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Late song learning in song sparrows

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In many oscine species, young males learn songs that match those of their first breeding-season neighbours. Because sharing songs with neighbours may be advantageous, selection should favour birds that retain the capacity to memorize new songs later in their first year as the birds cannot know for sure who their neighbours will be until spring. We investigated whether song sparrows, *Melospiza melodia*, from a sedentary western population were capable of acquiring new songs after their natal summer in a two-stage laboratory experiment. In the first stage (30–90 days of age), we rotated hand-reared males equally among one set of four live tutors that had been neighbours in the field (and therefore shared songs between them). During the second stage (140–330 days old), we removed two of the original tutors and replaced them with two new tutors (which did not share any songs with the original tutors). During stage two, subjects were not rotated, but were stationed next to only one of the four tutors (they could hear the other three at a distance). Eight of 12 subjects learned songs from tutors they only heard after they were 140 days old, and six subjects learned most of their songs from a late tutor. Thus, sedentary song sparrows are capable of acquiring many songs de novo in late autumn. These results are consistent with a song-learning strategy that provides young male song sparrows with a repertoire of songs they will share with their first breeding-season neighbours.

In many songbirds, young males learn songs that match those of their first-year neighbours (Nelson 1992; Payne & Payne 1993; Bell et al. 1998; Langmore 1999; Nordby et al. 1999). Several studies have indicated that sharing songs with one's neighbours may be advantageous (Payne et al. 1988; Beecher et al. 2000; Wilson et al. 2000). Because a young bird cannot know for certain who his neighbours will be until the onset of that first breeding season, it would seem advantageous that his ability to learn new songs remain open until that time. To date, however, field data have not been complete enough to pinpoint, for any species, the point at which a first-year male songbird loses his ability to learn new songs.

Laboratory studies of song learning, on the other hand, have clearly implicated the natal summer as a sensitive period for song memorization (e.g. Marler 1970; Marler & Peters 1987, 1988). This finding poses a paradox: if it is advantageous for the young bird to share songs with his first-year neighbours, and if these neighbours are not known for sure until the breeding season, selection should favour the ability to learn songs until then, or at least closer to the male's first breeding season than to the preceding natal summer. Marler & Nelson (Marler 1990; Nelson & Marler 1994) have developed a theory that addresses this paradox for species that are age-limited song learners (i.e. those species that do not change their song repertoire after their first year). In their 'action-based' model, Marler & Nelson propose that all song memorization takes place during an early sensitive period that occurs in the bird's natal summer, usually in the second and third months of life. According to this model, later in the bird's first year, when song is still plastic, the bird progresses through a period of selective attrition. During this time, a bird produces more song material than he will keep in his final repertoire and the action-based theory suggests that he selectively retains the songs that best match those of his first breeding-season neighbours. This attrition period is thought to occur between 6 and 11 months of age, and Marler & Nelson posit that birds do not acquire (memorize) new songs during this time, but instead use 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).

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A young male may not, however, 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 & 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 can (Marler & Peters 1982; Nelson et al. 1996a). In the case of the song sparrow, with its complex, multi-element songs, elements from different memorized songs could in theory be rearranged to resemble the songs of new neighbours.

Our previous three studies on song learning in song sparrows, two in the field, one in the laboratory, are consistent with the Marler–Nelson theory (Beecher et al. 1994; Nordby et al. 1999, 2000). Our studies suggest that young males learn songs in the neighbourhood where they will settle, and that social interactions later in a bird's first year influence song development such that males favour the songs of adults that are present and nearby in the young males' first breeding season over songs of adults that are no longer present or are further away. Neither our field studies nor the laboratory study, however, addressed the question of when young males are able to memorize songs. In our laboratory study, the same set of tutors were present throughout the study so subjects were not exposed to any new tutors after their natal summer. Birds in our study population are resident year-round and rarely do new birds enter the population as adults (Beecher 1996). Thus a young bird in the field will not experience new song tutors unless he moves from his postdispersal area to a new area in the autumn or spring. Although we cannot, of course, manipulate tutor exposure in field studies, one can make inferences from field data on birds that move, and we consider some of these cases below.

Young males in our sedentary study population in Washington generally establish their territories in autumn or later and almost all males settle on territories that are next to those of their song tutors (Beecher et al. 1994; Nordby et al. 1999). However, in the Nordby et al. (1999) field study, we identified six young males that settled on territories that were far removed from some or all of their song tutors. Two males appeared to have moved away from all of their tutors, and did so late in their first year of life (possibly as late as March or April of their first breeding season). The other four males settled on territories that were next to some of their tutors, but they had also learned songs from adults that were in a separate area of our study site. At least three of these males appeared to have moved earlier in their first year (by the end of October) to the area where they established territories. Adult males in this population produce song through mid-July, but then sing little or not at all during moult, which lasts through August. Following moult, there is an increase in song production in September and October. If males do not establish territories until after their natal summer, and have been moving about in other areas, it is possible that they would not hear their neighbours-to-be sing until autumn. That the young males that appear to have moved in late summer or autumn share some songs with their adult neighbours suggested to us that the period for song memorization may extend beyond the natal summer. In other songbird species it has been shown that males can acquire songs later in their first year, even as late as their first spring; these species include chaffinches, *Fringilla coelebs*, marsh wrens, *Cistothorus palustris*, and indigo buntings, *Passerina cyanea* (Slater & Ince 1982; Kroodsma & Pickert 1984; Payne & Payne 1997).

In the present experiment, we tested whether song sparrows were capable of learning songs de novo in the autumn 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 autumn, and assessed whether subjects learned songs from the new tutors. If song sparrows are unable to acquire new songs after their natal summer, we predicted, according to Nelson & Marler's (1994) selective attrition hypothesis, that subjects should 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, then they should produce very good imitations of the new tutors' songs. In either case, the two tutors that were present throughout the experiment should have the most influence overall because they would be present during the early sensitive period as well as during the selective attrition phase.

An additional 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, 2000). 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 and (4) 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, Washington, U.S.A.) between 10 and 25 May 1997 when they were 5–7 days old. Subjects were hand-raised as a group until they were 26–30 days old and then placed into individual wire-mesh cages (45 × 28 × 18 cm) equipped with wooden perches. Subjects were maintained on ad libitum 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 on 8 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. 2000). In that experiment,

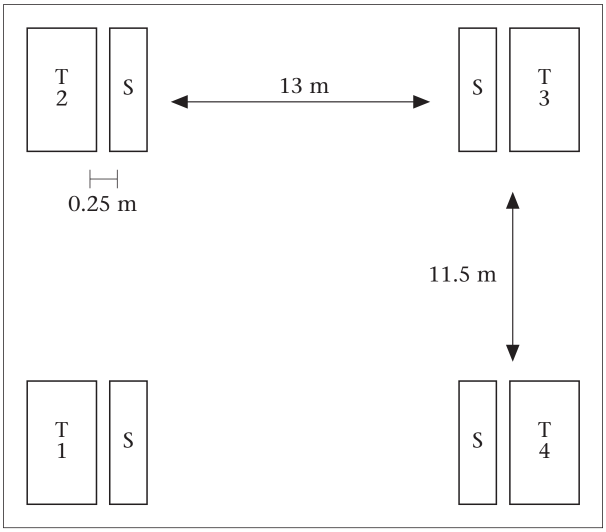

Figure 1. Schematic diagram of the spatial arrangement of tutor aviaries (T 1–4) and the subject cages (S). Subjects had visual contact only with the adjacent tutor and all birds were in auditory contact.

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 (1.47 × 0.71 × 1.83 m, containing a 1.0-m potted shrub and several wooden perches) and maintained on ad libitum water and food.

Experimental Design and Procedure

We conducted the experiment outside on the roof of Guthrie Hall at the University of Washington, Seattle. We placed four tutors in individual aviaries in four corners of an area of the roof and simulated field conditions by moving the subjects among these tutors on their pseudo-territories. Tutor aviaries were 11.5–17.4 m apart. When a subject was being exposed to a tutor, he was placed in a cubicle that was 0.25 m away from the tutor's aviary and open only on the side facing the tutor (Fig. 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 (Fig. 2). Stage I occurred between 7 June and 18 August 1997 when subjects were approximately 30–90 days old and corresponded to the sensitive period for song memorization found in eastern song sparrows (Marler & Peters 1987). During this stage, subjects were exposed only to Tutors 1, 2, 3 and 4 (the four tutors that had been neighbours in the field) and each subject was exposed to the tutors for 61 days. Because 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 from zero to three 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 3 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 and 18 April 1998 and corresponded to the later stages of song development. 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 that 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 1 January and 18 April 1998. Song sparrows produce little song in mid-winter so we did not expose subjects to the tutors during that time. 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, 18-mm 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. Because the subjects had begun to sing plastic song by this time, we wanted to limit possible within-cohort influence by having only one subject with each tutor at a time. We therefore divided the subjects into three groups of four birds (groups A, B and C) and exposed only one group 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, groups were rotated every 2 days and so subjects were with the tutors a third of the time. When subjects 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

Songs were recorded using a Sennheiser ME-88 or a Realistic 33-1056A omni-directional condenser microphone and a Sony TC-D5M or a Marantz PMD221 stereo-cassette recorder. We produced sonagrams of each subject and tutor's song types (including distinct variations) using a Kay DSP-5500 sonagraph.

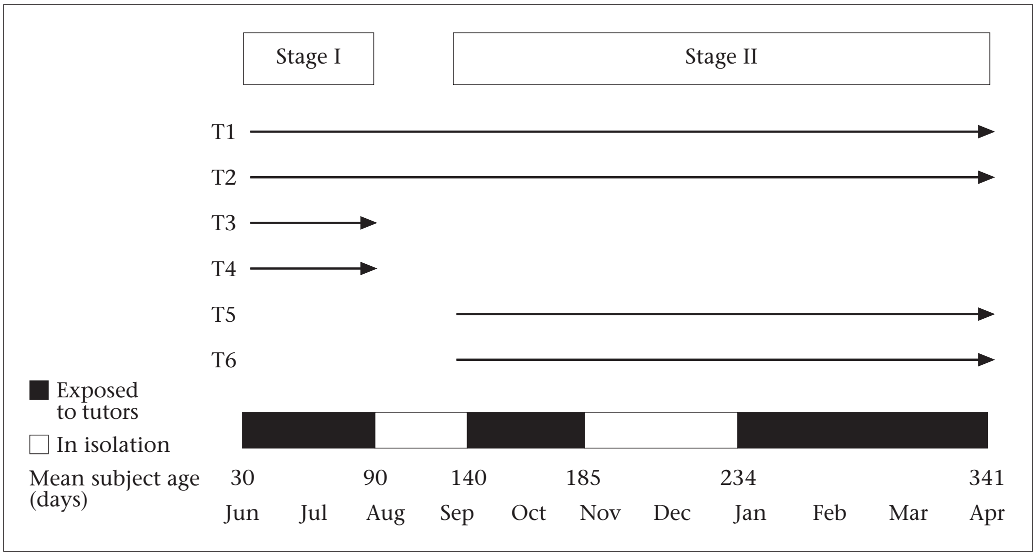

Figure 2. Experimental design. During stage I, all subjects were rotated equally among four tutors (T1–4). During stage II, subjects were stationed next to only one of four tutors (T1, T2, T5, or T6). Black arrows represent the period of time that a tutor occupied one of the four aviaries. Black bars 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.

We had specifically chosen Tutors 5 and 6 as the late-only tutors because they did not share any song types with the early-only or permanent tutors. We determined a priori 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 and occurred in the same order. We classified the 53 tutor songs into 38 different song types. Twelve of these song types were shared (i.e. songs were shared by two or more tutors) and 26 were unique song types (i.e. only one tutor sang that song type). Eleven of the shared song types were found among Tutors 1–4 (the four tutors that had been neighbours in the field). Tutors 5 and 6 shared only one song type that met our sharing criterion. No songs were shared between the late-only tutors (Tutors 5 and 6) and the other four tutors (Tutors 1–4).

In addition, we wanted to ensure that the late-only tutors shared few song elements with the other tutors as well. If subjects learned songs of the late-only tutors, we wanted to be able to detect whether subjects had memorized the songs de novo or if they had rearranged earlier-memorized elements to approximate the late-tutors' songs. Therefore, we conducted an analysis of sharing among the six tutors at the level of song elements. We cut sonagrams of their songs into their component elements and grouped the elements into one of four categories; introductory phrases, trills, buzzes or note complexes. Our method of categorization is similar to that used by Podos et al. (1992), with the exception that we did not include short simple notes in this analysis as they are common to most song sparrow songs and so did not contribute substantially to tutor identification in this study. Introductory phrases consisted of the first set of repeated notes at the beginning of the song. Elements, other than introductory phrases, containing a set of rapidly repeated notes were considered trills. Buzzes appeared as a single wide-band trace on the sonagram, either noisy or banded. Elements that contained one or more discrete tracings that were consistently produced together were categorized as note complexes. In Figure 3 we give an example of how we defined these four element categories. Elements were classified as shared or unshared on the consensus of two judges who were blind as to tutor. We classified the 254 tutor song elements into 169 different elements, 59 of which were shared (i.e. common to two or more tutors) and 110 of which were unique to a single tutor. Only 15 of the 169 elements (8.9%) were common to both late-only and either early-only or permanent tutors. In addition, of the late-only tutors' 16 song types, only two contained more than two elements that were classified as shared between the late-only and either the early-only or permanent tutors. Therefore, we were confident that we could distinguish between subject songs that were composed of elements learned from the early-only or permanent tutors and songs memorized after September.

We recorded each subject's crystallized song repertoire after 29 April 1998 when they were more than 344 days old. Sonagrams of each subject's song types (including distinct variations) were then visually matched by three judges to the song types of all six tutors and the subject's respective groupmates. One of the judges was blind as to tutor, and his judgements differed inconsequentially from those of the other two judges. We wanted to identify the bird that had the most influence on repertoire development and so looked for the tutor or groupmate that 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

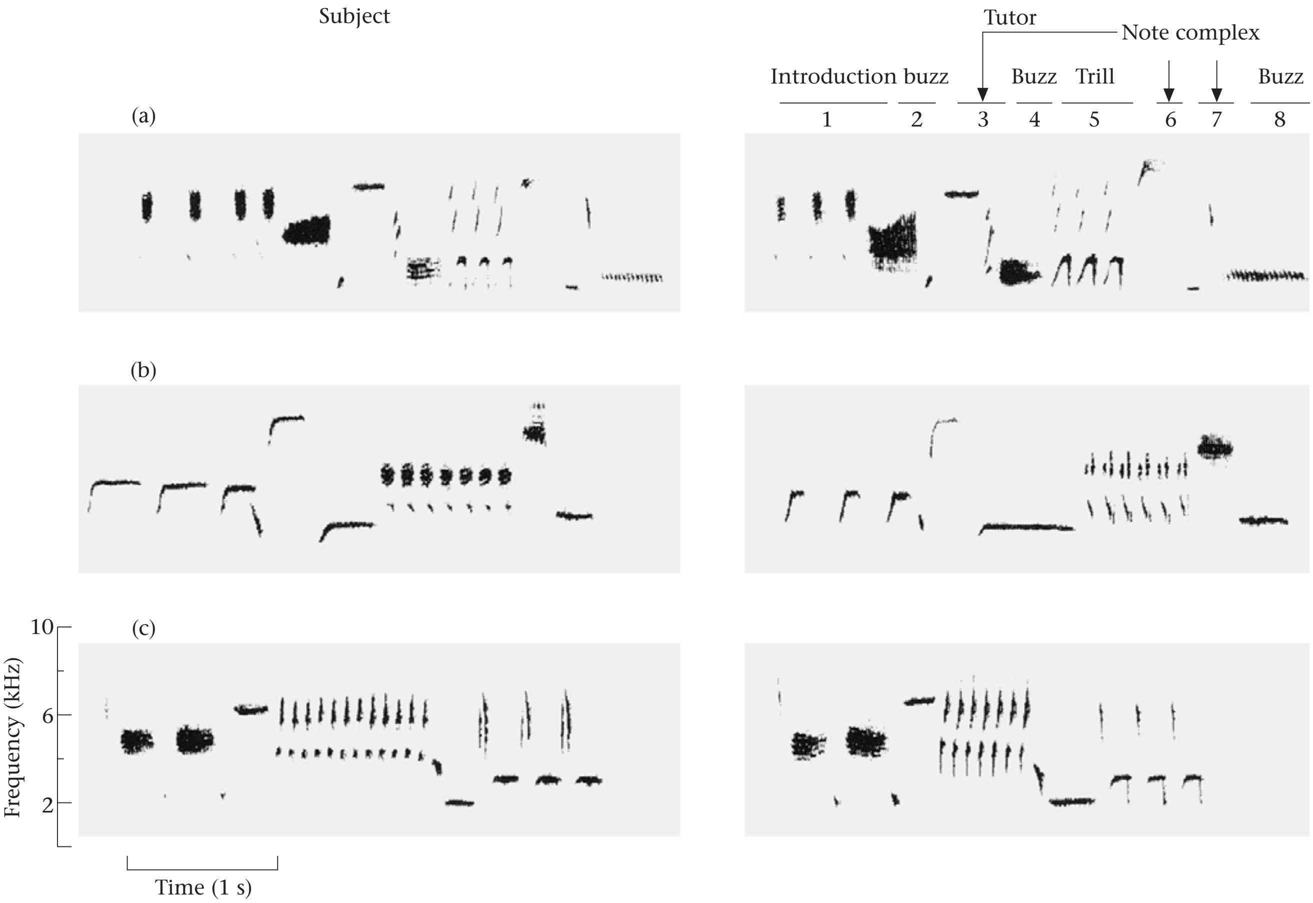

Figure 3. Examples of matching subject and tutor song types. All three tutor songs are those of Tutor 6, a late-only tutor. We rated song sung by subject (a) WE, as a 1 (≥90% of the elements within the subject's song matched those in the tutor's song) and (b) BA, and (c) RG, as 2s (70–89% of the elements matched those in the tutor's song). The categories of elements used in the tutor song-element analysis are indicated above the tutor song in (a). Elements 2, 3 and 5 were classified as shared between the late-only tutors and either the early-only or permanent tutors.

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 one case where a groupmate had a better matching song type than the 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. Finally, in 11 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 one of these cases 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=at least 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.

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

Table 1. Tutor scores, number of song types in each matching category and number of song types in subjects' repertoires

	Tutor scores*								
Subject	Tutor 1	Tutor 2	Tutor 3	Tutor 4	Tutor 5	Tutor 6	Cohort†	Element match‡	Song types in repertoire
Group A									
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 B									
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 C									
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	

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

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

‡These song types did not match any one tutor song type, but 50% or more of the elements were identified as tutor song elements.

§Indicates which tutor that subject was stationed next to during stage II.

Bold values indicate the highest tutor score for that subject.

one overall category score (e.g. 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?), 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. 2000) showed that males are more likely to learn songs if they are shared among their tutors. To examine the effect of song sharing we used the classification of shared and nonshared tutor songs outlined above and determined how many of the subjects' tutor-matching songs were among those we classified as shared and how many were not. The second variable we examined was tutor song rate. Results from our previous song-learning experiment (Nordby et al. 2000) 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 that sings the most. To sample tutor song rate we simultaneously recorded all four tutors that were present during each bout of tutor exposure at a random time every other morning for 45 min and counted how many songs they sang during each session.

RESULTS

Subject Repertoires

The size of subject repertoires ranged from five to eight song types, which is within the normal range for *M. melodia*. Using our matching criterion ($\geq$50% of the elements within the songs matched and were in the same order), we found that 69 of the 75 subject song types (92%) matched a tutor or groupmate song type (Table 1). Figure 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 12 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 1s ($\geq$90% of the elements in the song matched those in a tutor's song), 40% as 2s (70–89% of the elements matched), and 22% as 3s (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 1s, 36% were rated as 2s, and 32% were rated as 3s.

Late De Novo Song Learning and Tutor Influence

Surprisingly, Tutor 6 (a late-only tutor) was by far the most influential tutor overall; six 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). In contrast, the other late-only tutor, Tutor 5, had only a minor 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. 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 that learned songs from Tutor 6 (including three that 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 m.

The songs 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 few elements in common with Tutors 1–4. The tutor-element analysis we conducted showed that only 15 of the 169 tutor song elements were shared by Tutors 5 and 6 and tutors that were present during stage I. Two of the nine songs that subjects learned from Tutors 5 and 6 contained no shared elements, four songs contained only one shared element, one song contained two shared elements and two songs contained four shared elements each. If we exclude those shared elements from the analysis, however, the results of this experiment do not change. All subjects' songs still met our matching criteria (half of the elements in the same order) without including the shared elements. The song in Fig. 3a gives an example of one of the tutor songs that contained four shared elements, although the variation in the figure contains only three of them (elements 2, 3 and 5), and the subject's version of that song. This case is the closest we found to subjects possibly rearranging previously learned elements to create a match to a late-tutor's song. It is possible that the subject memorized three of the eight elements that comprise this song during stage I, but then he would have acquired the remaining five elements during stage II, and have learned to put them together in the proper order.

The two permanent tutors (Tutors 1 and 2), which 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 2 was the primary tutor for one subject and four subjects were influenced by him. Only one of the four subjects that 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 minimal 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.

Table 2. Percentage of tutor-matching songs that were tutor-shared songs

Subject	Song types in repertoire	Tutor matches*	Tutor shared†	%Tutor shared‡
Group A				
BA	7	7	2	29
RG	8	8	3	38
OA	6	5	3	60
WE	8	7	4	57
Group B				
WI	8	8	6	75
OB	6	1	1	100
PB	5	1	1	100
RI	7	5	1	20
Group C				
RB	5	4	2	50
WA	5	5	3	60
AP	5	3	0	0
GG	5	4	1	25
Mean				51

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

†Indicates the number of tutor-matching songs that were shared by two or more tutors.

‡Indicates the percentage of tutor-matching songs that were tutor-shared songs.

Learning of Tutor-shared Songs

We had classified the 53 tutor songs into 38 different song types, 12 (32%) were shared by two or more tutors and 26 (68%) were unique to a single tutor. 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 song types. We found that, on average, 51% of the subjects' tutor-matching songs were shared among tutors, which was significantly greater than expected (single sample one-tailed t test: $t_{11}=2.12$, $P<0.05$; Table 2, last column).

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 song type. 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

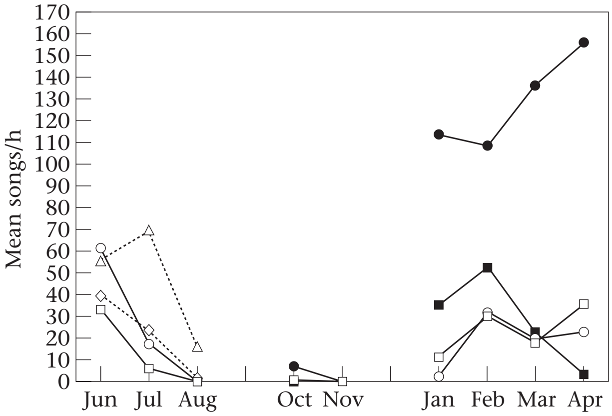

Figure 4. Mean tutor song rate per month for each tutor. We recorded the tutors only during the periods when subjects were being exposed to the them. Tutors 1 (□) and 2 (○) were present throughout the experiment, Tutors 3 (△) and 4 (◇) were present only during the first summer, and Tutors 5 (■) and 6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

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 (Fig. 4). 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 autumn 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 autumn but we only recorded him singing during early October. Neither Tutor 6 nor 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 a third of the samples for Tutor 2 due to technical problems.)

Song rates were higher overall during the second bout of tutor exposure in stage II, and again Tutor 6 had the highest song rate of the 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. 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 that they did not hear sing until they were 132–147 days old. Not only were subjects capable of learning new songs in the autumn, they were capable of learning a lot of song then. 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.

This experiment shows that the ability to memorize songs in sedentary western song sparrows extends at least into the fifth month. 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 & 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 & Pickert (1984) demonstrated that marsh wrens 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 (1999). 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.

If the sensitive period for song memorization for males in this experiment had been restricted to the natal summer, we predicted, according to Nelson & Marler's (1994) selective attrition hypothesis, that males would improvise songs from material they learned during that early sensitive period. However, the songs the subjects learned from the late-only tutors were comprised almost entirely 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 autumn or later. Interestingly, the two tutors that were present only during the subjects' natal summer 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 per cent 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 the subjects learned songs from the late-only tutors despite the fact that two other tutors were present throughout the experiment. Furthermore, two subjects learned more songs from a late-only tutor that they could not see, even though they were closer 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; (3) subjects had song interactions with the late-only tutors.

Although subjects in this experiment did not hear any of the late-only tutor songs until they were 4.5–5 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 6 weeks, as was done in previous experiments on song sparrows and white-crowned sparrows (Marler & Peters 1987; Nelson et al. 1996a), could have facilitated acquisition of the new songs.

We designed the present experiment to simulate the type of exposure to song that young males in a sedentary population may experience. In our study population, and in another sedentary population on Mandarte Island in British Columbia, male song sparrows establish territories in the autumn, or later, and then maintain most of the same neighbours through their first spring (Arcese 1987, 1989; Nordby et al. 1999). In nonmigratory populations, it may be that exposure to neighbour song during territory establishment in the autumn, followed by continued exposure to those songs, is more important than song exposure during the natal summer. Territorial behaviour and countersinging with neighbours by juvenile males in the autumn has been reported in other species (Kroodsma 1974; DeWolfe et al. 1989), and we have observed the same behaviour in our study population as well (J. C. Nordby & S. E. Campbell, unpublished data).

Because males from migratory populations do not normally experience continued exposure to song tutors during autumn and early winter, an investigation to determine whether young males from these and/or eastern populations could learn songs after their natal summer under a regime of tutor exposure similar to that used in the present experiment would add to our understanding of patterns of song learning. Similarly, an experiment in which eastern and western males were given the same tutor exposure would help clarify whether observed differences between eastern and western populations of song sparrows in patterns of song learning and song sharing (Marler & Peters 1987; Hughes et al. 1998; Hill et al. 1999; this study) have a genetic basis or if ecological factors such as the degree of philopatry and population turnover rates are more influential. However, because many song sparrows from eastern populations are nonmigratory (Davis & Arcese 1999), the effects of region and migratory status would have to be parceled out. While continued exposure to song may be necessary for late learning, it is most likely not sufficient; in the present experiment, Tutor 5, one of the two late-only tutors, had only a minor 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, which had the most influence overall on the subjects, produced an average of six times as much song during the autumn, winter and spring as any other tutor. In our previous experiment (Nordby et al. 2000), we also found a trend towards subjects learning more songs from the tutor that sang the most frequently, at least under certain conditions. In that experiment, half of the subjects rotated among all tutors throughout the entire experiment and so had equal exposure to all tutors. Each of those subjects chose the same adult male as their primary tutor, which produced twice as much song as the other tutors. However, the other half of the subjects were each stationed with one of the four tutors during the second half of the experiment and each subject learned most from the tutor he was next to.

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 (1987) found a relatively weak dosage effect (songs heard for 6 weeks were 1.5 times more likely to be imitated than songs heard for only 1 week). Nelson et al. (1996b) found a strong effect of tutor song dosage in the *Z. l. oriantha* subspecies of white-crowned sparrow. In another experiment, however, Nelson et al. (1996a) 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 (e.g. antiphonal singing) may have been the crucial factor that allowed them to acquire songs into the autumn. The fact that several subjects in this experiment learned songs from Tutor 6 even though they could not see him suggests that vocal interaction is more important than visual communication. Our sampling tapes (intended to permit measurement of tutor song rates) revealed antiphonal singing between Tutor 6 and the subjects, and among other tutors and subjects as well.

It has been suggested that results using live tutors differ from those 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 interactively sing 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; Beecher et al. 2000). We suggest that in future studies it may be profitable to try and simulate live tutors and key aspects of the natural social situation using tape tutors. The experiment could be set up so that the 'tutors' interact with one another from separate 'territories' and, ideally, with the tutees during the plastic song phase as well (antiphonal singing, song matching, etc.). This simulation would capture 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. If an interactive design can be made to work, it will be particularly interesting to contrast interactive and dosage effects. We suggest 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 replicated our previous findings regarding four of the components of the song-learning strategy of male song sparrows (Beecher et al. 1994; Nordby et al. 1999, 2000). First, males generally learned whole song types, that is 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 that found in our previous experiment (71%, Nordby et al. 2000), but less than 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 neighbours (Nice 1943), and by adults sharing many of the same song types (Hill et al. 1999; Wilson et al. 2000). However, the level of whole song sharing is less in some eastern populations (Kramer & Lemon 1983; Hughes et al. 1998).

Second, males learned songs from several tutors rather than 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 matched 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 neighbouring birds. We have found this same result in our previous laboratory experiment (Nordby et al. 2000) 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 learned songs that were 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, which 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, which were also present during the later stages of song development. Langmore (1999) found that male dunnocks prefer to learn song phrases that are shared by nearby males (although this result could be explained by the fact that there was 76% repertoire overlap between neighbours, and 60% overlap even among distant males).

Finally, males were influenced by other subjects in their group. At least half of the song sparrows 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's. 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. (2000) experiment several males developed songs that best matched the songs of other subjects in their group as well. In addition, as in that previous experiment, subjects did not hear one another sing until the autumn 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; Volman & Khanna 1995).

In summary, this experiment demonstrates that song sparrows in a sedentary population are capable of acquiring many new songs through their first autumn. Subjects in this experiment learned new songs as late as 5 months of age. Whether song sparrows can learn even later (e.g. in their first spring) needs to be tested experimentally. Being able to learn songs in late autumn 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.

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