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Social influences during song development in the song sparrow: a laboratory experiment simulating field conditions

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Oscine songbirds are exposed to many more songs than they keep for their final song repertoire and little is known about how a bird selects the particular song(s) to sing as an adult. We simulated in the laboratory the key variables of the natural song learning environment and examined the song selection process in nine hand-reared male song sparrows, *Melospiza melodia*, a species in which males sing 5–11 song types. During their second and third months (their presumed sensitive period), subjects were rotated equally among four live adult male tutors that had been neighbours in the field. Tutors were housed in individual aviary 'territories' in four corners of the roof of a building; subjects could see only one tutor at a time, but they could hear the others at a short distance. Later in their first year (months 5–12), half the subjects were again rotated among all four tutors and the other half were randomly stationed next to just one tutor. Results from this experiment confirm and extend the findings from our two previous field studies of song learning in this species. Young males in this experiment (1) learned whole song types, (2) learned songs from multiple tutors, (3) preferentially learned songs that were shared among their tutors, (4) learned songs that other young males in their group also chose, and (5) learned more songs from the tutor they were stationed next to during the later stage (stationary subjects). These last two results support the late influence hypothesis that interactions after a bird's sensitive period affect song repertoire development.

When learning songs 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 Marler & Peters (1981, 1982a, b, 1988b). They found that swamp sparrows, *Melospiza georgiana*, sang more songs during the rehearsal (or plastic song) phase of song learning than were kept for the final repertoire (two to four songs in this species). Marler & Peters traced the 'extra' or 'overproduced' songs back to tutor songs the bird had heard during his sensitive phase (which in the swamp sparrow is roughly months 2 and 3, the rehearsal phase is roughly months 9 and 10). Marler & Peters called the dropping of the extra songs 'selective attrition'. Subsequently, Marler (1990) and Nelson & Marler (1994) suggested that selective attrition would normally 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, *M. melodia*, a species in which each male sings 5–11 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 previously conducted two field studies of a sedentary Washington population to examine which songs, from which adults, a bird selects for his final repertoire (Beecher et al. 1994b; Nordby et al. 1999). From these studies we could make the follow generalizations. The young song sparrow (1) copies whole song types (versus recombining elements copied from different song types); (2) learns his songs from several older birds that were neighbours in his natal summer; (3) usually establishes his territory near his surviving tutor-neighbours the next spring; (4) preferentially learns song types shared by

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his tutors versus song types that were unique to particular tutors; (5) learns more songs from tutors that survived into the next spring (i.e. the young bird's first breeding season) than from tutors that died before then; and (6) learns more songs from the bird that was his nearest neighbour 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.

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 more closely 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 to earlier tape tutor studies (Marler & Peters 1987, 1988a) and our own preliminary laboratory studies with live tutors, both of 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 only one tutor after the natal summer, 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 than tutor-unique song types. Sharing is more unambiguously measured in our laboratory simulation because we are sure 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 or retain 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. 1999).

METHODS

Subjects

Subjects were nine males from four different broods. We collected the subjects from our study population in Seattle, Washington, on 3 May 1994 when they were 4–6 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 (45 × 28 cm and 18 cm high) 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.

Tutors

Tutors were four wild-caught adult males (referred to as tutors 1, 2, 3 and 4) that we collected from our study population in mid-October 1993. Each male was housed in an individual flight cage (1.47 × 0.71 m and 1.83 m high, containing a 1.0-m tall potted shrub and several perches) and maintained on ad libitum 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: 12-mm silastic tube implants on 17 May 1994, and 6-mm implants on 6 June 1994. We did not give tutor 1 testosterone because his song rate was similar to the song rate of males in the field. At the conclusion of the experiment, tutors were released in the area of their original territories in the field.

There was one additional adult male to which the subjects were exposed. He died 6 days into the experiment and was replaced by tutor 3. Subjects heard this fifth male for only 6 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 pseudoterritories. Tutor aviaries were 11.5–13.0 m apart, and when a subject was exposed to a tutor, his cage was 0.25 m away from the tutor's aviary and was placed in a cubicle that was only open on the side facing the tutor (Fig. 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.

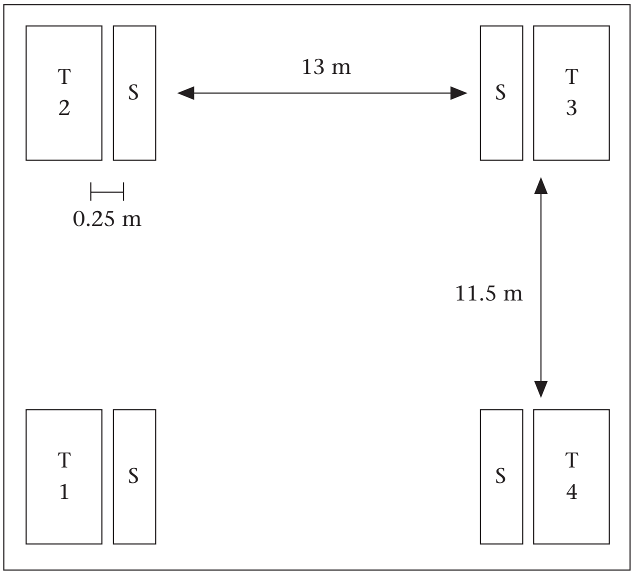

Figure 1. Schematic diagram of spatial arrangement of tutor aviaries (T1–4) and subject cages (S). Subjects had visual contact only with the adjacent tutor and all birds were in auditory contact.

The experiment was conducted in two stages (Fig. 2). Stage I occurred when subjects were 33–94 days old (1 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 3 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 laboratory and had no contact with tutors until the beginning of 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 the autumn 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 autumn and early winter because 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 groupmates throughout stage II.

During the autumn bout of tutor exposure, groups were switched every 4 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 autumn bout of tutor exposure during stage II, but was included in the stage I rotations and in the winter/spring rotations. During the autumn

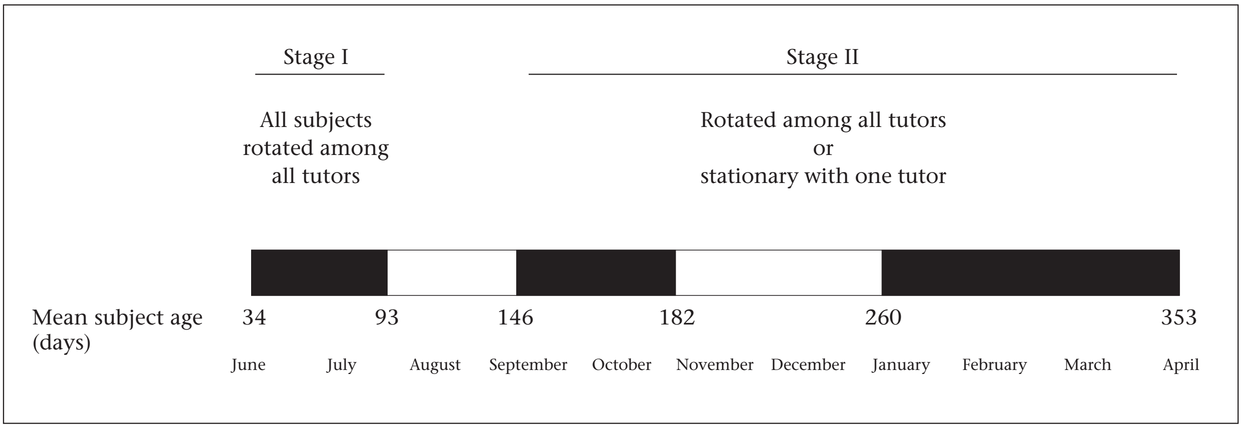

Figure 2. Experimental design. During stage I, all subjects were rotated equally among all tutors. During stage II, subjects were either rotated equally among all tutors or stationed next to one particular tutor. ■: The three periods when subjects were exposed to the tutors. □: The two periods when subjects were in acoustic isolation and which correspond to times of very low song rates in wild song sparrows.

he was housed with three females and one other juvenile male that 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 min and counted how many songs each one sang during each session. All songs were recorded using Realistic 33-1056A omni-directional, 600-Ω condenser microphones and Marantz PMD221 or AIWA AD-6350 stereo cassette recorders and analysed 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 behaviour, 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 behaviour 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 behaviour 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. 1994b; Nordby et al. 1999) 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, 2000) suggest the same, and hence we make this assumption in our present analysis.

We recorded each subject's crystallized repertoire after 1 May 1994 when they were more than a year old, using the 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 groupmates. We first wanted to identify which bird had the most influence on each subject's repertoire development, so we looked for the tutor or groupmate that had the most similar rendition of each subject's song types. The bird that 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 groupmate had equally similar versions of a song type, we gave the adult tutor sole credit. 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 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.

To quantify the amount of influence each tutor had on each subject, we gave each tutor a score based on the number of his song types that were matched by the 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 groupmate matches to determine how well these songs matched. Each subjects' matching song types were ranked on a three-point scale: 1: $\geq 90\%$ of the elements matched a tutor or groupmate song type; 2: 70–89% of the elements matched; and 3: 50–69% of the elements matched. We also analysed the unmatched song types, those that did not meet the criteria of matching any one tutor or groupmate 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 determined a priori which of the tutors' songs were 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 artefact 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.

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

	Tutor scores*								
Subject	Tutor 1	Tutor 2	Tutor 3	Tutor 4	Cohort	Song types in repertoire	Tutor or cohort match	Element match†	Invention‡
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

*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.
†These song types did not match any one tutor song type, but 50% or more of the elements were identified as tutor song elements.
‡Less than 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.
**Subject BR did not receive the autumn bout of tutor exposure during stage II.
Bold values indicate the highest tutor score for each subject.

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 groupmate. Three subjects had three nonmatching 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 groupmate 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 that did not reach crystallization until late April; the other five subjects had crystallized repertoires two or more weeks before then. Because 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 groupmate 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 groupmate matching song types as 1s ($\geq$90% of the elements matched), eight as 2s (70–89% of the elements matched), and only three as 3s (50–69% of the elements matched). Figure 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 that 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 (Table 1). The probability of obtaining this exact pattern of primary tutor influence for the stationary subjects was 1 in 256, or P=0.004. This result supports the late influence hypothesis that social interactions after the sensitive period can affect song development. The one exception was RI, which had the same score for his primary tutor and one of his groupmates. 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/h and the average rates for tutors 2, 3 and 4 were 8.9, 9.9 and 12.2 songs/h, 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 randomly (without regard to sharing), then the subjects' tutor-matching songs would, on average, contain the same fraction of shared song types (i.e. 27%). We found that, on average, 47% of their tutor-matching song types were tutor-shared songs, which was 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

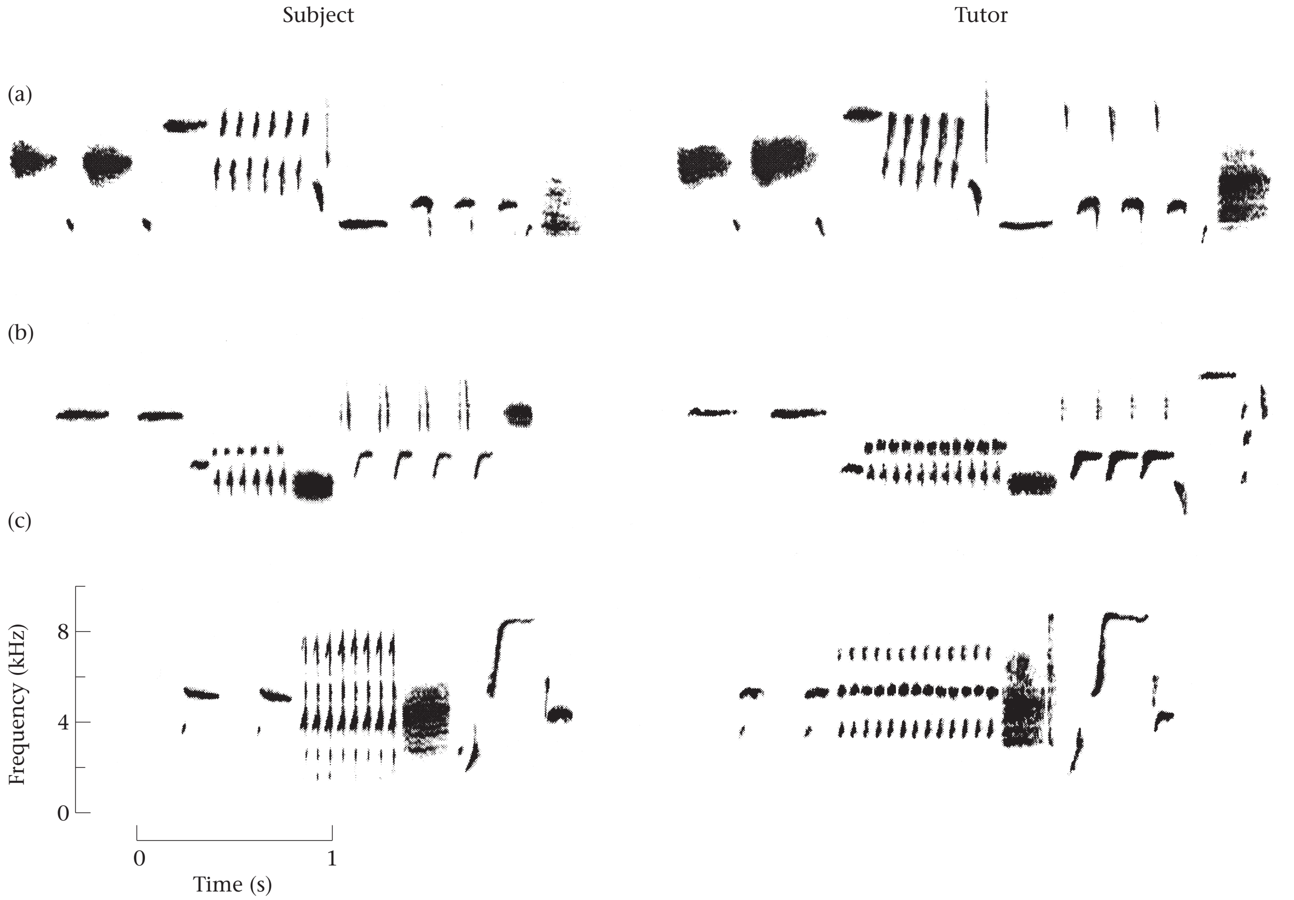

Figure 3. Examples of matching subject and tutor song types. Each row represents a different subject and tutor. We ranked songs (a) and (b) as 1s (≥90% of the elements within the subject's song matched those in the tutor's song) and song (c) as 2 (70–89% of the elements matched those in the tutor's song).

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 the expected 42% (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 groupmates influencing each other's repertoire development. For six subjects, at least one song type matched a groupmate's song type better than any of the tutors' song types. In one case, a subject (RI) learned a song that a groupmate (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 groupmates 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, and 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 groupmates. For this analysis we computed the expected percentage of sharing separately for each subject because the pool of 'neighbours' was slightly different for each subject (i.e. neighbours were

Table 2. Percentage of subjects' tutor-matching song types that matched shared songs

Subject	Repertoire size	A Tutor matches	B Tutor-shared	C Tutor-unique	D % Tutor-shared
Stationary					
AY	9	6	6	0	100
RP	9	7	6	1	86
RI	5	3	2	1	67
BY	9	6	2	4	33
Rotated					
BP	6	4	2	2	50
BR*	5	3	2	1	67
RG	5	3	2	1	67
RY	7	6	4	2	67
				Mean	67.12

A: The number of each subject's songs in which 50% or more of the elements matched those within a tutor song (=column B+column C).

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

C: The number of tutor-matching songs that were unique to a single tutor.

D: The percentage of tutor-matching songs that were tutor-shared songs (=column B/column A)*100).

*Subject BR did not receive the autumn bout of tutor exposure during stage II.

the four tutors and three or four other groupmates) and then used a within-subject paired test. Using the strict criterion for sharing, subjects learned significantly more shared songs than expected ($\bar{X}$ difference ± SE= 42.2 ± 7.0%, N=8; paired t test: t_7=6.46, P<0.001), and results were similar using the loose criterion ($\bar{X}$ difference ± SE=39.1 ± 4.3%, N=8; paired t test: t_7=9.80, P<0.001).

DISCUSSION

Results from this experiment confirm and extend the findings of our field studies of song learning in song sparrows (Beecher et al. 1994b; Nordby et al. 1999). First, young males in this study learned to sing good imitations of their tutors' song types. Collectively (and excluding IY), 71% of the subjects' song types matched a tutor (or groupmate) 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 groupmates chose. Finally, the Stationary subjects learned more songs from the tutor they were adjacent to during autumn, 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 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 laboratory study it still is less than we see in the field. For example, in our most complete field study (Nordby et al. 1999), 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.

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 three to five, Beecher et al. 1994b; Nordby et al. 1999), 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 because 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 which they did not have any visual or close auditory contact after they were 3 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

Whether we used the strict or the loose criterion for sharing, subjects had a clear preference for learning song types that were shared among their tutors. This finding is consistent with results from the Beecher et al. (1994b) study, which showed that song sparrows in the field learned more tutor-shared songs than tutor-unique songs. There are at least two possible mechanisms by which young males would preferentially select shared songs. First, young males may learn shared songs simply because they hear them more often than other songs. According to this 'dosage' hypothesis, a young male selects those songs that he hears more often without regard to the fact that he is hearing them from multiple birds. This hypothesis may also be one explanation for why subjects in the Rotated group had the same primary tutor. They may have learned most from tutor 1 because he sang more than the other tutors (although the dosage hypothesis fails to explain why birds in the Stationary group did not learn more from tutor 1). Marler & Peters (1987) found a relatively weak dosage effect in their tape tutor song learning study on song sparrows, while Nelson et al. (1996) found a strong effect of dosage for at least one subspecies of white-crowned sparrow, *Zonotrichia leucophrys oriantha*.

An alternative explanation for the preference for learning shared songs is that young males learn those songs specifically because they are shared by several birds. It may be the fact that more than one bird sings certain songs that are crucial, rather than how many times the song is sung. Perhaps the manner in which tutors use their shared songs influences the young males' song selection process. For example, if two adult neighbours (tutors) share a song, they are able to type-match each other during countersinging interactions (i.e. reply with the same song type). This use of shared songs in song sparrows has been documented in several field studies (Stoddard et al. 1992a; Nielsen & Vehrencamp 1995; Beecher et al. 1996, 2000).

We cannot distinguish between these two hypotheses in the present experiment because both conditions were simultaneously true; subjects heard shared songs more often and they were sung by more than one tutor. An experiment using tape tutors, in which 'singer' and number of songs are varied independently, is probably the only way to contrast these hypotheses.

Cohort Influences

A new finding from the present experiment was that subjects 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 groupmate's song type better than any of the tutors' song types and one subject learned one song that another groupmate 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 subject's song than to any tutor's song.

Interestingly, subjects were influenced by groupmates 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 they took 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 nonadjacent 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 that 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 groupmates' 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 that had been tutored by live adults converged on one another and developed similar songs (Cunningham & Baker 1983; Kroodsma & Pickert 1984; Slater et al. 1993). In addition, one field study by Payne & Payne (1993) showed that first-year male indigo buntings, *Passerina cyanea*, 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 5–12 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. 1994b; Nordby et al. 1999). 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 5 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. (1999) field study: young males learned more songs from tutors that survived into the young male's first spring than from tutors that 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 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. Also, studies of white-crowned sparrows in the field by DeWolfe et al. (1989) and Baptista & Morton (1988) showed that males 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 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 that 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 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 (1990) and Nelson & Marler (1994). Their theory proposes that song learning occurs in two stages. The first stage is a sensitive period which occurs when birds are roughly 1–3 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 & 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. (1999) 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 autumn or following spring as a result of social interactions with older birds. The young males in that study learned more songs from adults that were present throughout the young birds' first year than from those that 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 that 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 that survive the winter because those males are on average more vigorous in the young male's natal summer than are those that do not survive. 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 that survive into his first spring because he learns the songs of these neighbouring males after settling next to them in the autumn 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 summer 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 groupmate song type better than any of the tutors' song types. Subjects were unable to hear each other sing until the autumn, so any influence that subjects had on each other must have occurred during the later period. Thus our 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 favour of this hypothesis because one young bird learned a song invented by a groupmate that 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 expose young males to a new set of tutors during the later stage of song development.

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References

Arcese, P. 1987. Age, intrusion pressure and defence against floaters by territorial male song sparrows. *Animal Behaviour*, **35**, 773–784.

Arcese, P. 1989a. Territory acquisition and loss in male song sparrows. *Animal Behaviour*, **37**, 45–55.

Arcese, P. 1989b. Intrasexual competition, mating system and natal dispersal in song sparrows. *Animal Behaviour*, **38**, 958–979.

Baptista, L. F. & Morton, M. L. 1988. Song learning in montane white-crowned sparrows: from whom and when. *Animal Behaviour*, **36**, 1753–1764.

Beecher, M. D. 1996. Birdsong learning in the laboratory and field. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 61–78. Ithaca, New York: Cornell University Press.

Beecher, M. D., Campbell, S. E. & Burt, J. M. 1994a. Song perception in the song sparrow: birds classify by song type but not by singer. *Animal Behaviour*, **47**, 1343–1351.

Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994b. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences U.S.A*, **91**, 1450–1454.

Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. 1996. Repertoire matching between neighboring songbirds. *Animal Behaviour*, **51**, 917–923.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000. Song-type matching between neighbouring song sparrows. *Animal Behaviour*, **59**, 21–27.

Byers, B. E. & Kroodsma, D. E. 1992. Development of two song categories by chestnut-sided warblers. *Animal Behaviour*, **44**, 799–810.

Chaiken, M., Gentner, T. Q. & Hulse, S. H. 1997. Effects of social interaction on the development of starling song and the perception of these effects by conspecifics. *Journal of Comparative Psychology*, **111**, 379–392.

Clayton, N. S. 1987. Song tutor choice in zebra finches. *Animal Behaviour*, **35**, 714–721.

Cunningham, M. A. & Baker, M. C. 1983. Vocal learning in white-crowned sparrows: sensitive phases and song dialects. *Behavioral Ecology and Sociobiology*, **13**, 259–269.

DeWolfe, B. B., Baptista, L. F. & Petrinovich, L. 1989. Song development and territory establishment in Nuttall's white-crowned sparrows. *Condor*, **91**, 397–407.

Horning, C. L., Beecher, M. D., Stoddard, P. K. & Campbell, S. E. 1993. Song perception in the song sparrow: importance of different parts of the song in song type classification. *Ethology*, **94**, 46–58.

Kroodsma, D. E. & Pickert, R. 1984. Sensitive phases for song learning: effects of social interaction and individual variation. *Animal Behaviour*, **32**, 389–394.

Kroodsma, D. E., Albano, D. J., Houlihan, P. W. & Wells, J. A. 1995. Song development by black-capped chickadees (*Parus atricapillus*) and Carolina chickadees (*P. carolinensis*). *Auk*, **112**, 29–43.

Marler, P. 1970. A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative and Physiological Psychology*, **71**, 1–25.

Marler, P. 1990. Song learning: the interface between behaviour and neuroethology. *Philosophical Transactions of the Royal Society of London, Series B*, **329**, 109–114.

Marler, P. & Peters, S. 1981. Sparrows learn adult song and more from memory. *Science*, **213**, 780–782.

Marler, P. & Peters, S. 1982a. Developmental overproduction and selective attrition: new processes in the epigenesis of birdsong. *Developmental Psychobiology*, **15**, 369–378.

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

Marler, P. & Peters, S. 1987. A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*, a case of age-limited learning. *Ethology*, **77**, 125–149.

Marler, P. & Peters, S. 1988a. The role of song phonology and syntax in vocal learning preferences in the song sparrow, *Melospiza melodia*. *Ethology*, **77**, 125–149.

Marler, P. & Peters, S. 1988b. Sensitive periods for song acquisition from tape recordings and live tutors in the swamp sparrow, *Melospiza georgiana*. *Ethology*, **77**, 76–84.

Nelson, D. A. 1992. Song overproduction and selective attrition lead to song sharing in the field sparrow (*Spizella pusilla*). *Behavioral Ecology and Sociobiology*, **30**, 415–424.

Nelson, D. A. & Marler, P. 1994. Selection-based learning in bird song development. *Proceedings of the National Academy of Sciences U.S.A*, **91**, 10 498–10 501.

Nelson, D. A., Whaling, C. & Marler, P. 1996. The capacity for song memorization varies in populations of the same species. *Animal Behaviour*, **52**, 379–387.

Nielsen, B. M. B. & Vehrencamp, S. L. 1995. Responses of song sparrows to song-type matching via interactive playback. *Behavioral Ecology and Sociobiology*, **37**, 109–117.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 1999. Ecological correlates of song learning in song sparrows. *Behavioral Ecology*, **10**, 287–297.

O'Loghlen, A. L. & Rothstein, S. I. 1993. An extreme example of delayed vocal development: song learning in a population of wild brown-headed cowbirds. *Animal Behaviour*, **46**, 293–304.

Payne, R. B. & Payne, L. L. 1993. Song copying and cultural transmission in indigo buntings. *Animal Behaviour*, **46,** 1045–1065.

Payne, R. B. & Payne, L. L. 1997. Field observations, experimental design, and the time and place of learning bird song. In: *Social Influences on Vocal Development* (Ed. by C. T. Snowdon & M. Hausberger), pp. 57–84. Cambridge: Cambridge University Press.

Podos, J., Peters, S., Rudnicky, T., Marler, P. & Nowicki, S. 1992. The organization of song repertoires of song sparrows: themes and variations. *Ethology*, **90,** 89–106.

Slater, P. J. B., Richards, C. & Mann, N. I. 1991. Song learning in zebra finches exposed to a series of tutors during the sensitive phase. *Ethology*, **88,** 163–171.

Slater, P. J. B., Jones, A. & ten Cate, C. 1993. Can lack of experience delay the end of the sensitive period for song learning? *Netherlands Journal of Zoology*, **43,** 80–90.

Stoddard, P. K., Beecher, M. D., Campbell, S. E. & Horning, C. 1992a. Song-type matching in the song sparrow. *Canadian Journal of Zoology*, **70,** 1440–1444.

Stoddard, P. K., Beecher, M. D., Loesche, P. & Campbell, S. E. 1992b. Memory does not constrain individual recognition in a bird with song repertoires. *Behaviour*, **122,** 274–287.