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Song learning in the song sparrow (*Melospiza melodia*): ecological and social factors

Jennifer Cully Nordby

A dissertation submitted in partial fulfillment of the
requirements for the degree of

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Abstract

Song learning in the song sparrow (*Melospiza melodia*): ecological and social factors

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During song learning, songbirds are exposed to many more songs then they keep for their final song repertoire and little is known about how or why a bird selects the particular songs he sings as an adult. These studies examine the social and ecological factors that influence song learning and repertoire development in a sedentary Washington population of song sparrows (*Melospiza melodia*). In the first study, I examined the song repertoires of an entire cohort of males and compared them to those of potential song tutors. I found that a young male (1) learns whole song types, (2) learns songs from multiple tutors who were neighbors in his first year, (3) establishes a territory among or near these tutors, and (4) learns more songs from tutors who survive the winter. In the second study, I attempted to replicate in the laboratory the key variables of the natural song learning environment by exposing hand-reared male song sparrows to live adult tutors. Results from this experiment confirmed findings from the field study. In addition, this experiment showed that (1) interactions with a close neighbor after the natal summer affect song learning and (2) males preferentially learn songs that are shared among their tutors and other males in their same age cohort. In the third study, I examined whether song sparrows were capable of acquiring new songs after their presumed sensitive period for song memorization (30 – 90 days of age) by exposing them to new

tutors after their natal summer. Eight of 12 subjects learned songs from tutors they only heard after 140 days of age, and six subjects learned most of their songs from a late tutor. Thus, song sparrows are capable of acquiring many songs de novo in late fall, and may be capable of acquiring songs even later. Taken together, these studies demonstrate that young male song sparrows have a song learning strategy that provides them with a repertoire of song types they will share with their neighbors in their first-breeding season and that social interactions after the natal summer are crucial to song repertoire development.

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Chapter 1

ECOLOGICAL CORRELATES OF SONG LEARNING IN SONG SPARROWS

INTRODUCTION

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, 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 take 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 one 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 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 lab (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 five different hatch years. In the present study we monitored an entire cohort (all first-year males within our study area in one 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 3 - 4 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 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 vs. those who did not survive past 01 January. We chose 01 January as the cutoff date since 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. Since 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. The song sparrow habitat consists of mixed deciduous and coniferous woodland (including bigleaf maple, *Acer* *macrophyllum;* red alder, *Alnus rubra;* Douglas fir, *Pseudotsuga menziesii;* and western redcedar, *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 $100m^2$ to $7500m^2$.

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 since 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 three 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 pre-dispersal) 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 one 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 (one 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 3 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 non-tutor 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 non-tutor 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 six to 11 song types with a median of eight (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 1.1 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 one song type for 10 subjects, and for all but two song types for five 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. Since we were unable to identify tutors for over half of these two males' songs, they were included only in analyses which examined individual tutor influence (to give credit to those tutors we could identify), and not in analyses which examined subjects' song learning strategy (since 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 1.2). 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

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 since 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 1.3. 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 1.4). Twenty-eight of 39 subjects had tutors whose territories were 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 further removed (Figure 1.5). Results were similar for the exclusive set of tutors; 26 subjects replaced and/or were contiguous to one of their tutors, nine were 1 gap removed, and four were further removed.

Subjects Banded in 1992 vs. 1993

Results from the seven subjects who were banded in 1993 were similar to those who were banded in 1992. The only notable difference between the two groups appears in the inclusive number of tutors per subject (Figure 1.2). Results from subjects banded in 1993 were slightly weighted toward the higher numbers (two of the three subjects who had nine or ten tutors were banded in 1993). However, this difference is 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 in fact 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 Non-tutors

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 one subject, 25 tutored two subjects, and 28 tutored three or more subjects. Only seven of the birds who tutored two or more males were primary tutors for more than one 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 01 January 1993 with those who disappeared 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 01 January 1993, Figure 1.6). The total number of songs tutored ranged from 0.20 to 20.41 for males identified as tutors; non-tutors 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 vs. 1.21 songs, $n = 87$ vs. 35 respectively, $t = 3.56$, $p = 0.001$). This result holds even when we consider only those males identified as tutors ($t = 3.05$, $p = 0.003$), or exclude the one outlier male with a score of 20.41 ($t = 2.88$, $p = 0.005$). 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 01 January.

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, so as to avoid a confound 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, two tutors with 5 and 6 song types respectively excluded, F = 0.53, p = 0.71), nor by tutor's subsequent survival (measured from the subject's hatch year, 1-4 years, F = 0.41, p = 0.75, or from the tutor's hatch year, 2-8 years, F = 0.38, p = 0.89). There was a significant effect of tutor age (1, 2 , 3, or 4 or more years old in 1992, F = 3.95, p = 0.01); however, this effect does not persist when the one outlier male with a score of 20.41 (see Figure 1.6) is deleted from the sample (F = 2.07, p = 0.11).

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 01 January. There were no significant differences between these two groups on any of the four traits we measured; repertoire size (t = 1.03, p = 0.30), age in 1992 (t = 0.24, p = 0.81), years on territory past 1992 (t = 1.56, p = 0.12), and total years on territory (t = 1.49, p = 0.14).

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 vs. 2.93, n = 35 vs. 4 respectively, t = 2.61, p = 0.026).

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 a confound with the late influence effect). The results were the same. Primary tutor scores were not predicted by tutor repertoire size (7-11 song types, one tutor with 6 song types excluded, F = 0.87, p = 0.49), tutor age (1-5 years, F = 0.74, p = 0.57), years on territory past 1992 (1-4 years, F = 0.46, p = 0.71), or total years on territory (2-7 years, F = 1.08, p = 0.39).

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 = 0.37), age in 1992 (t = 1.43, p = 0.15), years on territory past 1992 (t = 0.43, p = 0.67) and total years on territory (t = 0.80, p = 0.43). Because some of the primary tutors had low tutor scores, we decided to compare the total tutor scores of the top 15 primary tutors (those with primary tutor scores of 4.0 or higher) to all other surviving males. Again, there were no significant differences: repertoire size (t = 1.52, p = 0.13), age in 1992 (t = 1.16, p = 0.25), years on territory past 1992 (t = 0.89, p = 0.38) and total years on territory (t = 0.18, p = 0.86).

We also examined one other correlate; the proximity of the 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 further (two or more gaps) away from him (n = 8) (Table 1, last column). 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 vs. 1 gap removed, $p = .04$; contiguous vs. further, $p < .001$).

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 ARYM, were banded near their identified tutors (in July and October, 1992, respectively) but subsequently established breeding territories that were more than 500m (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 was 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 600m (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 eleven 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 six subjects together, only 4% of the tutors in the areas they moved from died as 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 (1) is influenced by social interactions continuing beyond the sensitive period of the natal summer, and into the following spring, and (2) is 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 which 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 (vs. 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 which would explain why these subjects only learned songs from 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 respectively. 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, for instance, 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 study). Payne et al. (1988) also found that song sharing relates to fitness in indigo buntings, specifically that first-year males who share 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 late in the 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 since we identified tutors that were not present after 01 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 that he will share with his eventual neighbors. In a sedentary Oregon population of Bewick's wrens (*Thryomanes bewickii*), Kroodsma (1974) showed that following 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 carunculatus*). He too showed that following dispersal from the natal area, young males learned the songs of their new neighbors (repertoire size 1-4 songs). O'Loghlen (1995) showed that male brown-headed cowbirds returning for their second breeding season had modified their repertoires (3-8 songs) to match the local dialect.

Turning to species in which a male sings only one song type, Payne's studies (Payne and Payne, 1993; Payne, 1996) of a migratory population of indigo buntings showed that neighbors often sing the same song type, this pattern of song sharing arising because first-year males tended 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 over a mile away. Furthermore, the close song sharing among neighbors observed in sedentary populations of song sparrows (ours; 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., 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.

Figure 1.1

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

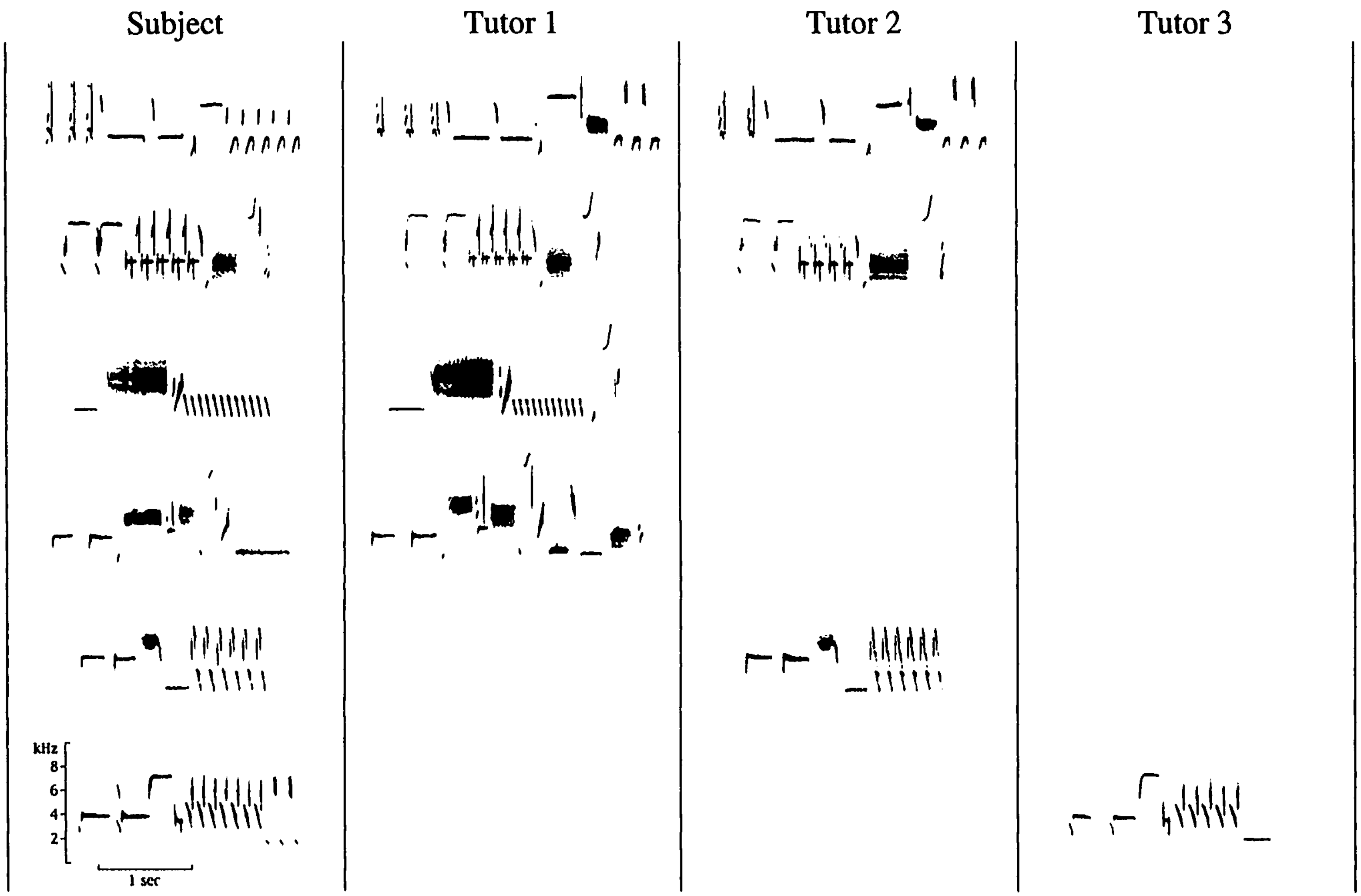
Subject
Tutor 1
Tutor 2
Tutor 3
kHz
8
6
4
2
1 sec

Figure 1.2
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).

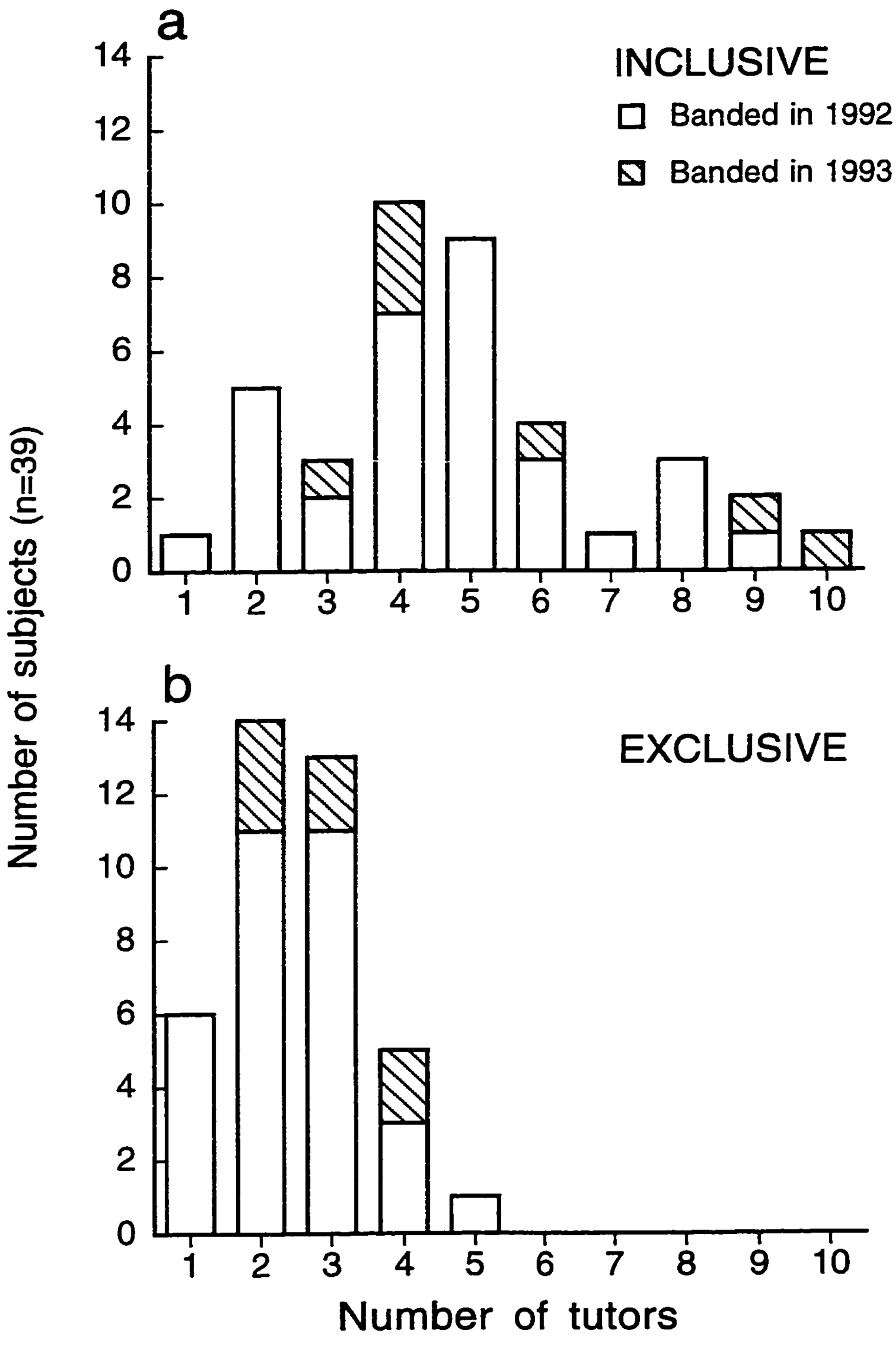
a
INCLUSIVE
□ Banded in 1992
▨ Banded in 1993
b
EXCLUSIVE
Number of subjects (n=39)
Number of tutors
0
2
4
6
8
10
12
14
1
2
3
4
5
6
7
8
9
10

Figure 1.3
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 (X's), and which was adjacent to his only surviving tutor (OGGM).

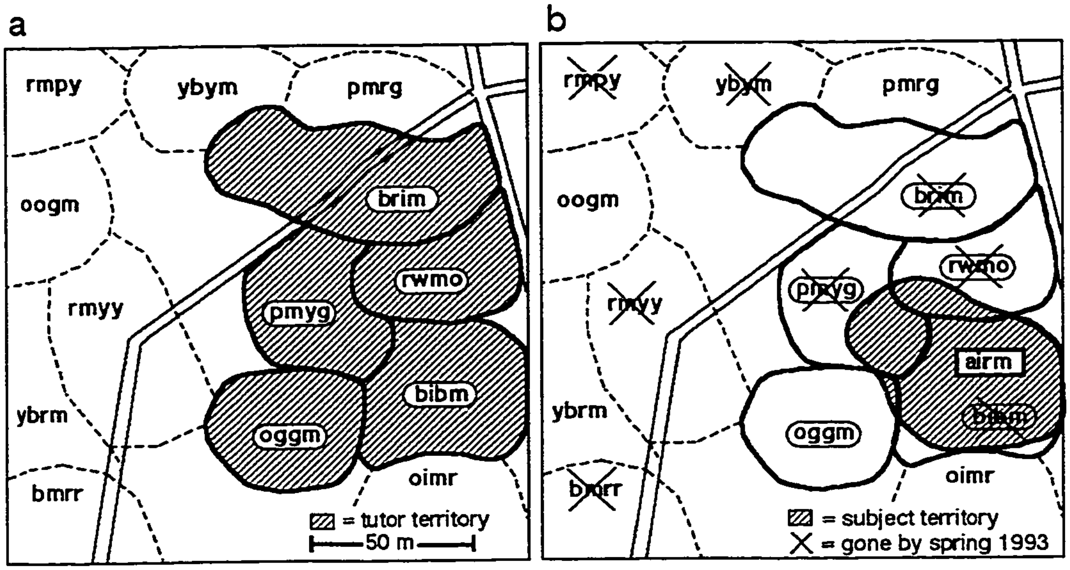
a
rmpy
ybym
pmrg
oogm
brim
rwmo
pmyg
rmyy
bibm
ybrm
oggm
oimr
bmrr
▨ = tutor territory
50 m
b
rmpy
ybym
pmrg
oogm
brim
rwmo
pmyg
rmyy
airm
ybrm
oggm
bibm
oimr
bmrr
▨ = subject territory
X = gone by spring 1993

Figure 1.4
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 non-tutor bird's territories.

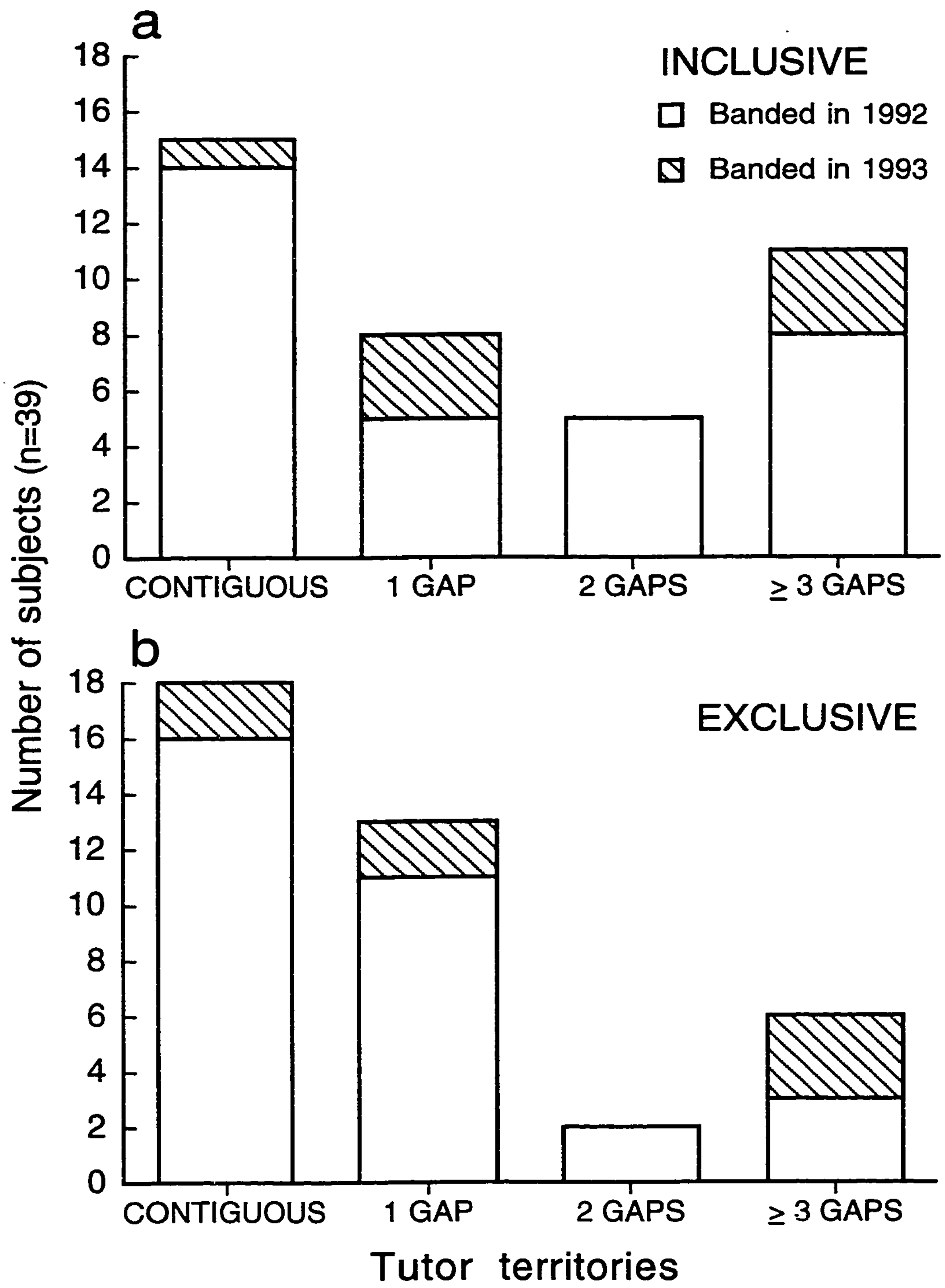
a
INCLUSIVE
☐ Banded in 1992
▨ Banded in 1993
18
16
14
12
10
8
6
4
2
0
CONTIGUOUS
1 GAP
2 GAPS
≥ 3 GAPS
Number of subjects (n=39)
b
EXCLUSIVE
18
16
14
12
10
8
6
4
2
0
CONTIGUOUS
1 GAP
2 GAPS
≥ 3 GAPS
Tutor territories

Figure 1.5
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 non-tutor bird's territory. Note: Subjects who replaced tutors may also have settled in territories contiguous to a surviving tutor, but were only categorized as "replaced".

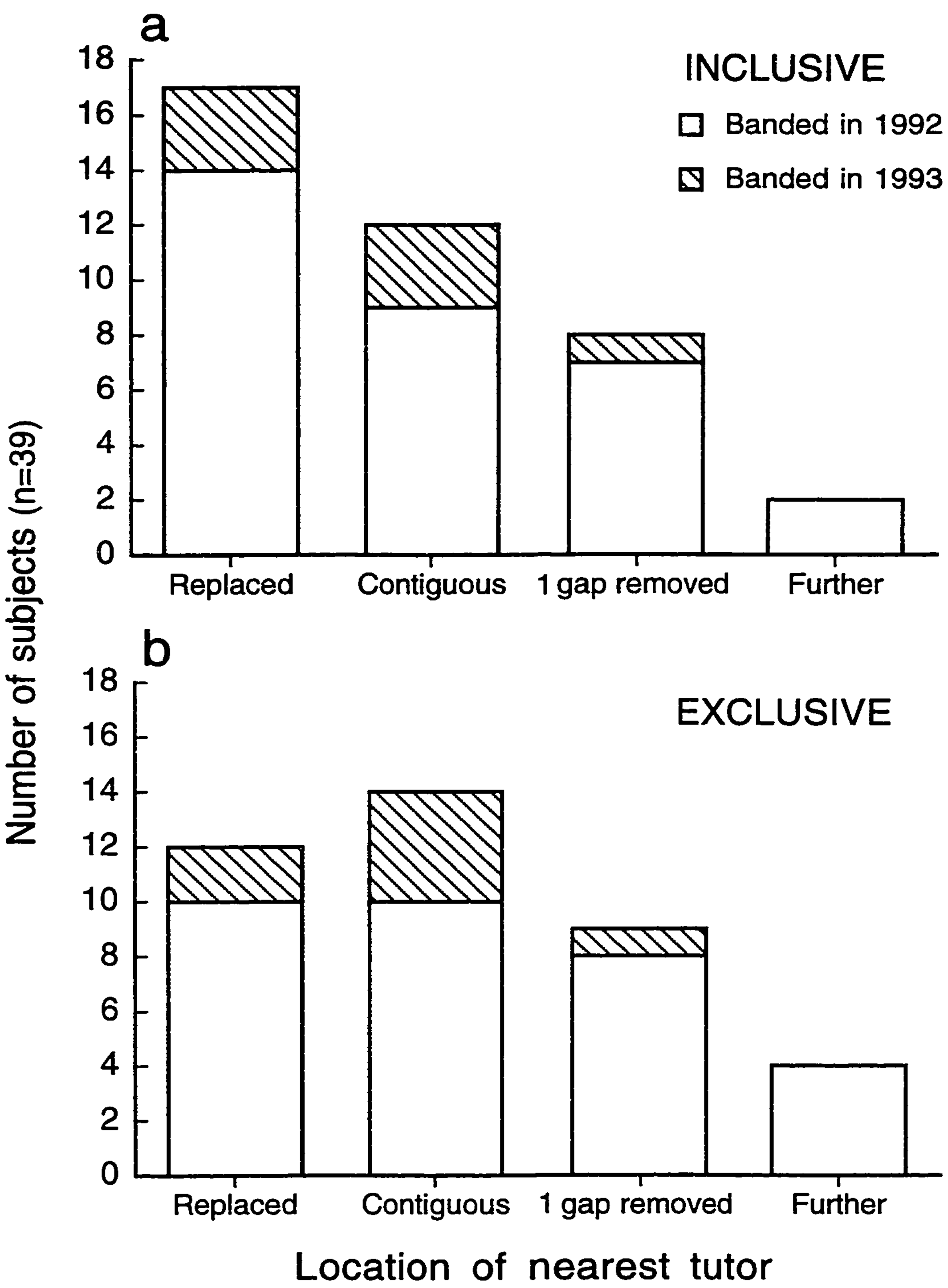
a
INCLUSIVE
□ Banded in 1992
▨ Banded in 1993
Number of subjects (n=39)
0
2
4
6
8
10
12
14
16
18
Replaced
Contiguous
1 gap removed
Further
b
EXCLUSIVE
0
2
4
6
8
10
12
14
16
18
Replaced
Contiguous
1 gap removed
Further
Location of nearest tutor

Figure 1.6

Frequency distribution of the total number of songs (inclusive analysis) tutored by adult males who survived past 01 January 1993 (shaded) and by those who did not (striped).

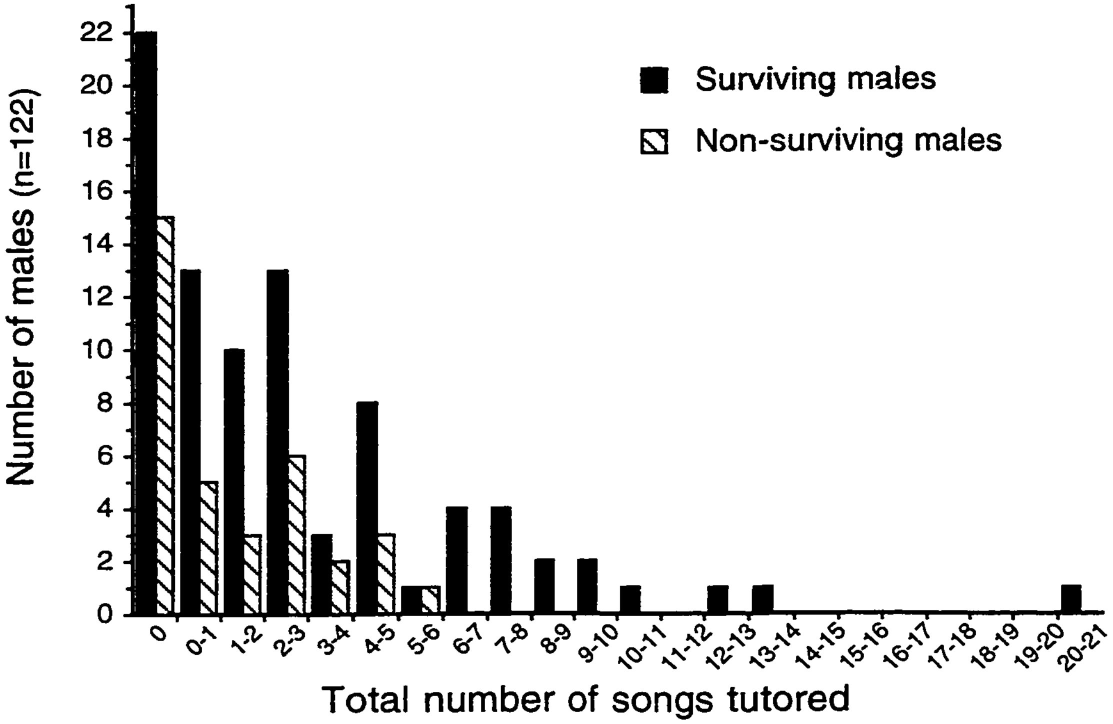
Number of males (n=122)
22
20
18
16
14
12
10
8
6
4
2
0
■ Surviving males
▨ Non-surviving males
0
0-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-10
10-11
11-12
12-13
13-14
14-15
15-16
16-17
17-18
18-19
19-20
20-21
Total number of songs tutored

Table 1.1
Tutor scores and proximity of each subject to his primary tutor in spring 1993

Subject	# of songs[a]		Tutor 1	Tutor 2	Tutor 3	Tutor 4	Tutor 5	Tutor 6	Tutor 7	Tutor 8	Tutor 9	Tutor 10	Proximity to Tutor 1[b]
GMYI	8	2	1.33	1.08	1.00	0.58	0.50	0.33	0.33	0.33	0.25	0.25	Further
GRRM	6	1	1.33	1.33	1.00	1.00	0.33						1 gap
YARM	7	1	1.33	1.25*	1.08	0.75	0.58	0.50	0.25*	0.25*			Further
ARYM	6		1.41	1.08	0.91	0.75*	0.66	0.50	0.33	0.33			Further
YYAM	9		2.20	2.00	1.53	1.00	0.83	0.53*	0.50	0.20	0.20*		Contiguous
ABGM	8		2.50	2.00	1.75	0.75	0.50*	0.50					Further
AIBM	8		2.50*	2.00*	1.50	1.50*	0.50						-
AIRM	9		2.50*	2.00	2.00*	1.50*	1.00*						-
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							Further
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						Further
RMIO	6		2.83*	1.83	1.33*								-
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*	0.25						Further
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*	0.75	0.25*						Contiguous
IOOM	10		3.33	2.25	1.25	0.83	0.83	0.75	0.75				Further
BRAM	11		3.83	3.16	1.83	1.33	0.83						1 gap
ORIM	7		3.91*	0.75	0.58*	0.50	0.33	0.33*	0.33	0.25			-
PPOM	8	1	4.00	1.50	1.00	0.50							Contiguous
BARM	10		4.16	2.33*	2.33	0.83	0.33						Contiguous
RAOM	10		4.20	2.20	2.00	0.70	0.70*	0.20*					Contiguous
YOAM	8	2	4.33	0.83	0.50	0.33*							1 gap
BAYM	6	1	4.50	0.50									1 gap
IAYM	10		4.82	3.82*	1.00*	0.33*							1 gap
IIAM	8		4.95	0.95*	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*	0.33							Contiguous
IAIM	8	1	6.00	1.00									Contiguous
OARM	7		6.25	0.25*	0.25	0.25							Contiguous
IMYY	8		6.33	0.83	0.50	0.33*							Contiguous
YMRR	8		6.50	0.50	0.50*	0.50*							1 gap
GARM	8		7.00	1.00*									Contiguous
GAYM	9		7.00	1.00	0.50	0.50*							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 column indicates subject's repertoire size, second column indicates number of songs for which we could not identify a tutor.

b Last column indicates the proximity of each subject to his primary tutor in spring 1993 (contiguous = adjacent territory; gap = large open space or another bird's territory; further = further than 1 gap; - = tutor not present in 1993).

* Indicates tutors who did not survive past 01 January 1993.

Chapter 2

SOCIAL INFLUENCES DURING SONG DEVELOPMENT
IN THE SONG SPARROW:
A LABORATORY EXPERIMENT SIMULATING FIELD CONDITIONS

INTRODUCTION

During song learning an oscine songbird is exposed to many more songs than he ultimately keeps for his crystallized song repertoire, which raises the question of how the bird selects the particular songs he keeps. That song selection is an active process was first suggested by the studies of Marler & Peters (1981, 1982a, b, 1988b) on swamp sparrows, *Melospiza georgiana*. They found that a bird sang more songs during the rehearsal (or plastic song) phase of song learning than he kept for his final repertoire (2-4 songs in this species). Marler & Peters could trace the 'extra' or 'overproduced' songs back to tutor songs the bird had heard during his sensitive phase (in the swamp sparrow the sensitive phase is roughly months 2 and 3, the rehearsal phase roughly months 9 and 10). Marler & Peters called the dropping of the extra songs selective attrition. Subsequently, Marler & Nelson (Marler 1990; Nelson & Marler 1994) suggested that normally selective attrition would occur as a result of social interactions early in the bird's first breeding season, with birds retaining those songs that best matched those of their new neighbours, and dropping those that matched less well. Evidence for this late influence hypothesis (as we will refer to it) has been found in several species (e.g., Kroodsma & Pickert 1984; DeWolfe et al. 1989; Byers & Kroodsma 1992; Nelson 1992).

Our field studies on the song sparrow, *Melospiza melodia*, a species in which each male sings 6-10 different song types, have identified a number of social variables that are critical in song selection. As shown by Arcese (1987, 1989a, b) in another Pacific Northwest population, young males, following dispersal, spend several months moving about, or 'floating', on the adjoining territories of several adult males. By the time they reach their first spring, these young males have established breeding territories, usually within this floater range. Using these observations as background, we conducted two field studies of a sedentary Washington population to examine the question of which songs, from which adults, a bird selects for his final repertoire (Beecher et al. 1994b; Nordby et al. in press). From these studies we could make the follow generalizations. The young song sparrow (1) copied whole song types (vs. recombining elements copied from different song types); (2) learned his songs from several older birds who were neighbours in his natal summer; (3) usually established his territory near his surviving tutor-neighbours the next spring; (4) preferentially learned song types shared by his tutors vs. song types that were unique to particular tutors; (5) learned more songs from tutors that survived into the next spring (i.e., the young bird's first breeding season) than from tutors who died before then; and (6) learned more songs from the bird who was his nearest neighbor the following spring than from his other surviving tutors.

We interpreted these results in terms of a theoretical song learning strategy, the goal of which is to maximize the number of songs the bird will share with his neighbours, especially his nearest neighbours, in his first breeding season. This overall goal is met by the bird preserving song types (rather than recombining elements to form new types), choosing songs from several neighbouring birds (rather than from just one of them), favoring songs the tutor-neighbours share, and favoring the songs of his nearest surviving neighbor.

We wanted to confirm and extend the conclusions from our field studies by bringing the hypothesized key features of the social context into the laboratory. In the present study, we simulated field conditions by placing four adult birds that had been neighbours in the field in four close aviary-based 'territories'. Young males were moved, during their presumed sensitive period, from tutor to tutor, simulating the movements of young floater song sparrows. When a young bird was placed near one of these adults, he could see only that adult but could still hear the other males. The major experimental manipulation was whether, following the early sensitive period, the young bird was stationed next to one tutor or was moved among all the tutor territories. The 'stationary' condition resembles the natural condition: some time between his natal summer and the following spring, the young bird establishes his territory, usually closest to his primary tutor. We made the following predictions.

1. Birds would learn whole song types, consistent with our field studies, and in contrast both to earlier tape tutor studies (Marler & Peters 1987, 1988a) and our own preliminary laboratory studies with live tutors which lacked many of the key features of our present simulation (M. D. Beecher, S. E. Campbell & J. M. Burt unpublished data, described in Beecher 1996).

2. Birds, even those stationed next to one tutor in fall and spring, would learn songs from more than one tutor. The field data show that birds usually learn from multiple tutors, and similar results in this experiment would provide further evidence that the song learning strategy is designed to give the bird songs of several of his neighbours (or neighbours-to-be).

3. Birds would learn more tutor-shared songs than tutor-unique songs. Sharing is more unambiguously measured in our lab simulation because we know that the young bird heard all tutor song types. In the field, several neighbours may have the same songs, but other distant birds may have also have somewhat similar songs, and we cannot know which adults the young males interacted with, or which of these songs he may have heard.

4. Birds stationed next to only one tutor after their sensitive period would copy more songs of that tutor than of other tutors. This would clarify one aspect of the field results, for we cannot tell in the field whether birds learn more from tutors surviving into the spring because they continue to

interact with them into the spring, or because these tutors were more active, vigorous birds during the natal summer and the learning occurred entirely during that period (Nordby et al. in press).

METHODS

Subjects

Subjects were nine males from four different broods. We collected the subjects from our study population in Seattle, Washington on 03 May 1994 when they were four to six days old. We hand-reared them in the laboratory as a group until they were 33-35 days old, and then placed them into individual wire-mesh cages (45cm x 28cm x 18cm) equipped with wooden perches. Subjects were maintained on ad lib water and food (Mazuri small bird maintenance diet, mixed seed, fresh greens, and egg/vitamin supplement) throughout the experiment.

Tutors

Tutors were four wild-caught adult males (referred to as Tutors 1, 2, 3, and 4) whom we collected from our study population in mid-October 1993. Each male was housed in an individual flight cage (1.47m x 0.71m x 1.83m, containing a 1.0m tall potted shrub and several perches) and maintained on ad lib water and food. These four birds had been adjacent neighbours in the field and shared several songs with one another. The song rates of tutors 2, 3, and 4 were initially low; to encourage vocal output we gave them subcutaneous implants of testosterone: 12mm silastic tube implants on 17 May 1994, and 6mm implants on 06 June 1994. We did not give Tutor 1 testosterone since his song rate was similar to the song rate of males in the field.

There was one additional adult male to whom the subjects were exposed. He died six days into the experiment and was replaced by Tutor 3. Subjects heard this fifth male for only six days (when they were 33-41 days old), and only five subjects had visual contact with him. We did not detect any influence from this male on the song repertoire of any subject, so we did not include him in further analyses.

Experimental Design and Procedure

We simulated natural conditions by placing the tutors outside in four corners of an area on the roof of a building at the University of Washington in Seattle, Washington and by having the subjects visit the tutors on these pseudo-territories. Tutor aviaries were 11.5 - 13.0m apart, and when a subject was exposed to a tutor, his cage was 0.25m away from the tutor's aviary and was placed in a cubicle that was only open on the side facing the tutor (Fig. 2.1). Each subject had visual contact only with the adjacent tutor, but all birds on the roof were in auditory contact. So, even though subjects could see only one tutor at a time, they could hear other tutors (and other subjects) at a short distance.

The experiment was conducted in two stages (Fig. 2.2). Stage I occurred when subjects were 33 - 94 days old (01 June - 28 July 1994) and corresponded to the presumed sensitive period for song memorization (Marler & Peters 1987). During this stage, we randomly rotated all subjects among all four tutors. All subjects remained on the roof with the tutors throughout this stage and were rotated every three days. There were two or three subjects with each tutor at a time, and each subject visited all tutors equally. At the end of Stage I, all subjects were brought into the lab and had no contact with tutors until the beginning of the Stage II. Subjects began singing plastic song in late August and we wanted to limit possible cohort influence. So, from that time on, when they were not being exposed to the tutors, subjects were housed in individual acoustic isolation chambers.

Stage II occurred when subjects were 145 - 354 days old and corresponded to the later stages of song development. During this stage there were two bouts of tutor exposure; the first occurred in Fall when subjects were 145 - 183 days old (19 September - 25 October 1994) and the second occurred in late winter and early spring when subjects were 259 - 354 days old (11 January - 14 April 1995). We did not expose subjects to the tutors in late fall and early winter since during this time the tutors, like males in the field, produced little song.

For Stage II of the experiment, we divided the subjects into two groups, 'Rotated' and 'Stationary'. The five subjects in the Rotated group were rotated equally among all four tutors, as they were in Stage I. Thus, during Stage II, these subjects had close visual and auditory contact with all tutors. The four subjects in the Stationary group were randomly assigned a particular tutor and only visited that one tutor throughout Stage II. These subjects had close auditory and visual contact with only one tutor, but could hear the other tutors at a distance.

In contrast to Stage I, during tutor exposure in Stage II, only one group, either the Rotated or Stationary group, was out on the roof with the tutors at any one time and the other group remained in isolation. We did this because the young birds were now singing and so could hear one another as well as the tutors, and we wanted to limit possible cohort influence by having only one subject with each tutor at a time. However, we also wanted to be able to detect cohort influence if it occurred, so, rather than mixing groups, we only had individuals from the same group out with tutors at the same time. With this design, subjects heard only the tutors and their cohorts throughout Stage II (we use 'cohorts' to refer to birds in the same group, Rotated or Stationary).

During the fall bout of tutor exposure, groups were switched every four days and subjects were with tutors 50% of the time. During the winter/spring bout, groups were switched every day and subjects were with the tutors 33% of the time (a group of females was included in the rotations, but was not part of this study).

One of the subjects in the Rotated group, BR, did not receive the fall bout of tutor exposure during Stage II, but was included in the Stage I rotations and in the winter/spring rotations. During the fall he was housed with three females and one other juvenile male who subsequently died. In our analysis, we included him in the Rotated group, but he is separately identified.

To monitor tutor song rate and test for any effect that differences in song rate had on repertoire development, we sampled each tutor's song rate during Stage I. We recorded all four tutors simultaneously twice a day, once in the morning and once in the afternoon, for 45 minutes and counted how many songs each one sang during each session. All songs were recorded using Realistic 33-1056A omni-directional, 600 ohm condenser microphones and Marantz PMD221 or AIWA AD-6350 stereo cassette recorders and analyzed on a Kay DSP-5500 Sonagraph.

Song Analysis and Identification of Tutors

Song sparrows sing with 'eventual variety' meaning that they sing one song type several times, varying each rendition slightly, before switching to the next type (e.g., AAA..., BBB...). In all our studies of song sparrow song, we use the bird's singing behavior, rather than our assessment of song similarity, to classify a bird's songs into different song types. That is, we classify different variations of a song as the same type if the bird sings them in the same bout. Podos et al. (1992) have shown that classifying types by the bird's singing behavior usually gives the same results as classifying by song similarity (which they measure in terms of 'minimal units of production'), and this has been our finding as well. Occasionally a bird will sing extreme variations on a type within a bout, and occasionally a bird will sing two rather similar song types in different bouts (treat them as two types), but these exceptions are rare. We cannot, however, use singing behavior in the same way to identify a song type that is shared between neighbouring birds or to identify a type that a young bird has copied from a tutor, so in these cases we must use our assessment of song similarity. In our two previous field studies of song learning in song sparrows (Beecher et al. 1994; Nordby et al. in press) we found that first-year males may blend two tutors' versions of what we considered a shared type, or they may sing both versions as variations of a single type, but they practically never sing them as two separate types. This observation suggests that song sparrows classify highly similar songs as the same song type. Our song perception and field playback experiments (Stoddard et al. 1992a, b; Horning et al. 1993; Beecher et al. 1994a, 1996, submitted) suggest the same, and hence we make this assumption in our present analysis.

We recorded each subject's crystallized repertoire after 01 May 1994 when they were more than a year old, using the same equipment described above. Sonagrams of each subject's song types, including distinct variations, were visually matched, based on the consensus of three judges, to those of all four tutors and cohorts. We first wanted to identify which bird had the most influence on each subject's repertoire development, so we looked for the tutor or cohort who had the most similar rendition of each subject's song types. The bird who had the best matching song type was identified as the tutor for that type, provided that his song type shared at least 50% of the elements in the subject's song type, in the same order. In cases where two adult tutors had equally similar versions of a song type, or if a subject sang both tutors' versions of the song type, we counted all birds in the tie as tutors. In cases where a tutor and a cohort had equally similar versions of a song type, we gave the adult tutor sole credit. In cases where a cohort had a better matching song type than any tutor, we gave half credit to the cohort and half credit to the tutor with the best match to reflect the origin of the song. There was one case where two subjects had a similar song type that was not in any of the tutors' repertoires. We scanned recordings of the plastic song of these two subjects and determined that one of the subjects had invented the song and the other had learned it from him.

In order to quantify the amount of influence each tutor had on each subject, we gave each tutor a score based on the number of song types he matched to each subject (devalued by the number of other tutors identified for those song types). For example, if he was the sole tutor for two types (2.00 credits) and shared credit with one other tutor for another type (0.50 credits), he would receive a score of 2.50 for that subject. To test the hypothesis that nearby tutors had greater influence on song development, we examined the repertoires of the Stationary subjects and compared the number of songs credited to the adjacent tutor to the number credited to other tutors.

We conducted a second analysis on the song types that were classified as tutor or cohort matches to determine how well these songs matched. Each subjects' matching song types were ranked on a three point scale: 1 = ≥ 90% of the elements matched a tutor or cohort song type, 2 = 70-89% of the elements matched, and 3 = 50-69% of the elements matched. We also analyzed the unmatched song types, those that did not meet the criteria of matching any one tutor or cohort song by at least 50%. If at least half of the elements within the song matched those from tutor songs (but not any one song) we categorized it as an 'element match'. If fewer than half of the elements were identified as tutor song elements we categorized the song as an 'invention'.

To test the hypothesis that subjects would preferentially learn songs that were shared among the tutors, we *a priori* determined which of the tutors' songs we considered shared via consensus of three judges. While we considered our assessment of sharing valid, we wanted to be confident that the results were not an artifact of the specifics of our evaluation. We therefore used two sets of criteria to determine sharing; one 'strict' (the first half and/or the last two-thirds of the elements in the songs matched) and the other 'loose' (the introductory element and at least two other elements matched). We then determined, using both criteria, how many of the subjects' tutor-matching song types were among those we classified as shared and how many were not.

RESULTS

Subject Repertoires

The size of subjects' repertoires ranged from five to nine song types, with a median of seven, which is within the normal range for *M. melodia* (Table 1). Five of the nine subjects had repertoires in which all but one or two songs matched those of a tutor or cohort. Three subjects had three non-matching song types each, and the ninth subject, IY, had no matching song types (Table 1). If we exclude IY, then 71% of the subjects' songs were considered tutor or cohort matches, 24% were element matches, and only 5% were inventions.

We cannot explain why IY had a different song learning pattern than the other eight subjects. The only correlate we are aware of is that his song repertoire crystallized later than most of the other subjects. IY was one of three subjects who did not reach crystallization until late April; the other five subjects had crystallized repertoires two or more weeks before then. Since IY did not learn any tutor song types but rather invented most of his song types, we excluded him from the analyses that were aimed at determining the relative degree of tutor or cohort influence on repertoire development.

In our analysis of how well the subjects' song types matched those of their tutors, we ranked 28 of the 39 tutor or cohort matching song types as 1's ($\geq$ 90% of the elements matched), eight as 2's (70-89% of the elements matched), and only three as 3's (50-69% of the elements matched). Figure 2.3 shows examples of matching subject and tutor song types.

Tutor Influence on Repertoire Development

All subjects (except IY) learned songs from two or more tutors, and tutor scores ranged from 0 to 5.25 (Table 1). We designated the tutor with the highest score for a subject as that subject's primary tutor (i.e., the tutor who influenced that subject the most). Within the Stationary group, each subject's primary tutor was the tutor he was stationed next to during Stage II which supports the late influence hypothesis that social interactions after the sensitive period can affect song development (Table 1). The one slight departure from this finding was subject RI who had the same score for his primary tutor and one of his cohorts. Interestingly, all the subjects in the Rotated group had the same primary tutor, Tutor 1. The one clear correlate of this finding is that Tutor 1 had the highest song rate, at least during Stage I. Over the 108 sampling sessions we recorded during Stage I, Tutor 1 sang over twice as many songs as any of the other tutors. Tutor 1's average song rate was 26.1 songs/hr and the average rates for Tutors 2, 3, and 4 were 8.9, 9.9, and 12.2 songs/hr respectively (Tutor 3 was not present for the first 11 sessions). We did not directly sample song rate during Stage II, but all tutors sang during winter and spring and it was our impression that Tutor 1 again sang the most.

Learning of Shared Songs

Using the strict criterion for determining sharing, we classified the 30 tutor songs into 22 different song types, six (27%) of which were shared and 16 of which were unique to a single tutor. If subjects learned tutor song types without regard to sharing, and assuming that they would not learn two shared songs as separate types, then we would expect that 27% of their tutor-matching songs on average would be tutor-shared songs. We found that, on average, 47% of their tutor-matching song types were tutor-shared songs which is significantly greater than expected (Single sample *t* test: $t_7 = 2.57$, $p < 0.05$). Results were even stronger using the loose criterion for sharing. We classified the 30 tutor songs into 19 different types, eight shared (42%) and 11 unique. On average, 67% of the subjects' tutor-matching song types were shared among the tutors; again this was higher than expected (Single sample *t* test: $t_7 = 3.53$, $p < 0.01$, Table 2). In addition, the tutor song type that was learned the most (by seven out of nine subjects) was the only song type that all four tutors had in common.

Cohort Influence on Repertoire Development

We found clear evidence of cohorts influencing each other's repertoire development. For six subjects, at least one song type matched a cohort's song type better than any of the tutors' song types. In one case, a subject (RI) learned a song that a cohort (BY) had invented. We also found that subjects within groups learned many of the same songs. We examined the subjects' 39 tutor-matching songs (using the strict criterion for sharing); in 20 cases three subjects within the same group learned the same song, in 13 cases two subjects within the same group learned the same song, and in only six cases did just one subject within a group learn a particular tutor song. In other words, if one subject learned a tutor song it was likely that one or two other cohorts learned that same song as well. Furthermore, this result was not due to subjects independently picking the same tutor songs (e.g., subjects might pick the same tutor song because they perceived it as more potent). Rather, there was little concordance between the two groups: within the Rotated group, five of six tutor songs (83%) were learned by two or more subjects, within the Stationary group, seven of 12 songs (58%) were learned by two or more subjects, but only five of 13 tutor songs (38%) were copied by one or more subjects in both groups. The results were nearly identical using the loose criterion for sharing. In 20 cases three subjects in a group learned the same song, in 15 cases two subjects in a group learned the same song, and in only four cases did just one subject in a group learn a tutor song. Five of six tutor songs (83%) were learned by two or more subjects in the Rotated group, eight of 11 tutor songs (73%) were learned by two or more subjects in the Stationary group, and only five of 13 tutor songs (38%) were learned by one or more subjects in both groups.

We therefore conducted a second analysis of the preference for learning shared songs, this time including the tutor-matching songs of cohorts. For this analysis we computed the expected percentage of sharing separately for each subject since the pool of 'neighbours' was slightly different for each subject (i.e., neighbours were the four tutors and three or four other cohorts) and then used a within-subject paired test. Using the strict criterion for sharing, subjects learned significantly more shared songs than expected (*X* difference ÒSE = 42.2 Ò7.0%, Paired *t* test: $t_7 = 6.46$, $p < 0.001$), and results were similar using the loose criterion (*X* difference ÒSE = 39.1 Ò4.3%, Paired *t* test: $t_7 = 9.80$, $p < 0.001$, Table 2).

DISCUSSION

Results from this experiment confirm and extend the findings of our field studies of song learning in song sparrows (Beecher et al 1994; Nordby et al. in press). First, young males in this study learned to sing good imitations of their tutors' songs. Collectively (and excluding IY), 71% of the subjects' song types matched a tutor (or cohort) song type (at least by half), and 55% were considered very good matches (90% or more of the elements matched). Second, subjects learned songs from multiple tutors. All subjects but IY learned songs from two, three or four tutors, and furthermore, they did so whether or not they had visual contact with their tutors after their natal summer. Third, subjects preferentially learned song types that were shared among their tutors. Fourth, subjects learned many of the same song types that their cohorts chose. Finally, the Stationary subjects learned more songs from the tutor they were adjacent to during fall, winter and spring. These last two results imply that social interactions after the sensitive period (months 2 and 3) can affect song development in this species. We will consider each of these findings in detail.

Preservation of Song Type

Subjects generally copied song types faithfully from their tutors, rather than recombining learned elements to form new songs, a finding that is consistent with our field results. We call this faithful copying 'preservation of song type' (Beecher 1996), as the song type is transmitted from one generation (tutors) to the next (tutees) in recognizable form. Although the degree of preservation of type found in this study is closer to the field results than it is to those of our earlier lab study (or of tape tutor studies, Marler & Peters 1987, 1988a) it still is less than we see in the field. For example, in our most complete field study (Nordby et al. in press), we found that 91% of learned songs could be traced to the song types of older tutors, as opposed to 71% in the present study.

Almost a third of the subjects' song types in this experiment were not considered tutor song matches. Most of these remaining song types were combinations of elements from different tutor song types, and only a few song types were completely invented. In most cases, the recombined or invented song type was not shared with other birds, but rather was unique to one subject. We know that young males are capable of precisely imitating tutor songs, so one possible explanation for creating new songs is that young males may be 'individualizing' their repertoires. It is extremely rare to find two song sparrows with identical repertoires in the field, and perhaps creating new songs is one way to facilitate individual recognition in this species.

There was also one subject in this experiment, IY, who did not learn any tutor song types. His repertoire was almost completely invented and several of the elements within his songs were, as far as we know, very atypical song sparrow elements. We could not find any obvious explanation for why this male had a song learning pattern that was so different from that of the other eight birds in this study.

Learning from Multiple Tutors

Subjects (except IY) copied songs from two to four adult tutors, which concurs with the findings from our field studies. The average number of tutors in this experiment was smaller than in our field studies (usually 3-5, Beecher et al 1994; Nordby et al. in press) but subjects in the present experiment had only four adult song models to chose from. Perhaps if we had presented them with several more tutors they would have learned songs from more birds than they did. It is perhaps not surprising that the Rotated subjects learned songs from multiple tutors since they had continued close social interactions with all four tutors throughout song development, but the Stationary subjects learned songs from multiple tutors as well. The fact that the Stationary subjects copied songs from tutors with whom they did not have any visual or close auditory contact after they were three months old suggests that learning from multiple tutors per se is a general goal of the song sparrow song learning strategy. We are aware of only one other species in which this question has been experimentally addressed: in zebra finches, *Taeniopygia guttata,* males learned from multiple tutors if exposed to them sequentially but not if exposed to them simultaneously (Clayton 1987; Slater et al. 1991).

Learning Preference for Shared Song Types and Cohort Influences

Whether we used the strict or the loose criterion for sharing, subjects had a clear preference for learning songs that were shared among their tutors. This finding is consistent with results from the Beecher et al. (1994) study which showed that song sparrows in the field learned more tutor-shared songs than tutor-unique songs. A new finding from the present experiment was that cohorts had pronounced effects on each other's repertoire development, and the preference for learning shared songs was even stronger when we included the songs of the other subjects within the group. We found that subjects tended to learn songs (tutor-shared or tutor-unique) that other young birds in their group had also chosen. In addition, six of the nine subjects had at least one song type that matched a cohort's song type better than any of the tutors' song types and one subject learned one song that another cohort had invented.

Developing a repertoire that is similar to those of cohorts is consistent with a song learning strategy designed to give the bird songs he shares with his neighbours in his first breeding season, for some of those neighbours can be other first-year birds. If song sparrows overproduce and 'shape' songs during their plastic song phase (not yet demonstrated) it is possible that cohorts could mutually influence each other, and in this experiment several birds did have at least one song that was more similar to another cohort's song than to any tutor's song. Overall, the Stationary subjects were influenced slightly more by cohorts than were the Rotated subjects. The fact that the Stationary subjects each heard the same three cohorts from the same location throughout Stage II may have facilitated interactions among these birds and may be one explanation for the larger cohort influence.

Interestingly, subjects were influenced by cohorts despite the fact that they had extremely limited visual contact with each other (birds within the same group had brief visual contact with each other when we moved groups into and out of isolation and when we gave them baths) yet were in close proximity and in continued visual contact with at least one tutor throughout the experiment. Subjects could hear each other only at a distance (similar to the relationship the Stationary subjects had with their three non-adjacent tutors) and yet they clearly attended to, and incorporated, the songs of these other young males when selecting songs for their final repertoire.

Several studies on other species have also shown that a young male's repertoire development can be influenced by birds within the same cohort. Most of these studies showed that young males who were raised in isolated groups (untutored) converged on one another and developed songs that were quite similar (e.g., Marler 1970; Byers & Kroodsma 1992; Slater et al. 1993; Chaiken et al. 1997). Studies using tape tutors have demonstrated that group-raised males developed some songs that were more similar to their group mates' songs than to the tutor songs (e.g., Kroodsma & Pickert 1984; Byers & Kroodsma 1992; Kroodsma et al. 1995). Only a few studies have shown that group-raised males who had been tutored by live adults converged on one another and developed similar songs (Kroodsma & Pickert 1984; Slater et al. 1993; Cunningham & Baker 1983). In addition, one field study by Payne & Payne (1993) showed that first-year male indigo bunting may sometimes learn songs from other first-year males at the start of the breeding season. In all the above studies, however, the young males had as much or more access (closer proximity and/or visual experience) to each other than they did to the adult tutors. The present experiment, to our knowledge, is the first demonstration that birds within a cohort influenced each other's repertoire development even though they had less exposure to one another than to adult tutors.

Learning Preference for Songs of Adjacent Tutor

All four of the Stationary subjects learned more songs from the tutor they were stationed next to during Stage II (when they were five to 12 months old) than they did from any other tutor. This result is similar to findings from our field studies in which we observed that a young male learns most of his songs from a particular tutor if, during the young male's first spring, that adult occupies an adjacent territory (Beecher et al. 1994 ; Nordby et al. in press). Several factors could have contributed to these results and there are many possible explanations for how this effect could have occurred. In the present study for example, Stationary subjects were in close proximity to the adjacent tutor, they saw only their adjacent tutor, and the amplitude of the adjacent tutor's songs was presumably greater than that of the other tutor's songs. Further studies would be necessary to determine the mechanism of this effect.

That young males in the present study learned more songs from the tutor they were stationed next to after they were five months old supports the late influence hypothesis that social interactions later in a young male's first year can affect song development. We also found evidence for the late influence hypothesis in the Nordby et al. (in press) field study: young males learned more songs from tutors who survived into the young male's first spring than from tutors who did not.

The effect of social influence during the later stages of song development has been reported in other songbird species as well. Nelson & Marler (1994) have shown that a white-crowned sparrow, *Zonotrichia leucophrys*, is more likely to retain a particular song he sings in his plastic song phase if he hears playback of that song during that rehearsal phase. Although that experiment provides only indirect evidence of late social influence (since tape tutors were used), studies of white-crowned sparrows by DeWolfe et al. (1989) and Baptista & Morton (1988) showed that males in the field do retain the song that best matches their neighbours in their first breeding season. A similar result was found by Nelson (1992) in field sparrows, *Spizella pusilla*. Some males returned from their first migration singing two or more song types, but retained the one song that most closely resembled the song of their near neighbours.

Other studies of the social influence on song learning have postulated that, under the right circumstances, birds may be able to actually learn new songs during the later phase of song development. In a laboratory study of marsh wrens, *Cistothorus palustris*, Kroodsma & Pickert (1984) demonstrated that males who were exposed to tape tutors during their early sensitive period were able to learn new songs from live tutors presented later in their first year. Payne & Payne (1997) made a strong case for late, de novo learning in indigo buntings, *Passerina cyanea*, and showed that males in the field may be acquiring the songs of their neighbours after they return from migration. O'Loghlen & Rothstein (1993) have documented that male brown-headed cowbirds, *Molothrus ater*, can alter their song between their first and second breeding season to match the local dialect, and suggest that these young males may first learn the local dialect during their first breeding season.

Timing of Song Learning

Although we were not testing the timing of song learning in this experiment, or our previous field studies, results for the most part are consistent with the 'action-based' model of song learning developed by Marler and Nelson (Marler 1990; Nelson & Marler 1994). In their theory, Marler and Nelson propose that song learning occurs in two stages. The first stage is a sensitive period which occurs when birds are roughly one to three months old. According to the model, birds memorize, or acquire, all their song material during this period. The second stage occurs later in the birds' first year when song is recognizable yet still plastic. At this time, Marler and Nelson propose that the birds select, from their earlier-memorized songs, the song or songs that best match the songs of their close neighbours. Social interactions with neighbouring birds during this stage are postulated to reinforce the selection of matching songs.

Evidence from the Nordby et al. (in press) field study is consistent with this hypothesis that the young birds memorize all their songs in their natal summer and 'select' among them in the fall or following spring as a result of social interactions with older birds. The young males in that study learned more songs from adults who were present throughout the young birds' first year than from those who did not survive the winter. However, we could not rule out two alternatives to the Marler-Nelson hypothesis for reasons which relate to the sedentary nature of our study population. Turnover in this population occurs only through the death of adults and the recruitment of first-year birds, hence any adult male who was present in a young male's first spring was also present during the young male's natal summer the previous year. The first alternative to the Marler-Nelson hypothesis, then, is that song learning and song selection are completed entirely within the hatch year. In this case, the young male learns more from adults who survive the winter because those males are on average more vigorous in the young male's natal summer than are those who do not survive the winter. The second alternative hypothesis is that additional learning (song memorization) takes place after the early sensitive period. That is, the young male learns more from adults who survive into his first spring because he learns the songs of these neighbouring males after settling next to them in the fall or following spring.

In the present experiment we were able to test the first alternative hypothesis by randomly placing the subjects next to a particular tutor during the later stage of song development. The results showed that close proximity to a tutor after the natal year led to a preponderance of that tutor's songs in the repertoire of the young male. In addition, several subjects had at least one song type that matched a cohort song type better than any of the tutors' song types. Subjects were unable to hear each other sing until the fall, so any influence that cohorts had on each other must have occurred during the later period. Thus the present experiment provides clear evidence against the first alternative hypothesis: learning of some form (whether selection or de novo memorization) takes place after the natal summer. The experiment does not, however, rule out the second alternative hypothesis that at least some songs may be learned de novo after the natal summer. In fact, it provides some evidence in favor of this hypothesis since one young bird learned a song invented by a cohort, who did not sing at all in the natal summer. Further experiments will be required to rigorously test the timing of song learning in song sparrows. The best way to determine whether they are capable of de novo song learning after their presumed sensitive period would be to conduct an experiment in which young males are exposed to a new set of tutors during the later stage of song development.

Figure 2.1

Schematic diagram of spatial arrangement of tutor aviaries (T 1-4) and subject cages (S). Subjects had visual contact only with the adjacent tutor and all birds were in auditory contact.

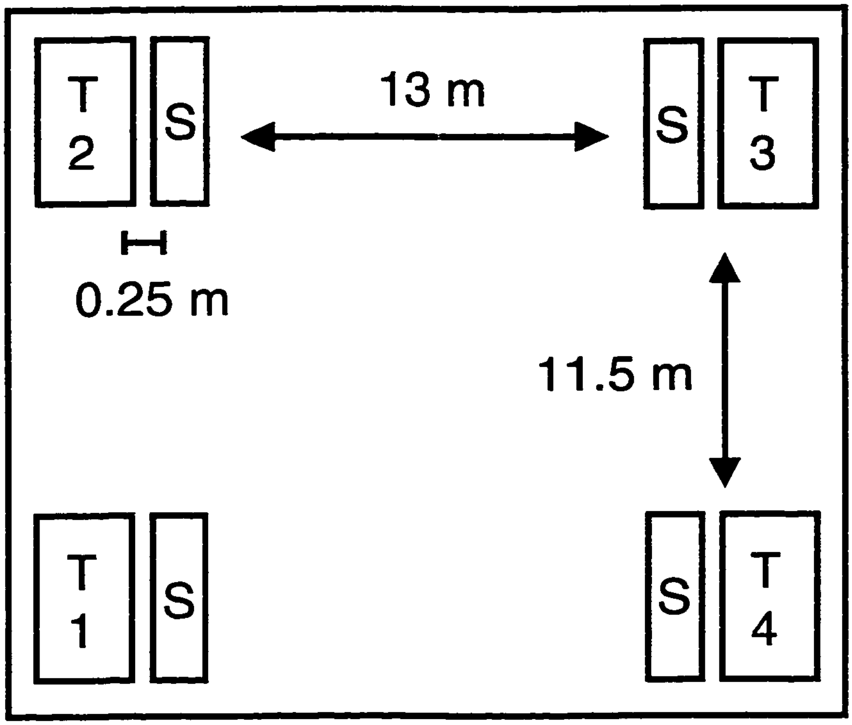
T 2
S
13 m
S
T 3
0.25 m
11.5 m
T 1
S
S
T 4

Figure 2.2

Experimental design. During Stage I, all subjects were rotated equally among all tutors. During Stage II, subjects were either rotated equally among all tutors or stationed next to one particular tutor. Black bars represent the three periods when subjects were exposed to the tutors. White bars represent the two periods when subjects were in acoustic isolation and correspond to times of very low song rates in wild song sparrows.

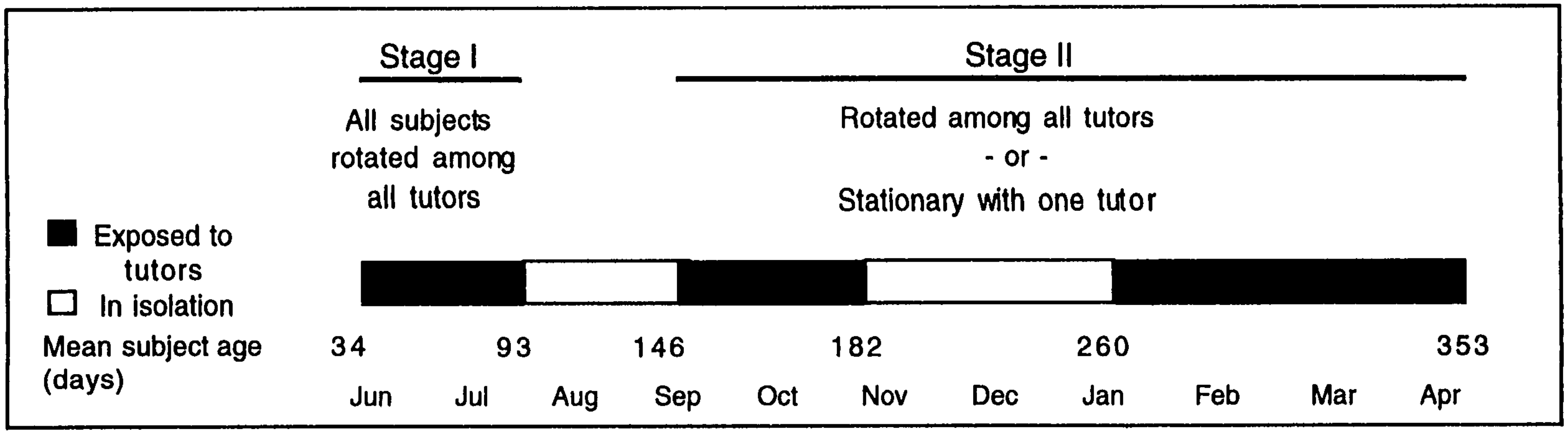
Stage I
All subjects rotated among all tutors
Stage II
Rotated among all tutors
- or -
Stationary with one tutor
■ Exposed to tutors
☐ In isolation
Mean subject age (days)
34
93
146
182
260
353
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr

Figure 2.3

Examples of matching subject and tutor song types. Each row represents a different subject and tutor. We ranked songs (a) and (b) as 1's ($\geq$ 90% of the elements within the subject's song matched those in the tutor's song) and song (c) as a 2 (70-89% of the elements matched those in the tutor's song).

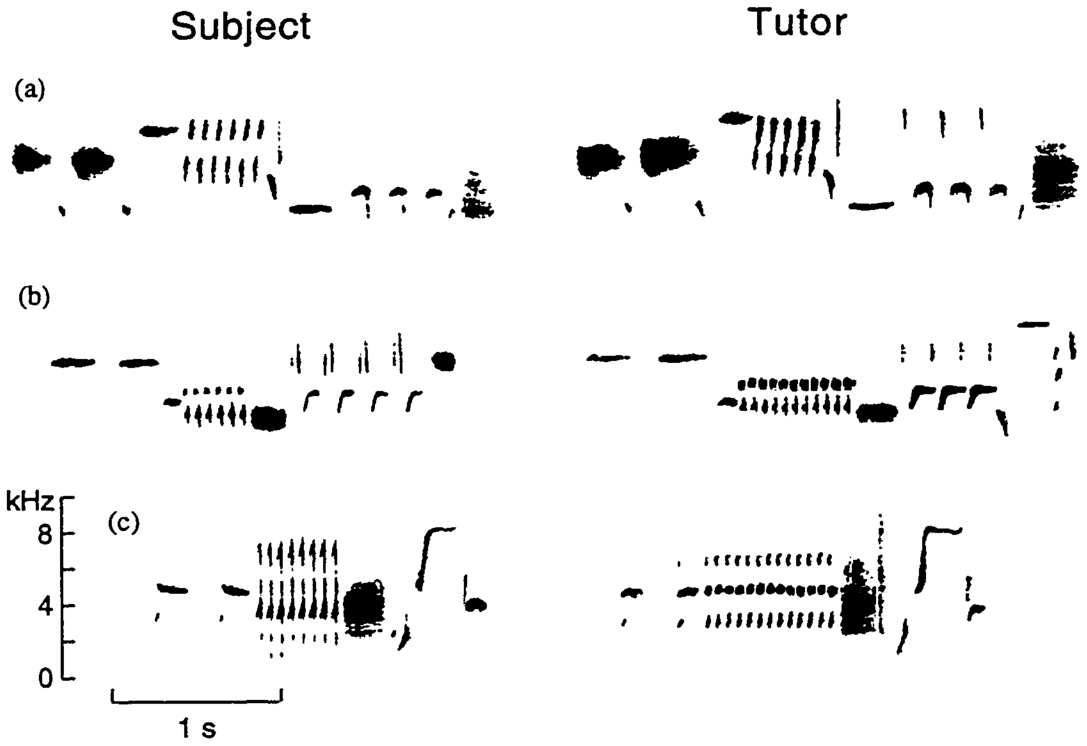
Subject
Tutor
(a)
(b)
(c)
kHz
8
4
0
1 s

Table 2.1. Tutor scores, number of song types in subjects' repertoires, and number of song types in each matching category.

Subject	Tutor 1	Tutor 2	Tutor Scores[a] Tutor 3	Tutor 4	Cohort	Song types in repertoire	Tutor or cohort match	Element match[b]	Invention[c]
Stationary									
AY	2.50*	1.75	-	1.25	0.50	9	6	2	1
RP	1.00	5.25*	-	0.25	0.50	9	7	2	0
RI	-	-	1.50*	1.00	1.50	5	4	1	0
BY	0.33	1.33	1.50	2.33*	0.50	9	6	2	1
Rotated									
BP	2.50	0.50	1.00	-	-	6	4	2	0
BR#	1.50	-	1.00	-	0.50	5	3	1	1
RG	1.50	0.50	1.00	-	-	5	3	2	0
RY	4.50	-	0.50	-	1.00	7	6	1	0
IY	-	-	-	-	-	8	0	3	5

a Tutor scores are the number of song types a tutor, or cohort, matches with a subject, devalued by the number of other tutors identified for those song types.

b These song types did not match any one tutor song type, but $\geq$ 50% of the elements were identified as tutor song elements.

c < 50% of the elements in these song types were identified as tutor song elements.

* Indicates which tutor that subject was stationed next to during Stage II.

_ Indicates highest tutor score for that subject.

Subject BR did not receive the fall bout of tutor exposure during Stage II.

Table 2.2. Proportion of subjects' song types that matched tutor-shared songs

Subject	Repertoire size	Tutor matches[a]	Tutor-shared[b]	Tutor-uniques[c]	Proportion tutor-shared	Proportion shared[d]
Stationary						
AY	9	6	6	0	1.00	1.00
RP	9	7	6	1	0.86	1.00
RI	5	3	2	1	0.67	1.00
BY	9	6	2	4	0.33	0.67
Rotated						
BP	6	4	2	2	0.50	1.00
BR*	5	3	2	1	0.67	1.00
RG	5	3	2	1	0.67	1.00
RY	7	6	4	2	0.67	1.00

a Indicates the number of each subject's songs in which ≥50% of the elements matched those within a tutor song.

b Indicates the number of tutor-matching songs that were shared by two or more tutors (using the loose criterion for sharing).

c Indicates the number of tutor-matching songs that were unique to a single tutor.

d Indicates the proportion of tutor-matching songs that were shared by two or more other birds (tutors and/or cohorts).

* Subject BR did not receive the fall bout of tutor exposure during Stage II.

Chapter 3

LATE SONG LEARNING IN SONG SPARROWS

INTRODUCTION

Many songbirds complete song development within their first year (Kroodsma 1996). In order to understand how young birds select the song(s) they will sing as adults it is important to know when, during this first year, they are capable of acquiring (or memorizing) songs. The predominant model of song learning in age-limited songbirds (i.e., those species who do not change their song repertoire after their first year) was developed by Marler and Nelson (Marler 1990; Nelson & Marler 1994). In their 'action-based' model, Marler and Nelson propose that all song memorization takes place during an early sensitive period that occurs entirely during a bird's natal summer, usually between one and three months of age. According to this model, later in the bird's first year, when song is recognizable yet still plastic, the bird progresses through a period of 'selective attrition'. During this time, a bird produces more song material than he has in his final repertoire and the action-based theory suggests that he will selectively retain the song that matches those of his first-breeding season neighbours. This attrition period is generally thought to occur between 6 and 11 months of age, and Marler and Nelson posit that birds do not acquire (memorize) any new songs during this time, but only utilize the earlier-memorized song material. This model is primarily based on, and is supported by, results from song learning experiments and field studies on white-crowned sparrows (*Zonotrichia leucophrys*), swamp sparrows (*Melospiza georgiana*), song sparrows (*Melospiza melodia*), and field sparrows (*Spizella pusilla*) (Marler & Peters 1981, 1982, 1987, 1988; Nelson 1992). However, a young male may not always settle in the same area where he learned his songs, particularly if he is from a migratory population, and therefore may not have memorized songs that match those of his territorial neighbours. In such cases, Marler and Nelson's theory could be extended to suggest that the young male would adjust or 'shape' his songs by combining elements from his plastic repertoire to form songs that match the songs of his present neighbours as best he could (Marler & Peters 1982; Nelson et al. 1996).

A competing model of song acquisition in age-limited song learning species suggests that birds can in fact memorize new songs after their natal summer (Payne & Payne 1997). Evidence for such 'late acquisition' of song, even as late as the bird's first spring, has been found in several songbird species including chaffinches (*Fringilla coelebs*), marsh wrens (*Cistothorus palustris*), and indigo buntings (*Passerina cyanea*) (Slater & Ince 1982; Kroodsma & Pickert 1984; Payne & Payne 1997). If having songs that are shared with neighbouring birds is a major goal of song learning, as Nelson & Marler (1994) suggest, then it would be adaptive for males to acquire songs as late as possible in their first year. Being able to learn new songs after their natal summer would increase their chances of sharing songs with those birds who will be their neighbours the following spring.

Our investigations of song development in a wild population of song sparrows support the idea that a young male's song learning strategy maximizes the number of songs he shares with his first-breeding season neighbours (Beecher et al. 1994; Nordby et al. 1999, in press).Through a combination of field and laboratory studies we have found that a young male song sparrow 1) learns whole song types, 2) learns songs from several adult males who are neighbours in the young bird's natal summer, 3) establishes his territory among or near his song tutors, 4) preferentially learns songs that are shared among his tutors, 5) preferentially learns songs of tutors who survive into the young male's first spring, 6) preferentially learns songs of a tutor to whom he has been adjacent throughout his first year, and 7) is influenced by which songs other young males in his age cohort learn to sing.

In all our studies, however, we were unable to determine when songs were first memorized because subjects were not exposed to any new tutors after their natal summer. In our field population, the birds are resident year round and rarely do new birds enter the population as adults (Beecher 1996). Thus, any adult male who is present in a young male's first spring was invariably also present during that male's natal summer. In a previous experiment (Nordby et al. in press) we found strong evidence of song tutors influencing song development after the young males' natal summer, but because the same four tutors were present throughout the experiment (from the subjects' natal summer through the next spring), we do not know when song memorization first occurred.

In an experiment using tape tutors, Marler & Peters (1987) examined the timing of song acquisition in song sparrows and found that 90% of song acquisition occurred before 90 days of age. There was some de novo song learning later, between 90 and 200 days of age. In most of these cases of late learning, however, the bird learned only a single syllable; in no case was a whole song learned after 90 days of age. While this study demonstrated that song sparrows may prefer to learn song material that they hear early in life, it does not demonstrate that males are incapable of learning songs they hear later in life. The subjects in that study were, by design, exposed to new songs (i.e., new 'tutors') every 1 to 6 weeks. Therefore, subjects in that experiment did not receive any reinforcement of songs during the later selective attrition phase.

In the present experiment, we tested whether song sparrows were capable of learning songs de novo after their natal summer by using live adult males as tutors. We exposed 12 hand-raised male song sparrows to one set of four tutors during the subjects' natal summer, then replaced two of the original tutors with two new tutors in the fall, and assessed whether subjects learned songs from the new tutors. According to Nelson & Marler's (1994) selective attrition hypothesis, subjects should not be able to acquire new songs after their natal summer but should, instead, use the song material they memorized earlier to improvise songs that resemble the songs of the new tutors. On the other hand, if males are capable of acquiring new songs later (the late acquisition hypothesis), then they should produce very good imitations of the new tutors' songs. In either case, the two tutors who were present throughout the experiment should have the most influence overall because they would be present during the presumed sensitive period as well as during the selective attrition phase.

A secondary goal of this experiment was to replicate some of our previous findings regarding how social influences affect song development (Beecher et al. 1994; Nordby et al. 1999, in press). Specifically we examined whether males 1) learned whole tutor songs, 2) learned songs from multiple tutors, 3) preferentially learned songs that were shared among their tutors, 4) preferentially learned songs of the tutor they were adjacent to after their natal summer, and 5) were influenced by other subjects in their age cohort.

METHODS

Subjects and Tutors

Subjects were 12 male song sparrows from seven different broods. We collected all subjects from nests in our study population (Discovery Park, Seattle, WA) between 10 – 25 May 1997 when they were five to seven days old. Subjects were hand-raised as a group until they were 26 – 30 days old and then placed into individual wire-mesh cages (45cm x 28cm x 18cm) equipped with wooden perches. Subjects were maintained on ad lib water and food (Mazuri small bird maintenance diet, mixed seed, fresh greens, and egg/vitamin supplement) throughout the experiment.

We used six adult male song sparrows as tutors. Four tutors had occupied adjacent territories in the field and shared several songs with one another (we refer to them as Tutors 1, 2, 3, and 4). We collected these four males from our study population in Seattle, WA on 08 November 1996. The two remaining tutors (Tutors 5 and 6) were hand-raised in 1994 as part of a previous song learning experiment (Nordby et al. 1999). In that experiment, these two birds learned their songs from four other wild-caught adult males. Tutors 5 and 6 shared one song with each other, but did not share any songs with Tutors 1 – 4. Each tutor was housed in an individual flight cage (1.47m x 0.71m x 1.83m, containing a 1.0m potted shrub and several wooden perches) and maintained on ad lib water and food.

Experimental Design and Procedure

We conducted the experiment outside on the roof of a building at the University of Washington in Seattle, WA. We had four tutors out on the roof at a time and simulated field conditions by placing the tutors in aviaries in four corners of an area of the roof and by having the subjects visit the tutors on these pseudo-territories. Tutor aviaries were 11.5 – 13.0m apart and when a subject was being exposed to a tutor, he was placed in a cubicle that was 0.25m away from the tutor's aviary and that was open only on the side facing the tutor (Figure 3.1). All birds on the roof (tutors and subjects) were in auditory contact , so even though subjects could see only one tutor at a time they could hear the other three as well.

The experiment was conducted in two stages (Figure 3.2). Stage I occurred between 07 June - 18 August 1997 when subjects were approximately 30 – 90 days old and corresponded to the presumed sensitive period for song memorization (Marler & Peters 1987). During this stage, subjects were exposed only to Tutors 1, 2, 3, and 4 (the four tutors who had been neighbours in the field) and each subject was exposed to the tutors for 61 days. Since the subjects' hatch dates were spread across 15 days, we staggered the start of the experiment so that each subject began this stage when they were 29 – 31 days old and finished when they were 89 – 91 days old. Thus there were 3 – 12 subjects on the roof at any one time, and 0 – 3 subjects with a particular tutor at any one time. All subjects were rotated among all four tutors and remained on the roof with the tutors the entire time. We randomly rotated the subjects every three days and each subject visited each tutor equally. At the end of Stage I we brought all subjects indoors. When the subjects were approximately 115 days old they began to sing subsong and from that time on, when they were not being exposed to the tutors, they were housed in individual acoustic isolation chambers.

Stage II occurred between 29 September – 18 April 1998 and corresponded to the later selective attrition stage of Nelson & Marler's (1994) song development model. We did not stagger the start date so subjects began this stage when they were 132 – 147 days old and finished when they were 333 – 348 days old. In late August (when all subjects were in isolation) we removed Tutors 3 and 4 and replaced them with Tutors 5 and 6 (the two hand-raised tutors who did not share any songs with Tutors 1 - 4). Thus, during Stage II, subjects were exposed to Tutors 1, 2, 5, and 6. There were two bouts of tutor exposure during this stage; the first bout occurred between 29 September and 13 November 1997 and the second bout occurred between 01 January – 18 April 1998. Song sparrows produce little song in mid-winter and these two bouts corresponded to the peak periods in adult song production that we observe in the field. Tutors 1 and 2 had song rates much lower than Tutors 5 and 6 at the beginning of the second bout of tutor exposure during Stage II. To encourage vocal output, we gave Tutors 1 and 2 subcutaneous, 18mm silastic tube implants of testosterone on 19 January 1998; both tutors' song rates increased by 28 January 1998.

In contrast to Stage I, during Stage II each subject was randomly assigned one particular tutor and only visited that tutor. During Stage II, then, subjects had visual and close auditory contact with only one tutor, but they could hear the other birds at a short distance. In addition, we wanted to limit possible within-cohort influence by having only one subject with each tutor at a time so we divided the subjects into three groups of four (groups A, B, and C) and only one group was exposed to the tutors at a time. Dividing the subjects into three groups also allowed us to have three independent 'replications' of the second stage of the experiment. During this stage, subjects were with the tutors a third of the time and when they were not being exposed to the tutors they were housed in isolation chambers.

With this experimental design we had three classes of tutors; Tutors 1 and 2 were present throughout the entire experiment and we refer to them as the 'permanent' tutors, Tutors 3 and 4 were present only during Stage I and we refer to them as the 'early-only' tutors, and Tutors 5 and 6 were present only during Stage II and we refer to them as the 'late-only' tutors.

Song Analysis and Tutor Identification

We recorded each subjects' crystallized song repertoire after 29 April 1998 when they were more than 344 days old. All songs were recorded using a Realistic 33-1056A omni-directional, condenser microphone and a Marantz PMD221 stereo cassette recorder, and analyzed on a Kay DSP-5500 Sonagraph. Sonagrams of each subjects' song types (including distinct variations) were then visually matched by three judges to those of all six tutors and the subjects' respective groupmates. We wanted to identify the bird who had the most influence on repertoire development and so looked for the tutor or groupmate who had the best matching song type to each of a subject's song types. Song types were considered 'matches' only if at least half of the elements were shared between the two songs and the elements occurred in the same order. If two or more adult tutors had song types that matched a subject's song type equally well, or if a subject sang both tutors' versions of a song type, then credit was split between all birds in the tie. In cases where a tutor and a groupmate had equally similar versions of a song type we gave sole credit to the adult tutor. In cases where a groupmate had a better matching song type than any tutor, we gave half credit to the groupmate and half credit to the tutor with the best match to reflect the source of the song. In a few cases a groupmate had the best matching song type but there was not a tutor song type that also matched. Most of the elements in these songs were identified as tutor song elements but they came from several different tutor songs. In these cases we gave sole tutor credit to the groupmate but recognized that these songs were not completely invented by the subjects but rather represented a rearrangement of various tutor song elements. We also found some cases where a subject's song type did not match any other bird's song type. In every case we could trace at least half of the elements within the song to various tutor songs. We classified these song types as 'element' matches.

After we classified all the song types, we conducted a second analysis on the tutor- and groupmate-matching song types to determine how well those songs matched. We rated each subject's song types on a three point scale: 1 = $\geq$ 90% of the elements in the song matched those in a tutor or groupmate song, 2 = 70 – 89% of the elements matched, and 3 = 50 – 69% of the elements matched.

In order to quantify the amount of influence each tutor had on each subject's repertoire development we assigned each tutor a score. For every subject, each tutor's score was based on the number of song types he matched to the subject, devalued by the number of other birds identified for those same types. For example, if a tutor had the best matching song type for two songs (2.0 credits) and shared credit with one other tutor for a for a third type (0.5 credits) his score would be 2.50 for that subject. We identified the tutor with the highest tutor score for each subject as that subject's 'primary' tutor, the tutor with the second highest score as that subject's 'secondary' tutor, and so on. We used the same scoring method for groupmate- and element-matching songs, but in these categories we added the scores together for one overall category score (i.e., the groupmate category score could represent the combined scores of two or more groupmates).

The above analyses, besides testing for late learning, also tested for learning whole songs (i.e., did subjects imitate tutor songs in their entirety?), learning from multiple tutors (i.e., did subjects learn songs from more than one tutor?), preferential learning from adjacent tutors (i.e., did subjects learn the most songs from the tutor they were stationed next to during Stage II), and cohort influences (i.e., did subjects have any songs that matched groupmate songs better than tutor songs?). In addition, we examined two other variables that we hypothesized might influence song repertoire development. The first variable was whether song types were shared among the tutors. Previous studies (Beecher et al. 1994; Nordby et al. in press) showed that males are more likely to learn songs if they are shared among their tutors. To examine the effect of song sharing we *a priori* determined which tutor songs we considered shared via consensus of three judges. Songs were considered shared if at least half of the elements in the songs matched. We then determined how many of the subjects' tutor-matching songs were among those we classified as shared and how many were not. Because we did not want our results to depend on the particulars of our sharing criterion, we conducted the same analysis using a looser sharing criterion (i.e., the songs had at least two elements in common). The results were the same using the looser criterion for sharing, so here we present just the results using our more strict criterion. The second variable we examined was tutor song rate. Results from our previous song learning experiment (Nordby et al. in press) suggested that tutor song rate may play a role in song selection and that, all else being equal, subjects learn more songs from the tutor who sang the most. To sample tutor song rate we simultaneously recorded all four tutors who were present during each bout of tutor exposure at a random time every other morning for 45 minutes and counted how many songs they sang during each session.

RESULTS

Subject Repertoires

The size of subject repertoires ranged from 5 – 8 song types which is within the normal range for *M. melodia*. Using our matching criterion (≥ 50% of the elements within the songs matched), we found that 69 of the 75 subject song types (92%) matched a tutor or groupmate song type (Table 1). Figure 3.3 shows examples of matching subject and tutor song types. Seven subjects had repertoires in which all song types matched a tutor or groupmate song type. Ten of the twelve subjects learned songs from more than one tutor, and while the remaining two subjects only learned songs from one tutor, they also had songs that matched the songs of their groupmates as well.

Overall, subjects tended to sing accurate imitations of tutor songs: we rated 38% of the 58 tutor-matching songs as 1's (≥ 90% of the elements in the song matched those in a tutor's song), 40% as 2's (70 – 89% of the elements matched), and 22% as 3's (50 – 69% of the elements matched). If we include the 11 groupmate-matching song types, then 32% of the subjects' song types were rated as 1's, 36% were rated as 2's, and 32% were rated as 3's.

Late De Novo Song Learning and Tutor Influence

Surprisingly, Tutor 6 (a late-only tutor) was by far the most influential tutor overall; 6 of the 12 subjects had Tutor 6 as their primary tutor, and 36% of the 75 subject song types matched songs in his repertoire (Table 1, Fig. 3.3). In contrast, the other late-only tutor, Tutor 5, had little influence on the subjects; three subjects learned one song each from him. In one of these three cases Tutor 6 had a song that matched the subject's song equally as well as Tutor 5's and they shared tutor credit, but, in the other two cases Tutor 5 was unambiguously identified as the tutor. The songs that the subjects learned from Tutors 5 and 6 were not created by rearranging elements they had heard earlier during Stage I because Tutors 5 and 6 had only a few elements in common with Tutors 1 - 4. Therefore, the subjects must have first learned (memorized) these songs during Stage II after they were 132-147 days old. Interestingly, because subjects did not rotate among the tutors during Stage II, four of the subjects who learned songs from Tutor 6 (including three who had him as their primary tutor) never had visual contact with Tutor 6 and heard him only from a distance of 11.5 – 17.4 meters.

The two permanent tutors (Tutors 1 and 2), whom we predicted would be the most influential tutors, did have the second and third highest total tutor scores overall (Table 1). Tutor 1 was the primary tutor for three subjects and eight subjects showed some influence from him, while Tutor 4 was the primary tutor for one subject and four subjects were influenced by him. Only one of the four subjects who had Tutor 1 or 2 as their primary tutor was stationed next to his primary tutor during Stage II -- although all subjects had close auditory and visual contact with these two tutors during Stage I. The two early-only tutors (Tutors 3 and 4) had relatively little influence on repertoire development. Six subjects showed only minor influence from Tutor 3 and no subject had any song type that best matched a Tutor 4 song type. Only three songs unambiguously identified Tutor 3 as a tutor, and in the other three cases Tutor 1 or 2 had a song type that matched the subject's song type equally well and so tutors shared credit for that song. Looking at all subject song types together, 38% of the 75 subjects' songs were learned from the late-only tutors, 34% were learned from the permanent tutors, and only 5% were learned from the early-only tutors. Looking just at the tutor-matching song types; 49% were learned from the late-only tutors, 45% were learned from the permanent tutors, and 6% were learned from the early-only tutors.

Learning of Tutor-shared Songs

Using our criterion for sharing ($\geq$ 50% of the elements in the songs match), we classified the 53 tutor songs into 12 shared song types (i.e., songs were shared by two or more tutors) and 26 unique song types (i.e., only one tutor sang that song type) for a total of 38 different tutor song types. Eleven of the shared song types were found among Tutors 1 – 4 (the four tutors who had been neighbors in the field). Tutors 5 and 6 shared only one song type that met our sharing criterion. We found no songs that were shared between the late-only tutors (Tutors 5 and 6) and the other four tutors (Tutors 1 – 4). If subjects learned song types randomly and without regard to sharing, then we would expect that, on average, 32% of the songs they learned from the tutors would be tutor-shared songs. We found that, on average, 51% of the subjects' tutor-matching songs were shared among tutors which is significantly greater than expected (Single sample 1-tailed *t* test: $t_{11} = 2.12$, $p < 0.05$, Table 2).

Adjacent Tutor Influence

In our previous experiment (Nordby et al. in press), we found that subjects learned the most songs from the tutor they were stationed next to during the later stages of song development (the period equivalent to Stage II in the present experiment). We did not find the same result in the present experiment; only four of the twelve subjects were influenced most by the tutor they were stationed next to during Stage II. However, if we examine the data from the tutors' perspective, we find that tutors tended to have greater influence on subjects who were next to them than on subjects who were not. For all four tutors present during Stage II, the mean tutor score was greater for adjacent subjects than for non-adjacent subjects (Figure 3.4). In addition, subjects tended to sing more faithful copies of tutor songs if they learned them from their adjacent tutor. Figure 3.5 shows the percentage of subject song types that we rated as number 1s ($\geq 90\%$ of the elements within the songs matched) for adjacent versus non-adjacent subjects; for Tutors 1, 2, and 6, the adjacent subjects tended to have a higher percentage of number 1 rated song matches.

Groupmate Influence

We found strong evidence of groupmates influencing repertoire development. Six subjects showed some unambiguous influence from groupmates as evidenced by having song types that matched a groupmate song type better than any tutor songtype. In fact, all but one of the 12 groupmate-matching songs were songs for which there was no matching tutor song (i.e., the subjects improvised the song by recombining elements from different tutor songs). Group B had the most groupmate influence; two subjects (OB and PB) developed repertoires that primarily matched groupmate song types and contained only one tutor-matching song type, as well as one or two element matches. A third subject in that group also had two groupmate-matching song types (Table 1). Group C had a moderate amount of groupmate influence, and there was no unambiguous groupmate influence in Group A. Note that groupmate scores reflect only those songs for which a groupmate had the best matching song type. In each group there were additional song types that we considered groupmate matches, but there were tutor song types that matched equally well, or better, and so the tutor was given sole credit.

Tutor Song Rate

During Stage I, Tutors 1 – 4 had similar song rates which were highest in June, declined through July, and finally dropped to little or no song produced during August (Figure 3.6). This pattern of song production is consistent with our observations of song output in the field. Tutor 3, an early-only tutor, had the highest song rate for most of Stage I and unlike the other three tutors, increased his song output during July and continued to sing during all of the sampling periods in August. Tutor 1, a permanent tutor, consistently had the lowest song rate throughout Stage I.

During the fall bout of tutor exposure in Stage II, the four tutors (Tutors 1, 2, 5, and 6) produced relatively little song but the range in song output was quite large. Tutor 6, a late-only tutor, had the highest song rate and produced almost nine times the amount of song during October as any other tutor. Tutor 1, a permanent tutor, also sang during the fall but we only recorded him singing during early October. Neither Tutor 6 or Tutor 1 sang during our sampling periods in early November. The two other tutors, Tutors

2 and 5, did not produce any song during our sampling periods throughout October and November. (Note: we missed approximately 33% of the samples for Tutor 2 due to technical problems.)

During the second bout of tutor exposure in Stage II, Tutor 6, again, had the highest song rate of all four tutors. He produced two to three times as much song during January and February as any other tutor, then continued to increase his song output during March and April while the other tutors mainly decreased song production. Tutor 5, the other late-only tutor, had the second highest song rate during January, February and March, but had the lowest song rate in April. Tutors 1 and 2 had very similar song rates, with Tutor 1 producing slightly more song overall than Tutor 2.

DISCUSSION

Results from this experiment demonstrate that song sparrows are capable of acquiring new songs after their natal summer. Eight of the 12 subjects in this experiment learned songs from a late-only tutor whom they did not hear sing until they were 132 – 147 days old. Not only were subjects capable of learning songs after their natal summer, they were capable of learning a lot of song late. Overall, 38% of the subjects' songs were learned from the late-only tutors (49% if we consider just the tutor-matching songs) and half of the subjects learned most of their songs from a late-only tutor. Furthermore, subjects were capable of producing very good copies of songs they learned late; 73% of songs learned were rated as matching a tutor song by 70% or more, and 27% were rated as matching by 90% or more.

These results support the 'late-acquisition' hypothesis that young males can learn new songs after their natal summer. This experiment shows that song sparrows can acquire several new songs as late as five months of age. They may be capable of learning new songs even later, which could be tested by exposing young males to new tutors in mid-winter or early spring. Petrinovich and Baptista (1987) tested the timing of song acquisition in young white-crowned sparrows and found that subjects were able to acquire songs from live adults they were exposed to after their presumed sensitive period had ended (at 50 days of age), but not from adults they were exposed to after 100 days of age. Kroodsma and Pickert (1984) demonstrated that marsh wrens who were exposed to new live tutors in their first spring were capable of learning songs then, and that at least one male learned half of his songs from the spring tutor. Chipping sparrows (*Spizella passerina*) and field sparrows are also capable of learning songs from live tutors in the spring, although only one or two individuals from each species did so in an experiment by Liu & Kroodsma (Liu & Kroodsma in press). Slater & Ince (1982), using tape tutors, demonstrated that chaffinches could also acquire songs in their first spring. Finally, in a field study, Payne & Payne (1997) argued that young male indigo buntings learned songs after they return from migration; however, it was not known precisely what songs these males had heard early in life.

Results from the present experiment do not support Nelson & Marler's (1994) 'selective attrition' hypothesis that males can only improvise songs from material they learned during a sensitive period early in life. The songs the subjects learned from the late-only tutors were comprised of elements that were not shared with any of the tutors present during the birds' natal summer. These new songs, and the elements within them, must have been first memorized during the fall or later. Furthermore, the two tutors who were present only during the subjects' presumed sensitive period had little or no influence overall, indicating that, given the right circumstances, primacy (a tutor being present early) is outweighed by recency (a tutor being present later). The two permanent tutors, as we predicted, had a great deal of influence on the subjects. Thirty-four percent of the subjects' songs were learned from the permanent tutors, and three subjects had one of the permanent tutors as their primary tutor. The permanent tutors were present during the entire song learning process and so had the advantage of being present both early and late. It is even more remarkable then, that subjects learned songs from the late-only tutors despite the fact that there were two other tutors who had been present throughout the experiment. Moreover, two subjects learned more songs from a late-only tutor whom they could not see, even though they were in closer proximity to, and could see a permanent tutor.

Factors Contributing to Late Learning

Several factors may have contributed to the result that song sparrows in this experiment learned songs de novo after their natal summer. We will focus on three of these; 1) subjects had prolonged and continued exposure to the late-only tutors' songs, 2) subjects heard more songs from the late-only tutors, and 3) subjects had live interactions with the late-only tutors.

Although subjects in this experiment did not hear any of the late-only tutor songs until they were four and a half to five months old, they continued to hear them throughout the rest of their song development. Prolonged exposure to new songs, as opposed to switching the song models at least every six weeks, as was done in previous experiments on song sparrows and white-crowned sparrows (Marler & Peters 1987; Nelson et al. 1996), could have facilitated acquisition of the new songs. This would make sense particularly if, as Nelson and Marler's (1994) model suggests, the goal of song learning is to develop a repertoire that matches first-breeding season neighbours. In our study population, and in another sedentary population on Mandarte Island in British Columbia, male song sparrows generally do not establish territories until the fall or later and then maintain most of the same neighbors through their first spring (Arcese 1987,1989; Nordby et al. 1999). Territorial behavior and countersinging with neighbours by juvenile males in the fall has been reported in other species as well (Kroodsma 1974; DeWolfe et al. 1989). In non-migratory populations, it may be that exposure to neighbor song during territory establishment in the fall, followed by continued exposure to those songs, is more important than song exposure during the natal summer. However, while continued exposure to song may be necessary for late learning, it is most likely not sufficient because in the present experiment Tutor 5, one of the two late-only tutors, had only minor (if any) influence on the subjects' repertoire development.

Not only were subjects exposed to the late-only tutors continually, they heard many more songs from the late-only tutors than from the permanent tutors (or the early-only tutors). In particular, Tutor 6, who had the most influence overall on the subjects, produced nine times as much song during the fall and two to three times as much song during the winter and spring as any other tutor (also, his spring song rate was ten times greater than his fall rate). In our previous experiment (Nordby et al. in press), we also found a trend toward subjects learning more songs from the tutor who sang the most frequently. In that experiment, half of the subjects continued to rotate among all tutors during fall, winter, and spring (equivalent to Stage II in the present experiment). All of the subjects who rotated chose the same male as their primary tutor, and that tutor produced twice as much song as the other three tutors. In a long-term field study of a wild population of song sparrows, Nice (1943), noted that the songs of one particular male were quite widespread and that he was a very prolific singer, particularly during fall and winter. It is notable here again that subjects in the present experiment did not learn more songs from Tutor 5, the other late-only tutor. Tutor 5 sang more than the permanent tutors, although his song rate was much lower than Tutor 6's. More importantly, perhaps, we did not record any song from Tutor 5 during the fall. While he may have produced song during this period, his song rate was considerably lower than that of Tutor 6 and Tutor 1 (a permanent tutor). Perhaps, as with prolonged exposure, high dosage of song is necessary but not sufficient to influence repertoire development if young males do not hear a tutor until fall or later.

The relative dosage of tutor songs was not a variable that we controlled in this experiment, but rather was the result of individual tutor differences in song production. Therefore, to verify that song dosage is an important factor in the song selection process for song sparrows or other species, one would need to experimentally manipulate the amount of song heard by subjects. Most previous studies of song learning have tended to emphasize the contrary observation that songs can be learned despite a very small number of presentations (e.g., as few as 15 repetitions in nightingales, *Luscinia megarhynchos*, (Hultsch & Todt 1989). Only a few studies have examined the effect of exposing young birds to higher dosages of tutor song. One study of song sparrows by Marler & Peters (1989) found a relatively weak dosage effect (songs heard for six weeks were 1.5 times more likely to be imitated than songs heard for only one week). Nelson et al. (1996) examined the effect of tutor song dosage on the timing of song acquisition in white-crowned sparrows and found that males did not learn new songs after 100 days of age even though they had heard the later songs five times more often.

Although prolonged exposure to song and high dosage of song may be necessary for young birds to learn tutor songs after their natal summer, these variables alone may not be sufficient. The fact that subjects were able to interact vocally with a live tutor may have been the crucial element that allowed them to acquire songs in the fall or later. The fact that several subjects in this experiment learned songs from Tutor 6 even though they could not see him suggests that vocal interaction, rather than visual communication, is a key factor. We have extensive recordings of tutor-subject and tutor-tutor singing interactions from this experiment and plan to conduct post hoc analyses of, for example, the difference in Tutor 6's interactions with subjects who learned a lot of song from him versus those who did not.

It has been suggested that using live tutors gives different results than using tape tutors, but there is considerable debate on this point (for a sampling of both sides of the debate see (Baptista & Gaunt 1997; Nelson 1998). To date, only live tutors have interactively sung with the young subjects during the plastic song phase. But as interactive playback studies have shown, it is possible to introduce many interactive social effects into playback designs (Nielsen & Vehrencamp 1995; Dabelsteen & McGregor 1996); J. M. Burt, S. E. Campbell & M. D. Beecher unpublished data). We suggest that it may be profitable to try and simulate live tutors and key aspects of the natural social situation using tape tutors. For example, one could simulate four singing neighbours by playing the recorded song repertoires of each of four birds from four separate locations (i.e., each simulated bird sings only from his territory). The physical layout would be identical to the present experiment, with the live tutors replaced with the appropriate song playback. Furthermore, the experiment could be set up so that the 'tutors' interacted with one another and, ideally, with the tutees during the plastic song phase as well (antiphonal singing, song matching, etc.). This simulation captures some features of the natural conditions, including spatial separation of singing adult males, clear definition of song types via shared song types, and interactive singing. Although an interactive song tutoring design may require considerable technical ingenuity, the concept is straight-forward. If an interactive design can be made to work, it will be particularly interesting to contrast interactive and dosage effects. Our intuition is that interactive effects will prove more important: that how the tape tutor 'uses' its songs (e.g., to reply to, type match or overlap the tutee; to respond to some but not others of the tutee's songs; to interact with the other tutors) will outweigh how often particular songs are played.

Song Learning Strategy of the Song Sparrow

Results from this experiment, for the most part, replicated our previous findings regarding five of the components of the song learning strategy of male song sparrows (Beecher et al. 1994; Nordby et al. 1999, in press). First, males generally learned whole song types, that is they accurately imitated a tutor's song rather than improvising new songs from learned elements. The percentage of songs that could be traced to adult tutors in this experiment (77%) was similar to results from our previous experiment (71%, Nordby et al.

in press), but is less than what we found in our field study (91%, Nordby et al. 1999). An additional 15% of the subjects' songs in this experiment matched the songs of groupmates, and only 8% of the subjects' songs were considered to be unique to one subject. Males in other populations of song sparrows also learn whole song types as evidenced by first-year males precisely imitating songs of their adult neighbors (Nice 1943), and by adults sharing many of the same song types (Hill et al. in press; Wilson, P. L., Towner, M. C., & Vehrencamp, S. L. unpublished data). However, the level of whole song sharing is less in some eastern populations (Hughes et al. 1998; Kramer & Lemon 1983).

Second, males learn songs from several tutors rather than learn songs from just one. Eight of 12 subjects in this experiment learned songs from two or more tutors. The remaining four subjects learned songs from only one tutor, but also had several songs in their repertoires that were considered to match the songs of other subjects in their group. The end result, for all subjects, was that males developed repertoires comprised of songs that matched the songs of at least two other birds. We have found this same result in our previous lab experiment (Nordby et al. in press) and two field studies (Beecher et al. 1994; Nordby et al. 1999). A field study of dunnocks (*Prunella modularis*) also showed that young males learn their songs from multiple tutors, and that these tutors consist of the male on whose territory they have settled and the neighbouring adults (Langmore 1999). In experiments investigating song tutor choice in zebra finches, *Taeniopygia guttata*, young males learned song material from more than one tutor if they were exposed to them sequentially, but not if exposed to them simultaneously (Clayton 1987; Slater et al. 1991).

Third, males preferentially learn songs that are shared among their tutors. Subjects in this experiment learned more tutor-shared song types than would have been expected if they had learned song types randomly. Interestingly, this result occurred despite the fact that Tutor 6, who was the most influential tutor overall, shared only a single song type with one other tutor. Seven subjects learned the song that Tutor 6 shared with Tutor 5 (the other late-only tutor), and most of the other tutor-matching song types that the subjects imitated were shared between Tutors 1 and 2 who were also present during the later stages of song development. Langmore (1999) found, in her study of dunnocks, that males preferred to learn song phrases that were shared by males nearby (although the result could be explained by the fact that there was 76% repertoire overlap between neighbours, and 60% overlap even among distant males).

Fourth, in our previous studies (Nordby et al. 1999, in press; Beecher et al. 1994) we found that subjects preferentially learned songs from tutors they were adjacent to during late fall, winter and spring. Half of the subjects in the Nordby et al. (in press) experiment were stationed next to only one of four tutors during the later stage (as all subjects were in the present experiment). The stationary subjects in the previous experiment learned most of their songs from the tutor to whom they were adjacent (the other rotated subjects learned the most from the tutor who sang the most, see discussion above). We expected to find a similar result in the present experiment, but only four of 12 subjects learned the most from their adjacent tutor. However, if we look from the tutor's perspective, there was a slight tendency for tutors to influence adjacent subjects more than distant subjects. We did not run any statistical analyses because of the small sample of tutors, but all four tutors who were present after the young males' natal summer tutored more songs to subjects who were adjacent to them than to distant subjects. Also, adjacent subjects tended to produce better imitations of tutor songs than did distant subjects.

Finally, males were influenced by other subjects in their group. At least half of the subjects had one or more songs that matched a groupmate's song better than any tutor song. In some cases a tutor also had a matching song but the subjects converged on one another to form a song that was more like one another. In other cases these songs were improvised from tutor song syllables but we did not know if one subject created the new song and was copied by another subject or if they somehow influenced each other in a reciprocal manner to create the new song. In the Nordby et al. (in press) experiment several males developed songs that best matched the songs of other subjects as well. In addition, as in that previous experiment, subjects did not hear one another sing until the fall so this influence must have occurred during the later stages of song development. Several studies of other oscines have also found that birds within the same cohort can develop songs that are alike, or, as in this study, are even more similar to each other's song than to the tutor song (Cunningham & Baker 1983; Kroodsma & Pickert 1984; Byers & Kroodsma 1992; Payne & Payne 1993; Slater et al. 1993; Kroodsma et al. 1995).

In summary, this experiment demonstrates that song sparrows are capable of acquiring many new songs after their presumed sensitive period for song learning. They can learn new songs as late as five months of age. Whether they can learn even later (e.g., in their first spring) needs to be tested experimentally. Being able to learn songs in late fall, or later, is consistent with a song learning strategy that provides young males with songs they will share with their first-breeding season neighbours. The specific mechanism by which tutors influence the timing of song acquisition and song selection is still unknown. Subjects in this experiment had prolonged and continued exposure to late tutor song, had a high dosage of late tutor song, and had live interactions with the late tutors all of which may be necessary for late acquisition to occur, although these factors alone are probably not sufficient.

Figure 3.1

Schematic diagram of spatial arrangement of tutor aviaries (T 1-4) and subject cages (S). Subjects had visual contact only with the adjacent tutor and all birds were in auditory contact.

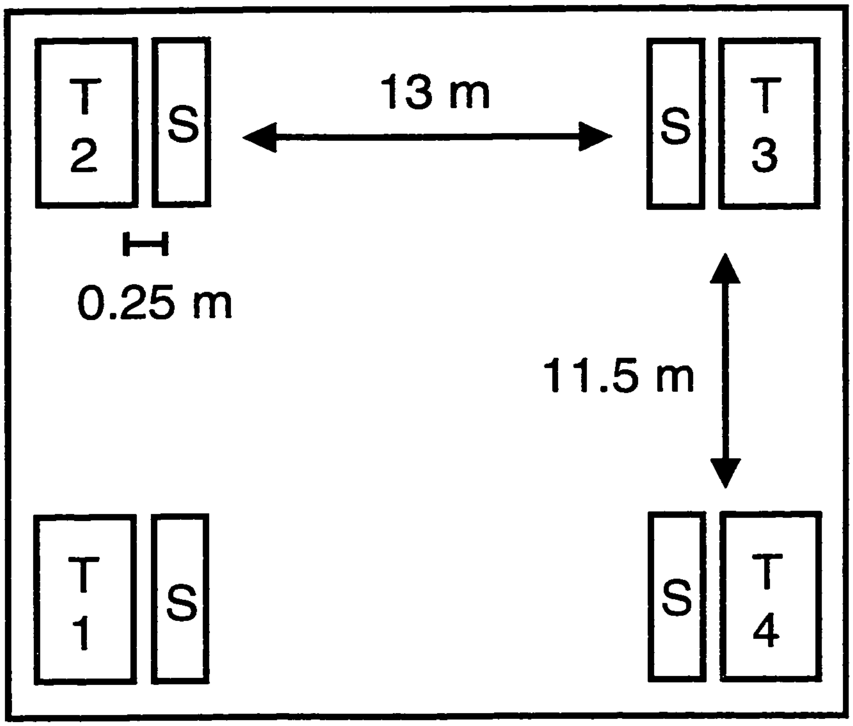
T 2
S
13 m
S
T 3
0.25 m
11.5 m
T 1
S
S
T 4

Figure 3.2

Experimental design. During Stage I, all subjects were rotated equally among four tutors (T1 – 4). During Stage II, subjects were stationed next to only one of four tutors (T1, T2, T5, or T6). Black arrows represent the period of time that a tutor occupied one of the four aviaries. Black bars represent the three periods when subjects were exposed to the tutors. White bars represent the two periods when subjects were in social and acoustic isolation and correspond to times of very low song rates in wild song sparrows.

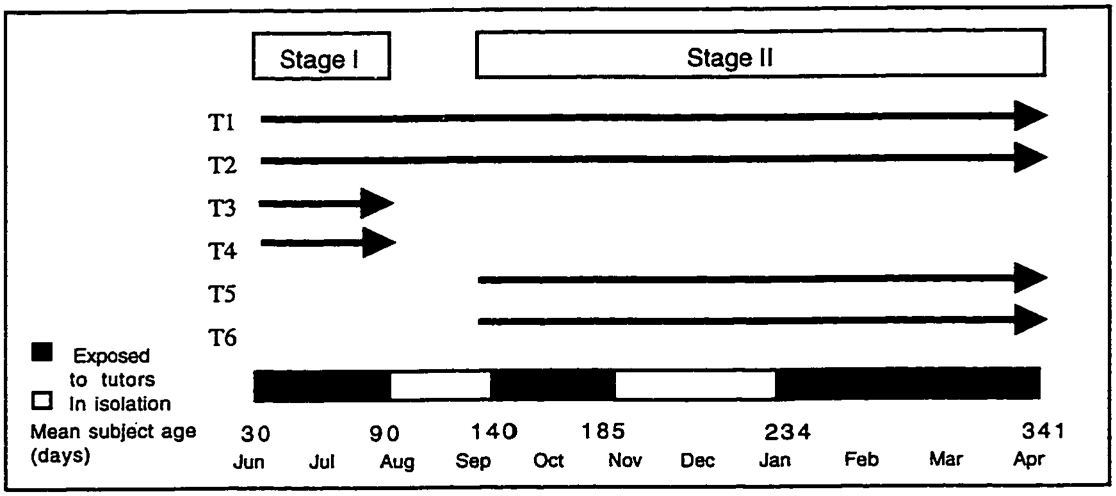
Stage I
Stage II
T1
T2
T3
T4
T5
T6
■ Exposed to tutors
□ In isolation
Mean subject age (days)
30
90
140
185
234
341
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr

Figure 3.3

Examples of matching subject and tutor song types. All three tutor songs are those of Tutor 6, a late-only tutor. We rated song (a), sung by subject WE, as a 1 (≥ 90% of the elements within the subject's song matched those in the tutor's song) and songs (b), sung by subject BA, and (c), sung by subject RG, as 2's (70-89% of the elements matched those in the tutor's song).

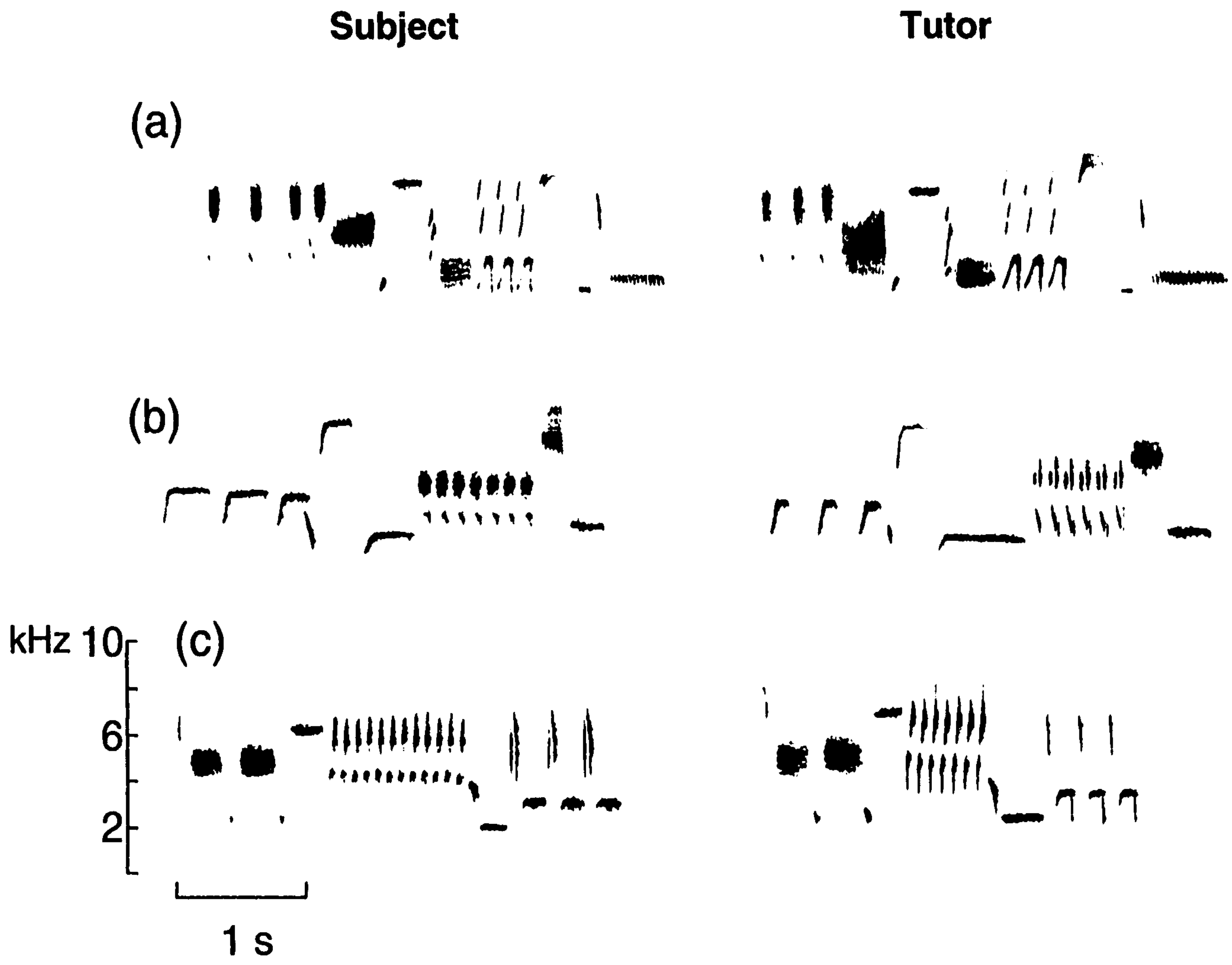
Subject
Tutor
(a)
(b)
(c)
kHz 10
6
2
1 s

Figure 3.4

Mean tutor score (+ SE) of each tutor present during Stage II for subjects who were adjacent to them (black bar, n = 3 per tutor) and subjects who were not (white bar, n = 9 per tutor). Mean tutor score is the number of song types a tutor matches with a subject, devalued by the number of other tutors identified for those song types.

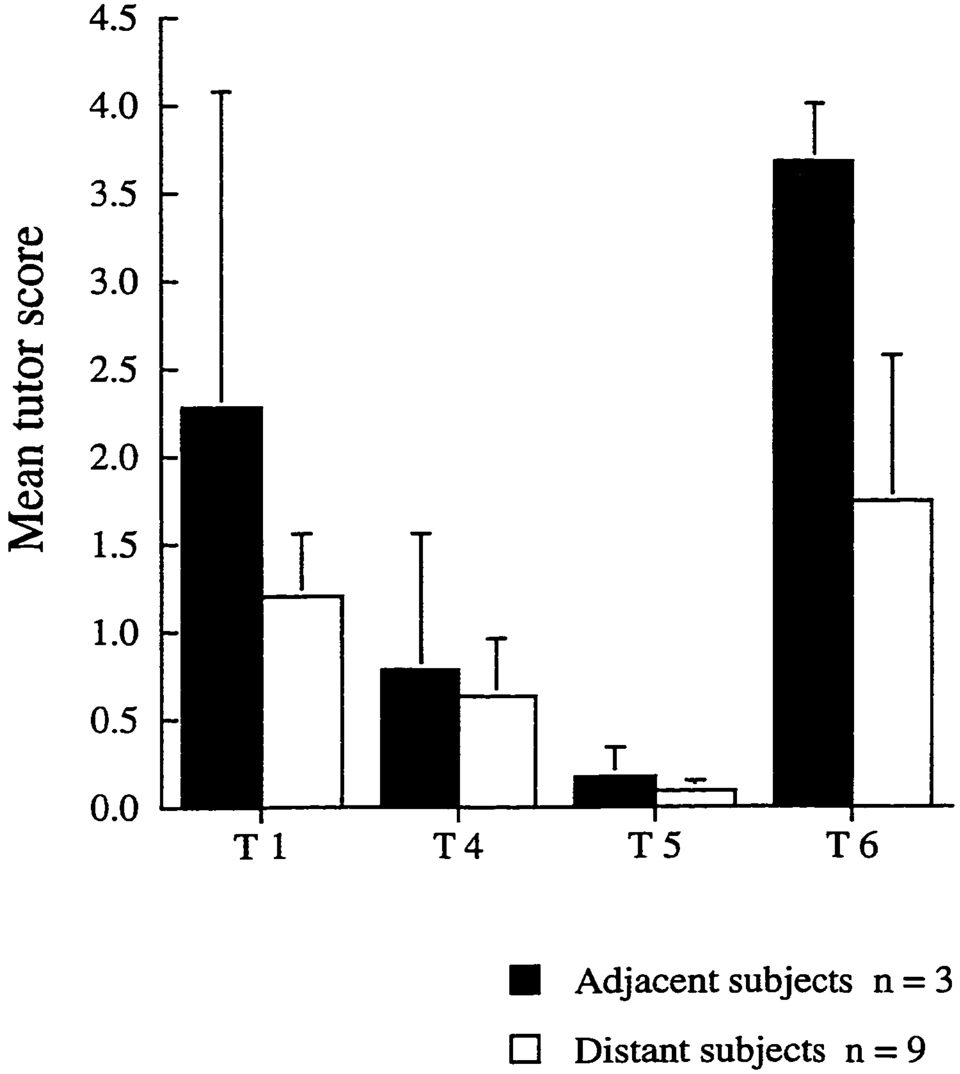
Mean tutor score
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
T 1
T 4
T 5
T 6
■ Adjacent subjects n = 3
□ Distant subjects n = 9

Figure 3.5

Percentage of subjects' tutor-matching song types (+ SE) that were rated as matching a tutor song by 90% or more (rating = 1) for each tutor present during Stage II, grouped by subjects who were adjacent to them (black bar) and subjects who were not (white bar). Numbers at the bottom of each bar indicate the sample size for that group.

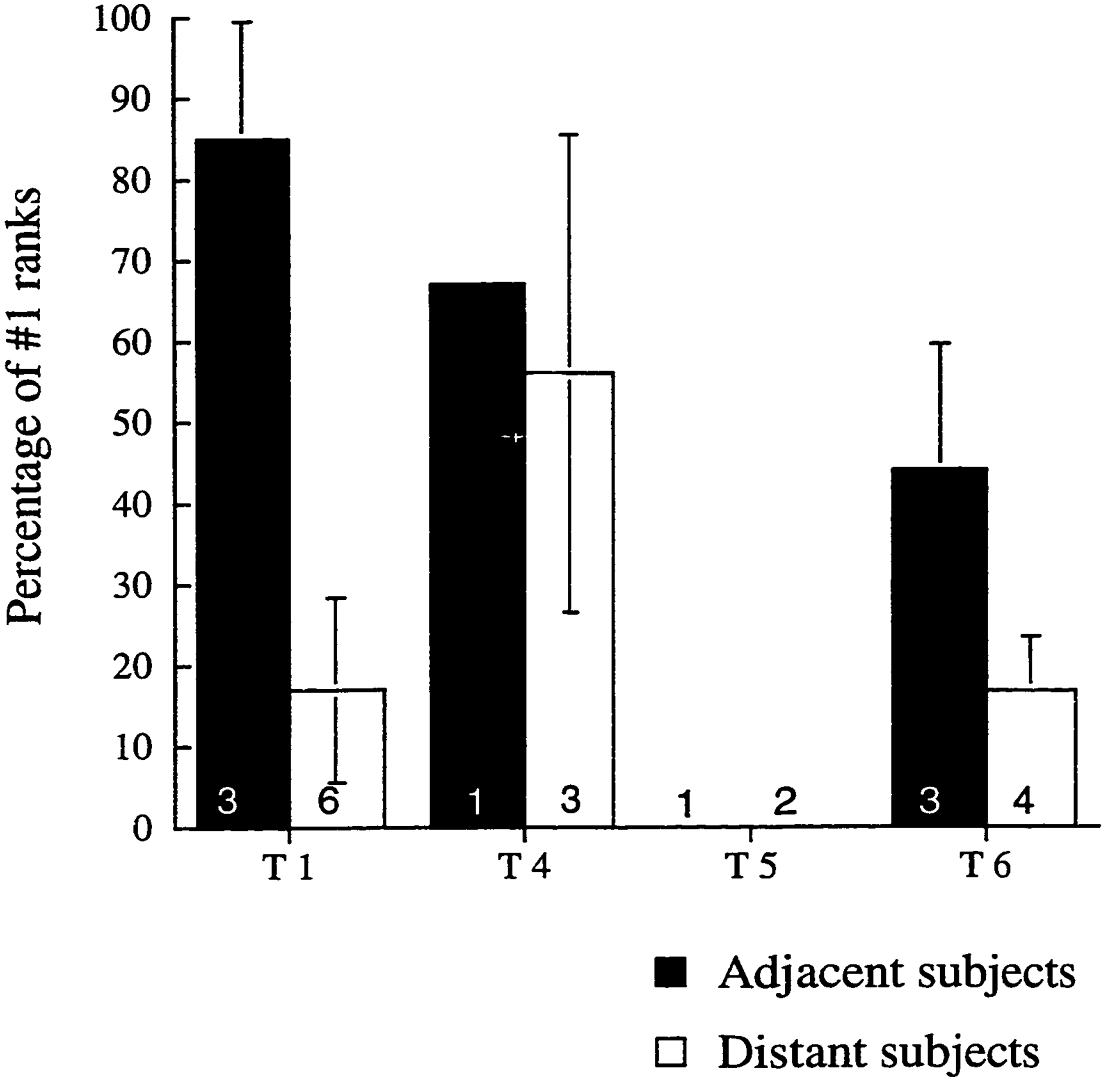
Percentage of #1 ranks
100
90
80
70
60
50
40
30
20
10
0
3
6
1
3
1
2
3
4
T 1
T 4
T 5
T 6
■ Adjacent subjects
□ Distant subjects

Figure 3.6
Mean tutor song rate per month for each tutor. We recorded the tutors only during the periods when subjects were being exposed to the them. Tutors 1 (□) and 2 (○) were present throughout the experiment, Tutors 3 (△) and 4 (◇) were present only during the first summer, and Tutors 5 (■) and 6 (●) were present during fall, winter and spring.

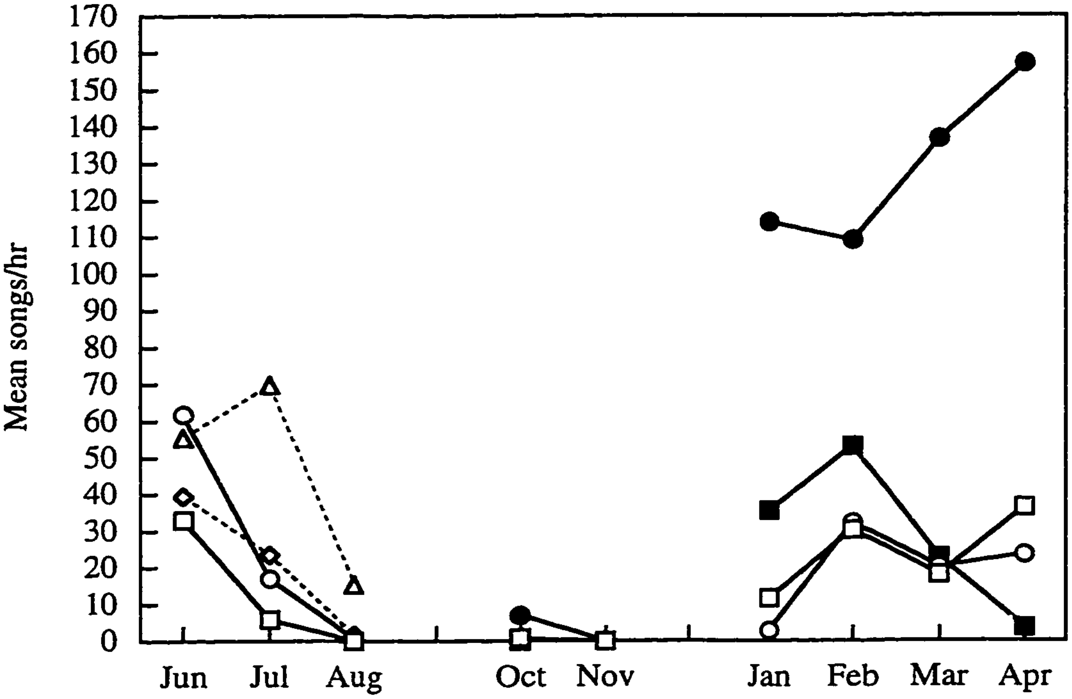
Mean songs/hr
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
Jun
Jul
Aug
Oct
Nov
Jan
Feb
Mar
Apr

Table 3.1. Tutor scores, number of song types in each matching category, and number of song types in subjects' repertoires.

	Tutor Scores[a]							Element	Song types
Subject	Tutor 1	Tutor 2	Tutor 3	Tutor 4	Tutor 5	Tutor 6	Cohort[b]	match[c]	in repertoire
Group 1									
BA	1.00*	-	-	-	-	6.00	-	-	7
RG	-	2.33*	0.33	-	-	5.33	-	-	8
OA	2.00	2.50	-	-	0.50*	-	-	1.00	6
WE	1.83	1.33	0.33	-	0.50	3.00*	-	1.00	8
Group 2									
WI	5.83*	1.83	0.33	-	-	-	-	-	8
OB	1.00	-*	-	-	-	-	3.00	2.00	6
PB	-	-	1.00	-	-*	-	3.00	1.00	5
RI	1.00	-	-	-	-	4.00*	2.00	-	7
Group 3									
RB	-*	-	0.50	-	-	3.00	1.50	-	5
WA	2.00	-*	1.00	-	0.50	1.50		-	5
AP	3.00	-	-	-	-*	-	1.00	1.00	5
GG	-	-	-	-	-	4.00*	1.00	-	5
Total	17.66	7.99	3.49	0.00	1.50	26.83	11.50	6.00	

a Tutor scores are the number of song types a tutor, or cohort, matches with a subject, devalued by the numbe identified for those song types.

b These song types matched a groupmate's song type better than any tutor song type.

c These song types did not match any one tutor song type, but ≥ 50% of the elements were identified as tutor s

* Indicates which tutor that subject was stationed next to during Stage II.

_ Indicates highest tutor score for that subject.

Table 3.2. Proportion of tutor-matching songs that were tutor-shared songs.

Subject	Song types in repertoire	Tutor matches[a]	Tutor shared[b]	% Tutor shared[c]
Group A				
BA	7	7	2	0.29
RG	8	8	3	0.38
OA	6	5	3	0.60
WE	8	7	4	0.57
Group B				
WI	8	8	6	0.75
OB	6	1	1	1.00
PB	5	1	1	1.00
RI	7	5	1	0.20
Group C				
RB	5	4	2	0.50
WA	5	5	3	0.60
AP	5	3	0	0.00
GG	5	4	1	0.25
			Mean	0.51
			SE	0.09

a Indicates the number of each subject's songs in which ≥50% of the elements matched those within a tutor song.

b Indicates the number of tutor-matching songs that were shared by two or more tutors (using the strict criterion for sharing).

c Indicates the proportion of tutor-matching songs that were tutor-shared songs.

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CURRICULUM VITAE

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Education

University of Washington	Ph.D., Psychology	1999
University of Washington	Grad. Concentration, Conservation Biology	1996
University of Wisconsin	B.S., Zoology	1989

Research Experience

Doctoral Dissertation Research — Sept. 1992 – July 1999
Department of Psychology, University of Washington
- Ecological correlates and adaptive significance of song learning in song sparrows (*Melospiza melodia*).

Research Biologist — Oct. 1991 - Aug. 1992
Center for Wildlife Conservation and The Nature Conservancy, Seattle, Washington
- Statewide population survey and development of captive propagation protocols for the state-endangered western pond turtle (*Clemmys marmorata*).

Senior Research Assistant — Sep. 1990 - Aug. 1991
Department of Psychology, University of Wisconsin — Jan. 1989 - Aug. 1989
- Parental behavior, mate choice, and sexual development in California mice (*Peromyscus californicus*).

Research Assistant — Jan. 1990 - Feb. 1990
Outback Research Station, University of New South Wales
- Demography and ranging behavior of red kangaroos (*Macropus rufus*) and euros (*Macropus robustus*).
  Advisor: Prof. David Croft

Research Assistant — Jun. 1988 - Dec. 1988
Department of Entomology, University of Wisconsin
- Life cycles, host plant associations, and parasitism of leaf-mining insects.
  Advisor: Prof. Dan Mahr

Awards and Grants

American Association of University Women: American Fellowship, 1998-99

National Science Foundation: Dissertation Improvement Grant, 1997

Animal Behavior Society: Founders' Memorial Award, 1994

Teaching Experience

Guest Lecturer, University of Washington:

Psychology as a Social Science	Autumn 1997
Comparative Animal Behavior	Autumn 1995

Teaching Assistantships, University of Washington, 1992-1998:

Comparative Animal Behavior	8 quarters
Elementary Psychological Statistics	1 quarter
Psychology as a Social Science	1 quarter

Professional Affiliations and Service

Animal Behavior Society
    Conservation Committee, 1997-present

Society for Conservation Biology
    President, Puget Sound Chapter, 1994-1995

International Society for Behavioral Ecology

University of Washington: Graduate Certificate Programs in Conservation Biology
    Steering Committee, 1996-1999

Invited Seminar Presentations

University of Wisconsin: Behavioral Interdisciplinary Seminar, September 1998

Publications

Nordby, J. C., S. E. Campbell, J. B. Burt & M. D. Beecher. (in press) Social influences during song development in the song sparrow: a laboratory experiment simulating field conditions. *Animal Behaviour*

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NON-REFEREED STATE AGENCY REPORT:

Nordby, J. C. (1992) Inventory survey of the western pond turtle (*Clemmys marmorata*) in Washington. Report to The Nongame Wildlife Program, Washington Department of Wildlife, Olympia, Washington.