



Song Learning in Song Sparrows: Relative Importance of Autumn vs. Spring Tutoring

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Received: January 2, 2010
Initial acceptance: February 21, 2010
Final acceptance: March 22, 2010
(S. Foster)

doi: 10.1111/j.1439-0310.2010.01782.x

Abstract

We examined 'late' song learning in song sparrows (*Melospiza melodia*), i.e., song learning that occurs after the first few months, or classical sensitive period, of the natal summer. Fledgling juveniles were brought into the laboratory at 2–3 mo of age and exposed to computer-simulated song tutors in three different time periods: late in the natal summer, the autumn, and the next spring. As expected, the birds' final repertoires consisted mostly of songs heard in the field, but 30% of the birds' songs were influenced by songs heard in the laboratory (selective retention) and another 8% were learned *de novo* in the laboratory. Parallel results were obtained for a second group of birds who received laboratory tutoring only in the spring. In fact, the results suggested that autumn tutoring may even be inhibitory. We conclude that the songs a young song sparrow hears in his first spring may be critical to his final repertoire development, indicating that the song learning process in song sparrows is longer and more flexible than previously supposed.

Introduction

In many songbirds, the memorization phase of song learning is restricted to a 'sensitive period' in the bird's first year (review in Beecher & Brenowitz 2005; Catchpole & Slater 2008). In a classic example, Marler (1970) showed that white-crowned sparrows (*Zonotrichia leucophrys*) have a sensitive period for song learning at 15–50 d of age. Although it appears that this sensitive period may be extended in this species when live tutors are used in place of tape recordings (Baptista & Petrinovich 1986), song memorization in this species is typically completed in the natal summer. Even in such a 'closed-ended learner,' however, song learning can continue in other ways beyond the classical sensitive period of the natal summer. Nelson & Marler (1994) showed that song learning in white-crowned sparrows continued into the following spring, but that at that time it took on a different, 'selective' form: having memorized several different conspecific songs the previous (natal)

summer, the bird retained only the one song that best matched the songs sung by his spring-time and future neighbors. Nelson and Marler called this process 'selective attrition,' emphasizing which songs were eliminated, but it could equally well be called 'selective retention,' emphasizing which song is kept. Nelson and Marler assumed that in the field, selective attrition results from the young bird's attempts to song-match his new territorial neighbors, i.e., to reply with a song type that matches or is similar to his neighbor's song. This assumption is consistent with the observation that sharing songs with territorial neighbors is generally helpful for territorial birds, particularly in the context of counter-singing interactions (Beecher et al. 1997; Searcy & Beecher 2009). We should note that while the white-crowned sparrow case is the most widely cited example of song learning, the song learning process varies widely in different songbird species. In particular, in some songbirds song learning continues after the bird's first year (O'Loughlen & Rothstein 2002;

Beecher & Brenowitz 2005; Catchpole & Slater 2008).

Our study species, the song sparrow, *Melospiza melodia*, has been described as a fairly typical closed-ended learner, and differs from the white-crowned sparrow mainly in that song sparrows males have not one song but a song repertoire of 6–12 different songs. Research on song sparrows to date has indicated that the sensitive period for song memorization concludes in the natal summer (Marler & Peters 1987), that late learning continues into the following spring mainly in the form of selective attrition (Nordby et al. 1999, 2007), and that the song repertoire does not change in subsequent years (Nordby et al. 2002). We should note that numerous differences in singing in eastern and western populations of song sparrows have been found, which have suggested to some that the song learning process as well may be different in the two subspecies (Hughes et al. 1998; and see review in Beecher 2008).

In the present study, we examine late song learning in western song sparrows, i.e., song learning occurring in the bird's first year of life after the classically defined sensitive period has ended. We ask whether late learning occurs primarily in the autumn of the bird's natal year, or the following spring, shortly before the bird begins his first breeding season. We are guided by the hypothesis that it is advantageous for a bird beginning his first breeding season to have songs that he shares with (that are very similar to those of) his territorial neighbors. Shared songs play a key role in neighbor–neighbor interactions, with effective communication depending on the ability of a male to sing song types that match those of his neighbors (review in Beecher 2008). Song sharing with neighbors is a good predictor of territorial success in western song sparrows (Beecher et al. 2000; Wilson et al. 2000), better in particular than song repertoire size, and so we start with the hypothesis that song learning in song sparrow is adapted to maximize the number of songs he shares with birds who will be his territorial neighbors in his first breeding season.

Song learning occurring in the late-learning period (in our population from mid-July to the following March or April) can be of two kinds. The simplest possibility is that late-learned songs are learned *de novo*, just like songs learned in the first few months. Alternatively, as Nelson and Marler have suggested, songs heard late may influence which of the earlier memorized songs the bird keeps ('selective retention') and which he drops ('selective attrition'). Our ability to infer whether a particular example of late

song learning is a result of selective retention rather than *de novo* learning requires that the pool of early tutor songs be different from the pool of late tutor songs. This condition generally does not occur in sedentary populations such as ours, because the adult singers available for late learning will come from the same pool that was available in the natal summer. However, we can arrange these circumstances in the laboratory. If the two tutor pools are distinct, we can conclude that a juvenile has learned a song *de novo* late if it resembles a song from the late tutor pool better than it does any song from the early tutor pool. If on the other hand, it does not closely resemble any song in the late pool, we can still conclude that this song was selectively retained if it (a) resembles some song in the late pool better than the songs the subject dropped (selective attrition, e.g., Nelson 1992, 2000; Nordby et al. 2007), or (b) resembles a late pool song better than it does other 'control' tutor songs the bird did not hear, or were heard in a period hypothesized to be unfavorable for song learning. In the present study, we used the second criterion. We brought birds in from the field as juveniles after the approximate end of the early sensitive period and then exposed them in the laboratory to a different set of songs across different phases of late learning, and in particular, in autumn and spring. Given our hypothesis that birds should seek to increase sharing with spring neighbors, our prediction was that subjects would preferentially learn songs presented in the spring, either *de novo* or by selective retention, rather than in autumn.

We have previously identified late learning in field studies of our western population of song sparrows: first-year birds learn more songs from older birds that are present both in the natal summer and the following spring than they do from adults who do not survive overwinter (Nordby et al. 1999). However, because this was a field study of a sedentary population, we could not tell whether the late learning was because some songs that had been heard and memorized in the natal year were heard again the following spring and thus selectively retained, or because these songs were heard for the first time the following spring and learned *de novo* at that time. In a laboratory experiment (Nordby et al. 2001), we exposed hand-raised song sparrows to six live song tutors, two present in June and July ('early-only' tutors), two present in October and again January through March ('late-only' tutors), and two present throughout (except for November and December). The two late-only tutors shared no songs with the other four tutors present early, thus

we could identify *de novo* learning if it occurred. The subjects actually learned the most songs from the two late-only tutors, and the fewest from the two early-only tutors, and the analysis identified that the learning was almost entirely *de novo* learning. Since the late-only tutors sang very little in October, we suspected that the late learning had occurred when all tutors sang at high rates from January through March, but our design did not allow us to distinguish between what was learned in the autumn and what was learned in the spring.

A young song sparrow presumably has to start song learning when he fledges in May or June, but several factors might favor pausing the song learning process in mid-summer and resuming the following spring. First, in our western, sedentary study population, not much good adult song is heard in this period. Adult singing tapers off by about Jul. 15, and essentially ceases in the month of August when adults are in full molt. Adult singing revives in September, but generally occurs at relatively low levels, and also is sometimes somewhat degraded compared with breeding-season song (Smith et al. 1997). Moreover, in some resident populations (including ours), migratory conspecifics will appear in the late summer and autumn, and presumably it would be disadvantageous for a young resident male to learn these population incorrect songs. Finally, much of the autumn singing we hear is by advanced hatch-year juveniles (sub-song and sometimes early plastic song), and these songs too would be poor models of population-appropriate song. Adult singing virtually ceases again by mid October and does not revive until after the winter solstice. Singing rates are generally high from January on, particularly in periods of warm or sunny weather.

A second reason that song learning in spring might be favored over song learning in the late summer and autumn follows from the hypothesis that it is advantageous to have songs shared with birds who will be your eventual territorial neighbors: adult birds encountered in the spring are much more likely to become the young bird's territorial neighbors than are those encountered in the earlier period. Many of the adult males the young bird encounters in late summer or autumn will not survive the winter: in our population, depending on the severity of the winter, 30–50% of adults do not survive. In contrast, the adult males the young bird encounters in January or February are highly likely to survive into the breeding season, and, moreover, they are more likely to be future territorial neighbors, as by this time the young song sparrow has

decreased the size of his home range and is it attempting to establish his breeding territory (Nordby et al. 1999; Templeton, C. N., Campbell, S. E. & Beecher, M. D., unpublished data). If song memorization concludes when the bird has 'enough' songs, as appears to happen in marsh wrens (Kroodsma 1978; Kroodsma & Pickert 1980), then it might behoove the young bird to stop memorizing songs in mid-summer, before he has reached 'capacity,' and resume in the spring when the birds he encounters are very likely to be his future neighbors.

The present study was designed to determine the relative importance of two different phases of late song learning: autumn and spring. We brought young birds (estimated 2–3 mo old) in from the field in early July and exposed them to varying schedules of computer-simulated tutor song playback in the laboratory. This procedure gives a strong advantage to the sensitive early learning phase, for a young bird that has heard songs from adult birds in the real world for a month or two will be expected to retain those songs in preference to the songs he later hears from loudspeakers in a laboratory chamber. Therefore, we expected that late learning would be limited, and that probably most of it would reflect selective retention of songs memorized in the field rather than learned *de novo* from our computer tutors. We tested two specific hypotheses about late learning. The 'dosage' hypothesis was that the young bird would learn more songs from song tutors he heard the most, irrespective of season. The 'spring effect' hypothesis, based on the arguments given above, was that the young bird would learn more songs from song tutors he heard in the spring than from those he heard in the autumn.

Methods

Study Design

To evaluate the dosage and spring effect hypotheses, 17 young song sparrows were brought in from the field near the end of the early learning period (mid-July) and were exposed to a completely new set of songs in the laboratory. Digitized songs were presented in a bird's chamber, from four independent loudspeakers, each representing one 'virtual tutor' computer simulation of a singing adult bird (designated Tutors 1, 2, 3, and 4; further details below). Twelve of the subjects (group 1) were exposed to the virtual tutors from Jul. 20 through Nov. 1 (summer–autumn tutoring phase), and again Dec. 24 through Mar. 23 (spring tutoring phase). Five

additional subjects (group 2) heard no tutor songs throughout the summer–autumn tutoring phase but were tutored like group 1 during the spring tutoring phase.

The four virtual tutors each represented a different combination of seasonal presentations. For group 1 birds, Tutor 1 was heard only in the late summer (Jul. 20–Aug. 31), Tutor 2 was heard in late summer and again in the autumn (Sept. 1–Nov. 1), Tutor 3 was heard in late summer and again in the spring (Dec. 24–Mar. 23), and Tutor 4 was heard in late summer, autumn, and spring. The reason that all tutors were presented in the late summer, i.e., were not part of the experimental manipulation, was because we feared that without summer tutoring in the laboratory, the advantage to the field tutors would be overwhelming, and we would get no laboratory learning at all. Hence, our experimental manipulation was only with respect to the autumn and spring periods (one tutor heard in both periods, one in spring only, one in autumn only, and one in neither). Group 2 birds, who received no late summer (or autumn) tutoring, were included in part to provide a check on this fear.

The four virtual tutors were each assigned one of four unique song repertoires (A, B, C, and D) derived from recorded adult song sparrow songs. The tutor-repertoire assignments were counter-balanced across subjects (for one subject, Tutor 1 was assigned repertoire A, while for another subject Tutor 1 had repertoire B, etc.; see Table 1).

Considering just the group 1 subjects, the predictions from hypothesis 1 (dosage) and hypothesis 2 (spring effect) are shown in Fig. 1. In addition, if neither summer nor autumn tutoring is effective, we

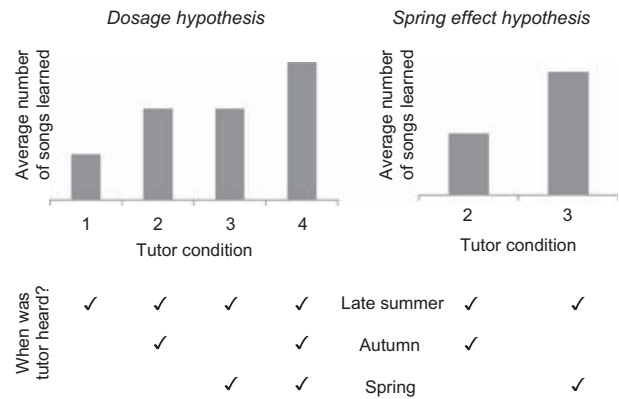


Fig. 1: Relative learning scores predicted by our two late-learning hypotheses for group 1 birds. Note that the two hypotheses are independent, i.e., the Dosage hypothesis makes no prediction about Tutor 2 vs. Tutor 3 (autumn vs. spring), whereas the spring effect hypothesis predicts that learning will be greater for Tutor 3 (spring) than Tutor 2 (autumn).

would expect the group 2 birds to learn as many laboratory songs as the group 1 birds.

Subjects

We brought 12 juvenile male song sparrows in from a local sedentary population in Discovery Park, Seattle WA between Jul. 13th and 17th, 2007; these birds we call Group 1. We captured an additional five birds during the last week of July; we refer to these birds as Group 2. All of the birds were independent from their parents and approximately 2–3 mo of age at the time (estimated average hatch dates 15 April–15 May). Subjects were maintained on a Seattle photoperiod using an astronomical timer. At the end of the study, birds were transferred to flight aviaries for 2 wk and then released at the capture site. Some of the birds were seen on territory in the field the following year.

Each subject was individually housed in a cage within an acoustic isolation chamber. Six group 1 and all five group 2 subjects were kept in smaller cages (dimensions 23 × 26 × 40 cm) within small isolation chambers, and the remaining six group 1 subjects were housed in larger cages (dimensions 30 × 30 × 60 cm) within large chambers. Each group 1 small-chamber subject was treatment matched to a large-chamber subject. Each chamber was equipped with a microphone, and four amplified speakers fixed to the four corners of the chamber. Output from each speaker was independently controlled by a computer running the virtual tutor playback software written by John Burt.

Table 1: Experimental design. Two of 12 subjects from group 1 are shown, as are two of five subjects from group 2

	Virtual tutor condition	Summer	Autumn	Spring	Repertoire
Group 1	1	✓			A
Subject 1	2	✓	✓		B
	3	✓		✓	C
	4	✓	✓	✓	D
Group 1	1	✓			C
Subject 2	2	✓	✓		D
	3	✓		✓	A
	4	✓	✓	✓	B
Group 2	5			✓	A
Subject 1	5			✓	B
Group 2	5			✓	C
Subject 2	5			✓	D

Stimuli and Apparatus

Songs used for tutoring playback in this study were extracted from high quality recordings of males used in a previous laboratory learning experiment. The songs were fully crystallized and were from a combination of live tutors captured in Skagit, WA (approx. 95 km from the Seattle population), and the subjects of the prior experiment who learned from them. The population distinctiveness of the Skagit-derived tutoring songs, compared with Seattle songs, made it easier for us to distinguish songs the subjects learned *de novo* in the experiment from songs the subjects had memorized in the field from their natal population (we had recorded virtually all the songs of birds in the population present in the subject's hatching summer). Songs were prepared for use as tutoring stimuli using the Syrinx-PC sound analysis application (John Burt, <http://www.syrinxpc.com>).

Tutoring songs were organized into four distinct repertoires (A, B, C, and D) for the four computer-simulated ('virtual') playback tutors. Each repertoire consisted of nine different song types, with 8–10 unique renditions of each type. Playback renditions were chosen to represent the song type as sung by the original singer. Thus, we tried to create repertoires that were typical of a real song sparrow (Stoddard et al. 1988; Podos et al. 1992). The song types in each repertoire were selected so as to include shared songs across all pairs: specifically, each virtual tutor shared two different song types with each of the three other tutors. Thus, each tutor had a repertoire consisting of six shared songs and three unique songs. Song sharing is common in our population and creating repertoires with shared song types allowed us to simulate natural singing interactions of real adult males (Beecher 2008; Burt & Beecher 2008). Each of the four virtual tutors was associated with its own particular speaker of the four in the chamber throughout the year-long experiment.

The virtual tutor song tutoring program, written in MATLAB by John Burt, presented a subject with songs from two virtual tutors at a time on a given day. Tutoring playback began in the morning 15 min after chamber lights turned on, and continued throughout the day, until a total of 200 songs had been sung by each tutor (the song limit was usually reached between 10:00 and 13:00 h). In general, the virtual tutor model was programmed to sing like a live song sparrow: cycling through its repertoire during solo singing bouts, pausing periodically, and counter-singing with its virtual tutor 'neighbor.' During counter-singing bouts, virtual tutors used

shared types to repertoire match and type match each other, as is common among western song sparrows. We are building evidence that listening to these sorts of adult interactions is important for song learning (Beecher et al. 2007; Templeton et al. 2009). All song types, and, within types, all renditions of a type, were presented with equal frequency. During and after tutoring sessions, a microphone in each chamber recorded the subjects' singing. In this experiment, the virtual tutors interacted only with each other and did not interact with subjects.

Song Learning Analysis

We examined recordings of each subject from the last 3 d of his spring tutoring sessions in March. Our previous studies have shown that song sparrows' songs crystallize by early March (Nordby et al. 2000, 2001). Each tutee's repertoire was independently scored against the four virtual tutors' repertoires by three judges (BN, MB, and JB), and the consensus judgment taken. In accordance with the theory of song learning described in the Introduction, we differentiated between two kinds of song learning. True 'copies,' evidenced by close similarity of the fine details of tutor and subject songs, were considered to reflect *de novo* learning. 'Similarity matches,' in contrast, were similar only in overall organization, and hypothesized to reflect selective retention (Nelson & Marler 1994) of songs which subjects memorized earlier in the field. Examples of true copies and similarity matches are shown in Fig. 2. In similarity matches, the general pattern of organization of the elements in the songs is similar between tutor and subject (which gives the two songs a similar sounding cadence), but the actual elements are different. In contrast, in true copies the elements themselves and the order in which they occur, match the tutor song precisely (Fig. 2a). For example, in the similarity match shown in Fig. 2b, both songs begin with two buzzes, followed by a low-high pair of pure notes, another buzz, a trill, a high note complex (upsweep followed by down sweep), and a low buzz; a few extra elements in the upper song are not present in the lower song. Despite the similarity of the overall pattern of song elements, however, none of the elements are identical; the trills are probably the most similar, but the trill rate is higher in the upper song. We assume that the song was heard in the field and memorized, and then was selectively retained because of its similarity to one of the lab tutor songs. Selective retention has been

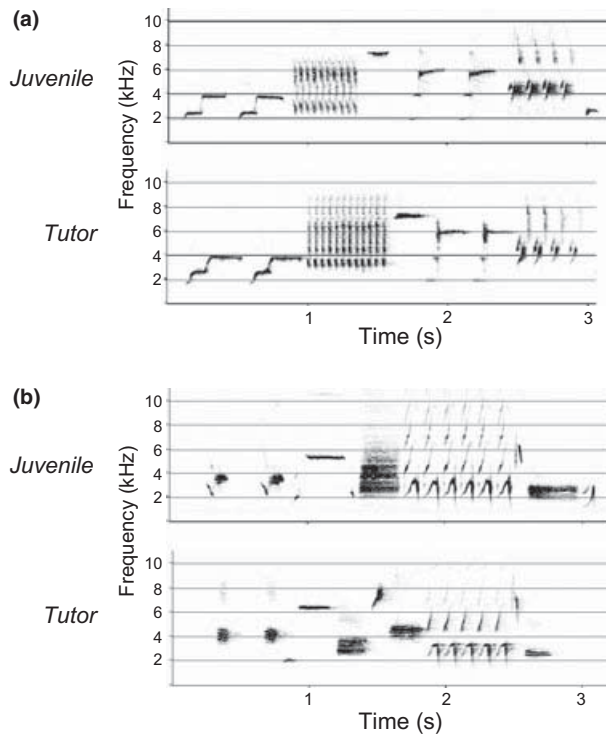


Fig. 2: Two examples of the two types of song learning and the score associated with each. (a) Example of a full match with computer tutor's song (*de novo* memorization), score 1.0 for tutor. (b) Example of a similarity match (inferred selective retention), score 0.5 for tutor.

detected this way in several previous studies (Nelson 1992, 2000; Nordby et al. 2007).

For each subject, we counted and weighted the number of songs learned from each tutor as follows. A subject song classified as a true copy of a unique lab tutor song (a song type shared with no other lab tutor), counted as one song learned from that tutor. A subject song classified as only a similarity match to a unique lab tutor song was attributed to that tutor but given only half weight (0.5); this can be thought of as splitting credit for the learned song between the lab tutor whose song it resembled and the unknown field tutor from whom the subject originally learned the song). Songs classified as copies of a tutor shared song were split between the

two tutors that shared that song (each counted 0.5) and songs classified as similarity matches to a shared song were split between the two lab tutors that shared that song (each counted 0.25). In unusual cases where a subject combined portions of two tutor songs to form a new song, the score was also divided equally among the two tutors. After scoring all subjects' songs, we compared the number of songs learned in each of the four tutor conditions for the group 1 birds.

Statistical Analysis

For the group 1 birds, we carried out two planned comparisons to test the 'dosage' and 'spring effect' hypotheses, as diagrammed in Fig. 2. We applied the planned comparisons to each subject by multiplying the subject's score for a given condition (Tutor 1, 2, 3, or 4) with the coefficient for that condition (Table 2) and summing these, so that each subject received a single score for each planned comparison. These scores were then compared with zero by means of a single-sample *t*-test. The two planned comparisons were orthogonal to each other, so we tested each at the significance level of 0.05 (Sokal & Rohlf 1995, pp 229–242). Because the two predictions were explicit as to direction, the statistical tests were one-tailed.

Results

Within Group 1

The 12 birds in group 1 crystallized a total of 113 songs. We classified 43 of them (38%) as learned from lab tutors or retained because of the influence of lab tutors: 34 (30% of the total) were selectively retained and nine (8% of the total) were learned *de novo*.

The first planned comparison provided no support for the dosage hypothesis, ($t = 0.69$, $p = 0.26$, Fig. 3). The spring effect hypothesis, however, was supported by the test of the second planned comparison ($t = 2.16$, $p < 0.03$, Fig. 3). Thus, subjects had a higher learning score for computer tutors that they

	Tutor 1 (late summer only)	Tutor 2 (late summer and autumn)	Tutor 3 (late summer and spring)	Tutor 4 (all three seasons)
Hypothesis 1: dosage Spring = Autumn > 0	-2	0.5	0.5	1
Hypothesis 2: spring effect Spring > Autumn	0	-1	1	0

Table 2: Hypotheses and coefficients for planned comparisons

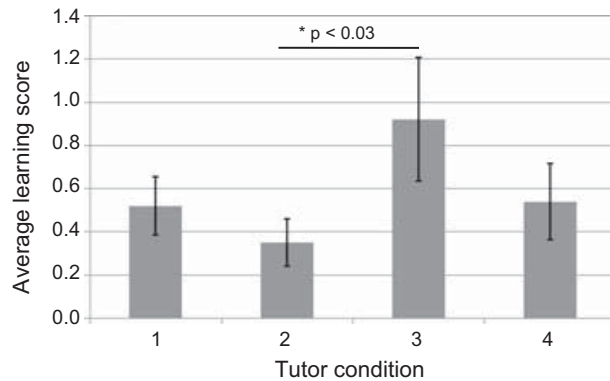


Fig. 3: The results do not support the dosage hypothesis but do support the spring effect hypothesis (Tutor 3, spring, >Tutor 2, autumn). Group 1 birds.

heard only in the spring than those they heard only in the autumn (note that all tutors were also heard in late summer).

Group 1 vs. Group 2

Group 2 birds, who heard no songs in the laboratory from the time they arrived in the laboratory in July until Dec. 24, nevertheless learned more songs from laboratory tutors than did group 1 birds (tutor scores 2.50 vs. 2.17 per bird) but the difference was not significant ($t = 0.84$, $p = 0.22$). Group 2 birds crystallized a total of 39 songs: 18 (46% of the total) were selectively retained, and three (8% of the total) were learned *de novo*.

Discussion

In this study, we sought to refine our understanding of late learning in song sparrows, and to determine the relative importance of spring learning vs. autumn learning. We presented virtual tutors in different combinations to 17 juveniles and examined subjects' crystallized repertoires for evidence of song learning. For the 12 group 1 birds, we found no evidence for the dosage hypothesis that birds are more likely to learn songs they hear more. Our results supported the second hypothesis that spring tutoring is more influential than autumn tutoring: subjects' repertoires had more in common with the songs they heard in the spring than with the songs they heard in the autumn. An additional five subjects heard computer tutors in the spring only, yet they learned a comparable number of songs. These two sets of results taken together imply that at least under the conditions of this experiment, late learn-

ing – whether it is selective retention of earlier memorized songs or *de novo* learning – occurs largely, and perhaps entirely, in the spring.

To the best of our knowledge, only one study has examined a species known to add songs after the natal summer and asked whether those songs are learned in the autumn or spring period. Thielcke & Krome (1991) captured juvenile chaffinches in August and September (late summer – early autumn) and tape-tutored them with chaffinch songs on Oct. 15 to Nov. 13, Dec. 18 to Jan. 16, or Mar. 15 to Apr. 13. All birds had acquired species-typical song repertoires (one to five songs) by the time they were brought into the laboratory, so none of them 'needed' to add a song to their repertoires. Nevertheless, although no birds learned the autumn song, one bird learned the winter song, and seven of 10 birds learned the spring song. These results suggest that chaffinches are insensitive to song heard in the late summer or autumn, a pattern similar to what we have found for song sparrows.

Closer inspection of our results (Fig. 3) actually suggests that tutoring in the late summer and autumn may have had an inhibitory effect, since Group 1 birds learned less from tutors heard in the late summer and autumn ('Tutor 2') than they did from tutors heard in the late summer only ('Tutor 1'), and less from tutors heard in the late summer, autumn, and spring ('Tutor 4') than they did from tutors heard in the late summer and spring only ('Tutor 3'). As with the group 2 vs. group 1 difference (more songs learned by birds who heard nothing from early summer until next spring), these differences are not significant but all three trends are in the same direction, suggesting a learning bias against songs heard in late summer and autumn. This hypothesis deserves future study.

The argument we advanced in the Introduction that learning song in late summer or autumn might be selected against is even stronger in the case of migratory populations. We have studied such a migratory population 80 km away from our main study population in Seattle, but 900 m higher (at Snoqualmie Pass, WA, Hill et al. 1999). In this population neighboring song sparrows share songs, but because they have left the population by late summer, they do not have the opportunity to learn from future neighbors after departure. Indeed, in some migratory populations, birds begin to leave the breeding grounds by mid-July and are migrating or on the wintering grounds by autumn. Although we have little natural history information on the singing behavior of birds on the winter migration grounds,

we can predict that if it is advantageous for birds to have population-typical songs during the breeding season – and there is considerable evidence on this point in song sparrows (Beecher et al. 2000; Searcy et al. 2003) – then learning songs during late summer and autumn would be selected against. In a migratory species, one might predict that birds should ignore, or actively avoid learning, songs heard in late summer or autumn, and restrict their late song learning to the following spring, when they will have returned to the breeding grounds. Again, future studies should contrast late summer and autumn learning with spring learning, ideally in combination with a comparison of migratory and sedentary populations.

Finally, we should comment on one design feature of the present experiment. The use of shared songs among our four virtual tutors was intended to add verisimilitude to our computer (virtual) tutoring stimulus. This feature was realistic, reflecting the fact that neighboring song sparrows in our population typically share songs, and use them preferentially in singing interactions (Burt & Beecher 2008), but it had the unfortunate side-effect of blurring the determination of which songs were learned in which time period. For example, a song shared between an autumn tutor and a spring tutor had to be credited one-half to each when in fact it might have been learned only from the spring tutor. This problem is clearest in the case of group 2 birds for whom two of the virtual tutors were heard in the spring only and two of the tutors were never heard at all. Although their learning scores were higher for the virtual tutors they heard than for those they never heard, the never-heard tutors nonetheless sometimes earned 'credit' based on song sharing. Thus, the design we used was conservative with respect to our hypothesis and so we may have underestimated the true difference between spring and autumn tutoring.

In conclusion, we have demonstrated that spring is the most salient late-learning period for song sparrows. In addition, our group 2 birds provide the first definitive evidence that young song sparrows can learn new songs *de novo* as late as the beginning of their first mating season. These results argue for the importance of future research on a fine-scale analysis of the timing of late learning, ideally in the context of a comparison of migratory and sedentary populations.

Acknowledgements

This research was supported by grants to MDB from National Science Foundation (IOS-0733991) and the

University of Washington Bridge Fund. CNT was supported by an NIH Auditory Neuroscience traineeship and a UW Biology Tunicliffe fellowship.

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