anim Behav 47:317–329.

Marler P, 1990. Song learning: the interface between behaviour and neuroethology. Phil Trans R Soc Lond B 329:109–114.

Marler P, Peters S, 1982. Structural changes in song ontogeny in the swamp sparrow *Melospiza georgiana.* Auk 99:446–458.

Marler P, Peters S, 1987. A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*: a case of age-limited learning. Ethology 76:89–100.

McGregor PK, Krebs JR, 1989. Song learning in adult great tits (*Parus major*): effects of neighbours. Behaviour 108:139–159.

McGregor PK, Krebs JR, Perrins CM, 1981. Song repertoires and lifetime reproductive success in the great tit *Parus major.* Am Nat 118: 149–159.

Morton ML, 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain white-crowned sparrow. Condor 94:117–133.

Mountjoy DJ, Lemon RE, 1995. Extended song learning in wild European starlings. Anim Behav 49:357–366.

Mountjoy DJ, Lemon RE, 1996. Female choice for complex song in the European starling: a field experiment. Behav Ecol Sociobiol 38: 65–71.

Nelson DA, 1992. Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). Behav Ecol Sociobiol 30:415–424.

Nelson DA, Marler P, 1994. Selection-based learning in bird song development. Proc Natl Acad Sci USA 91:10498–10501.

Nielsen BMB, Vehrencamp SL, 1995. Responses of song sparrows to song type matching via interactive playback. Behav Ecol Sociobiol 37:109–117.

Nottebohm F, 1991. Reassessing the mechanisms and origins of vocal learning in birds. Trends Neurosci 14:206–211.

O'Loghlen AL, 1995. Delayed access to local songs prolongs vocal development in dialect populations of brown-headed cowbirds. Condor 97:402–414.

O'Loghlen AL, Rothstein SI, 1993. An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. Anim Behav 46:293–304.

Payne RB, 1996. Song traditions in indigo buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds.) Ithaca, New York: Cornell University Press; 198–220.

Payne RB, Payne LL, 1993. Song copying and cultural transmission in indigo buntings. Anim Behav 46:1045–1065.

Payne RB, Payne LL, 1997. Field observations, experimental design, and the time and place of learning bird song. In: Social influences on vocal development (Snowdon CT, Hausberger M, eds). Cambridge, Cambridge University Press; 57–84.

Payne RB, Payne LL, Doehlert SM, 1988. Biological and cultural success of song memes in indigo buntings. Ecology 69(1):104–117.

Searcy WA, Andersson M, 1986. Sexual selection and the evolution of song. Annu Rev Ecol Syst 17:507–533.

Slater PJB, Ince SA, 1982. Song development in chaffinches: what is learnt and when? Ibis 124:21–26

Smith GT, Brenowitz EA, Beecher MD, Wingfield JC, 1997. Seasonal changes in testosterone, neural attributes of song control nuclei, and song structure in wild songbirds. J Neurosci 17(15):6001–6010.

Smith JNM, 1988. Determinants of lifetime reproductive success in the song sparrow. In: Reproductive success: studies of individual variation in contrasting breeding systems (Clutton-Brock TH, ed). Chicago: University of Chicago Press; 154–172.