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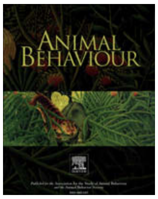

Song development in the grasshopper sparrow, *Ammodramus savannarum*

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Adult male grasshopper sparrows sing two structurally and functionally distinct songs: buzz song and warble song. To investigate how these songs develop, we tutored three groups of young males in the laboratory: one with recordings, one with live adult tutors and one with no song (isolate birds). We used visual scoring of spectrograms, principal components analysis of acoustic measures and spectrogram cross-correlation to analyse the results. Tape-tutored and live-tutored birds developed structurally normal buzz songs and largely normal warble songs. Isolate birds developed moderately normal buzz songs along with one or two more atypical songs. Neither buzz songs nor warble songs were accurately imitated by any of the tape-tutored birds. Live-tutored birds imitated buzz songs, but not warble songs, more closely than did tape-tutored birds. We also examined buzz songs in a population of grasshopper sparrows in the field. Comparisons of buzz songs of yearling males with those of their social fathers and with those of their first-breeding-year territorial neighbours indicate that sons do not imitate songs of their social fathers, and imitate songs of their immediate territorial neighbours only to a limited degree. Overall our results suggest that grasshopper sparrow song does not develop by imitation but that exposure to conspecific song is important for normal song development. Differences in development of the two song types may relate to both acoustic structure and function of these songs.

Studies of songbird vocal development have documented considerable variation across species in what is learned in song, and when. Examples of features of song learning that vary across species include the extent to which songs are imitated versus improvised or invented, the tendency to mimic other species, the number of songs that are learned, and the stages of life at which song learning occurs (e.g. Kroodsma 1988; Slater 1989). Broadly, these song-learning features are thought to vary because each species has a unique evolutionary history and set of life history traits. Birdsong ethologists are interested in understanding this variation in a functional sense. Selection is expected to optimize the relationship between ecological or life history features and the specific mechanisms by which song learning proceeds.

The extent of imitation in song development may be correlated with breeding site fidelity, and thus the likelihood that an individual bird will interact with the same neighbours through time (Kroodsma et al. 2002). In *Cistothorus* wrens, for example, male North American sedge wrens, *C. platensis*, display low breeding site fidelity within and between years, share few song types with neighbours (Kroodsma & Verner 1978), and have been found to improvise or invent songs when tutored in the laboratory (Kroodsma et al. 1999a). Two other species, the marsh wren, *C. palustris* (Verner 1976) and the Merida wren, *C. meridae* (Kroodsma et al. 2001) show higher breeding site fidelity and greater song sharing between neighbouring males, suggesting that song develops by imitation in these two species. Indeed, when tutored in the laboratory, marsh wrens were found to imitate song models (Kroodsma & Pickert 1984). Populations of sedge wrens in Central and South America, which are sedentary, also show neighbour song sharing and microgeographical song variation and thus are presumed to learn song by imitation (Kroodsma et al. 1999b, 2002). In combination, these studies indicate that among *Cistothorus* wrens, song develops by means other than imitation only in populations of wrens with low breeding site fidelity.

The grasshopper sparrow, *Ammodramus savannarum*, shows low breeding site fidelity in much of its range in North America (Vickery 1996). If a correlation between breeding site fidelity and song imitation holds generally across songbird families, this species would be expected to develop song by improvisation or invention. Investigating this question was one of our goals in the current study.

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Grasshopper sparrows and their song are interesting in several additional respects. First, songs of this species are unusually high-pitched (6–10 kHz) and contain an extremely rapid sequence of frequency- and amplitude-modulated notes (Fig. 1a). We investigated whether such high, rapid songs are learned by imitation, and if so, how accurately. Second, grasshopper sparrows are unusual among emberizids in that adult males sing two song types that differ in both structure and function (Vickery 1996). The primary song, identified here as the 'buzz song', consists of two to four very brief introductory notes at different frequencies, followed by a high-pitched, rapidly modulated sequence of notes (here, the buzz 'segment') lasting approximately 1 s (Fig. 1a). Buzz song is thought to serve both inter- and intrasexual territorial advertisement functions, based on (1) when it is produced in the season and breeding cycle (Smith 1959), (2) evidence that unpaired territorial males produce only this song type (B. Lohr, personal observation) and (3) the observation that the majority of songs given by males in response to song playback are buzz songs (Vickery 1996).

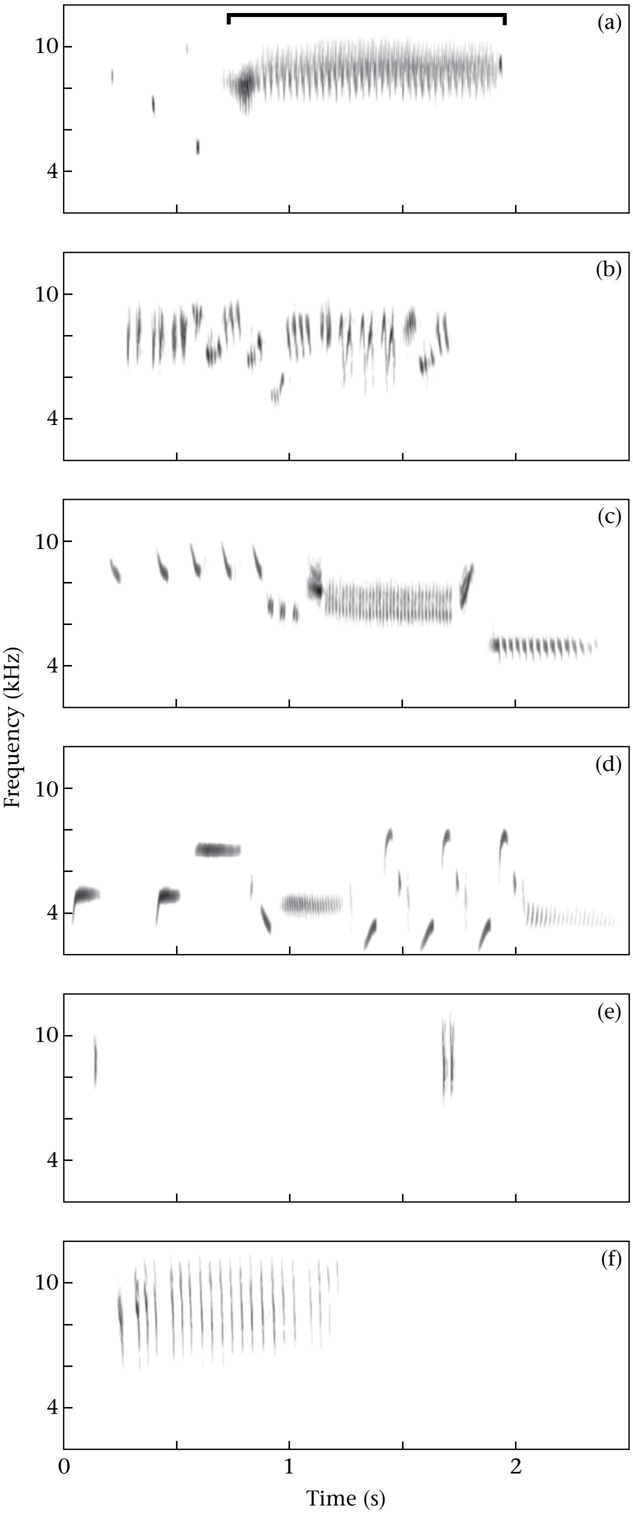

Figure 1. Six stimulus types used in laboratory experiments with young grasshopper sparrows: (a) grasshopper sparrow buzz song, with buzz segment indicated by bracket, (b) grasshopper sparrow warble song, (c) Savannah sparrow song, (d) song sparrow song, (e) grasshopper sparrow tic–tillic call, (f) grasshopper sparrow trill call. All six types were used in the early vocal response test. Types (a)–(d) were used as tutor models in the tape-tutoring experiment.

The second song type, or 'sustained song' of Vickery (1996), identified here as 'warble song', contains multiple short notes of variable structure (Fig. 1b). Some of these notes are repeated twice or more in sequence before the next note is produced, and the entire sequence may be repeated two or more times. The buzz and warble songs are often sung separately, but are also commonly produced with the buzz song immediately preceding the warble song. Because males sing the warble song much more frequently after pairing (Vickery 1996), and because a female call (the 'trill') and male warble songs may be produced in response to one another (Smith 1959), this song type may have female-directed functions such as pair bond maintenance or female reproductive stimulation. Each male grasshopper sparrow has an individually distinctive repertoire of one buzz song and one warble song (Smith 1959; Vickery 1996), both of which appear to remain stable over the course of a male's life.

The production of two functionally distinct song types is unusual in sparrows. While some sparrows produce 'flight songs' in addition to territorial signals (e.g. swamp sparrows *Melospiza georgiana*: Nowicki et al. 1991), the two song types in the grasshopper sparrow may be more analogous to the functionally distinct song categories produced by some New World warblers. In chestnut-sided warblers, *Dendroica pensylvanica*, for example, songs in one category are thought to serve as intrasexual signals and songs in the other as intersexual signals (Byers 1996a). Byers & Kroodsma (1992) documented differences in how chestnut-sided warblers learn songs of the two categories. In particular, they found that development of the intrasexual song was dependent on social interaction, while learning of the intersexual song was not. We wanted to investigate whether differences exist in learning of the two grasshopper sparrow song types, and if so, whether they parallel those observed in the chestnut-sided warbler, to the extent that the functional categories may be similar in these two species. We began by investigating early recognition of song types by fledgling grasshopper sparrows to determine whether we could find evidence for a predisposition to attend to one or both types of conspecific song for memorization. We then analysed the songs developed in a controlled laboratory setting using tape tutors, live tutors and isolate birds having no exposure to song. Finally, we assessed song imitation in a field setting with a banded population of grasshopper sparrows under long-term study, where both territorial neighbours and social fathers of second-year (SY) males could be identified.

METHODS

Subject Rearing and Care

Birds were collected as nestlings in 2004 and 2005 (details below), syringe-fed Kaytee Exact® Hand-Feeding Formula (Kaytee Products, Inc., Chilton, WI, U.S.A.) hourly during daylight for the first 2 weeks after collection, then gradually weaned to a diet of hardboiled egg mixed with Kaytee Nestling Food and Avia vitamins. Water and seed (5:1:1 canary seed, red millet and white proso millet) were made available during weaning. Once weaned, birds were fed ad libitum seed and water, and were given fresh food several days a week including soaked seed, fruit, vegetables, mealworms and vitamins. Baths were given three times a week, and housing and all procedures met the standards of The Ohio State University ILACUC. Room lighting timers were adjusted approximately every 5 days to follow the natural photoperiod for Columbus, Ohio, U.S.A. Survival of laboratory birds was 100% throughout the study, and upon the study's completion, all birds were transferred to researchers at other institutions, under Federal permits, for further study.

Sound Stimuli

We used six stimulus types in these experiments (Fig. 1). Grasshopper sparrow songs of both buzz and warble types ($N = 14$ each) were originally recorded in Ohio and Maryland except for one warble song from Montana. Savannah sparrow, *Passerculus sandwichensis*, and song sparrow, *Melospiza melodia*, songs ($N = 14$ each) were from geographically widespread locations in northern North America. Grasshopper sparrow calls of three types ($N = 4$ each) were recorded in Maryland, Ohio and Arizona: the 'tic' call, the 'tillic' call and the 'trill' call. The first two were assembled into tic–tillic stimuli consisting of a single, short 'tic' note followed 1.5 s later by a doublet 'tillic' note; both of these are alarm and contact calls. The trill call contains rapidly repeated frequency downsweeps, and is thought to function in announcing presence at the nest and maintaining the pair bond (Vickery 1996). Each stimulus was recorded from a different bird. Stimuli were originally recorded on open reel, analogue cassette or digital audiotape using a range of recording equipment; some stimuli were obtained from the archive of the Borror Laboratory of Bioacoustics at The Ohio State University. All stimuli were digitized in SIGNAL 3.1 or 4.0 (Engineering Design, Belmont, MA, U.S.A.) at a sample rate of 50 kHz, and either played directly from a PC or transferred to audiocassettes for use in tape-tutoring experiments (see below).

Fledgling Response to Playback

Subjects were 15 grasshopper sparrows collected as nestlings, 4–6 days old, from four nests in Queen Anne's County, Maryland, on 29–31 July 2004. An additional nestling, a 2-day-old runt, was present in one of the four broods collected. This bird survived to be included in the tape-tutoring study but was not tested for early response to playback.

We housed broods separately in $48 \times 25 \times 30$ cm cages until after fledging. At 12–13 days of age, individuals were housed singly inside sound-attenuating chambers (Industrial Acoustics Corporation, New York, NY, U.S.A.). Testing began on the third day after this transfer, when birds were 15–16 days old. On the day of testing, a bird heard sound stimuli at approximately hourly intervals between 0830 and 1400 hours Eastern Standard Time (EST).

Each fledgling heard six stimuli (Fig. 1): one each of normal grasshopper sparrow buzz and warble songs, songs of Savannah sparrow and song sparrow, and adult grasshopper sparrow tic–tillic and trill calls. Four exemplars of each stimulus type were used in the experiment. Each exemplar was presented to three or four subjects, and each subject heard a unique combination of exemplars with stimulus types presented in a unique sequence.

Stimuli were played using Syrinx-PC software (John Burt, Seattle, WA, U.S.A.; www.syrinxpc.com) on a PC laptop, and broadcast into the chambers through small loudspeakers (Radio Shack). We monitored trials in real time using headphones connected to microphones mounted in the sound chambers, and we simultaneously recorded all trials on audiocassette. Trials began with a 2 min preplayback period, after which stimuli were presented at 10 s intervals for 2 min (total 12 repetitions). Monitoring and recording continued for a 2 min postplayback period. We recorded the number of vocalizations produced by the fledglings throughout the trials.

We found no correlation between call rate during preplayback and during the 2 min playback period, so calls recorded during the playback period were not adjusted by the preplayback rate. In addition, calling rate was usually zero during the postplayback period, so only calls produced during the playback itself were analysed. Wilcoxon signed-ranks tests were used in pairwise comparisons of responses to different stimulus types.

Tape Tutoring

Following the playback tests, the 16 fledgings from 2004 remained in the individual sound chambers. Beginning at 20 days of age, they were tape-tutored daily for 60 days. Tutor songs included four types: normal grasshopper sparrow buzz and warble songs, Savannah sparrow songs, and song sparrow songs. All tutor exemplars were different from those used in the test of fledgling response to playback, but both sets of songs were included in the analysis of tutor effects (described below).

In the initial tutor series (August–October), six exemplars of each song type were used. These were presented in six blocks containing one exemplar of each tutor song type. The particular exemplars included in each block differed for each bird. Each block of four songs was presented for 10 days, such that birds heard different tutor exemplars at different ages. On each 60 min side of a 2 h cassette tape, all four songs in a block were recorded for 13 min at a rate of five songs per min, with 2 min silent intervals between song types. The four songs were recorded in different orders on sides A and B of each tape, and both sides of the tape were played once per day, at various times in the morning (before 1200 hours EST). The first side of the tape played each day was alternated, so that the first song heard was not the same every day. The order of song types on each side of the tape varied across birds, but was the same for all blocks within birds. After autumn tutoring ended, we genetically sexed all birds using the method of Griffiths et al. (1998). The seven males remained in their sound chambers through the winter, and beginning on 25 January, we recorded each of them twice weekly for an hour in the morning.

A new tutor series began on 9 February 2005. In this spring tutoring, the same four types of songs were used as in the autumn tutoring, but each bird now heard two exemplars of each type, both of them novel. Not all birds heard the same two exemplars. Each side of a 2 h tape contained one exemplar of each song type, and we alternated the first side played each day. Songs were presented at a rate of five songs per min for 11 min, with 4 min of silence between song types. A longer silent interval than in the autumn was used in the hopes of recording more of the young bird's vocalizations in the intervals between series of songs. The same tape was used for a given bird throughout the spring (if imitation occurred during the spring, we were not interested in finer resolution of the timing than this). Both tutoring and recording continued until crystallized song was recorded from all birds in June.

Live Tutoring

On 28 July and 4 August 2005, 11 nestling grasshopper sparrows, 4–6 days old, were collected from four nests at the Tri-Valley Wildlife Area in Muskingum County, Ohio. These birds were group housed initially and sexed by 18 days of age. Five of the birds were males. Three males were then moved at 19 days of age into individual cages in a room with two adult males (Br9 and Br16) from the 2004 cohort. These two adults were chosen from among the tape-tutored birds to serve as live tutors based on subjective judgement of their crystallized buzz and warble songs. The buzz songs sung by both birds appeared normal, and while both birds' warble songs contained fewer notes than the average wild-type warble song, neither contained any atypical notes. We chose to use captive, laboratory-reared birds as live tutors rather than wild-caught adults for strategic and ethical reasons: we felt the laboratory-reared birds would be less stressed in captivity and more likely than wild-caught adults to thrive and to sing in this environment, and it minimized the number of birds collected for the experiment.

The three young males and two adults were housed in a room together from August 2005 through June 2006. The adults had stopped singing by early August, and supplementary tape tutoring was done for 60 days during August–October so that the young birds would hear at least some song during this time. We used three 1-hour tapes, with each 30 min side containing repetitions of one buzz and one warble song type (this sequence repeated twice: 7 min of buzz song, 30 s of silence, 7 min of warble song, 30 s of silence), for a total of six songs of each type in the supplementary tutoring. On average, one side of one randomly chosen tape was broadcast in the room daily, at various times of day.

We began recording all birds in this room as a group twice weekly starting on 15 February 2006. The young birds heard live adult song throughout the spring: adults resumed singing their crystallized songs by early March and continued through June. All five birds were moved to individual sound chambers on 13 June and recorded until 22 June, when recordings of each bird's crystallized songs had been obtained.

Isolate Birds

Two of the males collected in 2005, also group housed initially and sexed by 17 days of age, were moved to individual sound-attenuation chambers on 16 August, when one (Br22) was 16 days old and the other (Br21) was 25 days old. Prior to this time, these two birds were not exposed to any song in the laboratory, and through June 2006, these two males remained individually housed and were not tutored. We recorded them for 1 h twice weekly beginning on 15 February 2006, until crystallized songs were recorded from each bird by the end of June.

Song Analysis: Laboratory-tutored Birds

We used visual judgement of spectrograms and quantitative computer analysis techniques to assess the extent to which the adult repertoire of the tutored birds contained imitations of the tutor song models. Tutor songs included in analysis for the tape-tutored birds were autumn tutor songs, spring tutor songs and songs used in the fledgling response test (10 songs from each category, buzz and warble, of which each bird had heard nine). Tutor songs included in analysis for the live-tutored birds were songs of the two live tutors and the six songs used on the supplemental autumn tutor tapes (all live-tutored birds had heard all eight of each type).

We found that buzz songs produced by laboratory-reared birds were often preceded by long strings of short introductory-type notes varying in frequency, and were only occasionally delivered with a species-typical stereotyped sequence of about four introductory notes (see Fig. 1a). Our analyses of buzz songs therefore focused on the much longer buzz segment of the song that follows the introductory notes and that appeared to be delivered in a stereotypical manner. We used three methods to compare subjects' crystallized buzz songs to the tutor models: principal components analysis (PCA) on acoustic measurements, visual spectrogram analysis and spectrogram cross-correlation. Analysis of warble songs consisted of visual spectrogram analysis and spectrogram cross-correlation of individual notes.

We measured eight acoustic features of buzzes using SIGNAL 4.0: duration of the buzz segment following the introductory notes; dominant frequency of the entire buzz segment, of the first 100 ms, and of the last 30 ms of the buzz segment; high and low shoulder frequencies with amplitude 20 dB lower than peak; and duration of three subjectively identified 'major cycles' and three 'minor cycles' within the buzz segment. These latter two measurements were taken on 200 ms portions of the buzz note (Fig. 2). Measurements were made on all tutor songs and on 10 songs from each subject. Using SPSS software (SPSS, Chicago, IL, U.S.A.), we ran one PCA for the tape-tutored birds and their tutor songs (2004–2005 group), and a second for the live-tutored birds and their tutors plus the two isolate birds (2005–2006 group). In each case, three PCs with eigenvalues greater than 1 were obtained. We calculated Euclidean distances between these PC values for subject and tutor songs, and used the shortest resulting distances to identify closest matches and to compare imitation accuracy across treatment groups.

For visual analysis of buzz songs, the first two PC values for all 10 crystallized buzzes of a given subject bird, from the above PCA, were first graphed on a scatter plot. The most central-looking point was

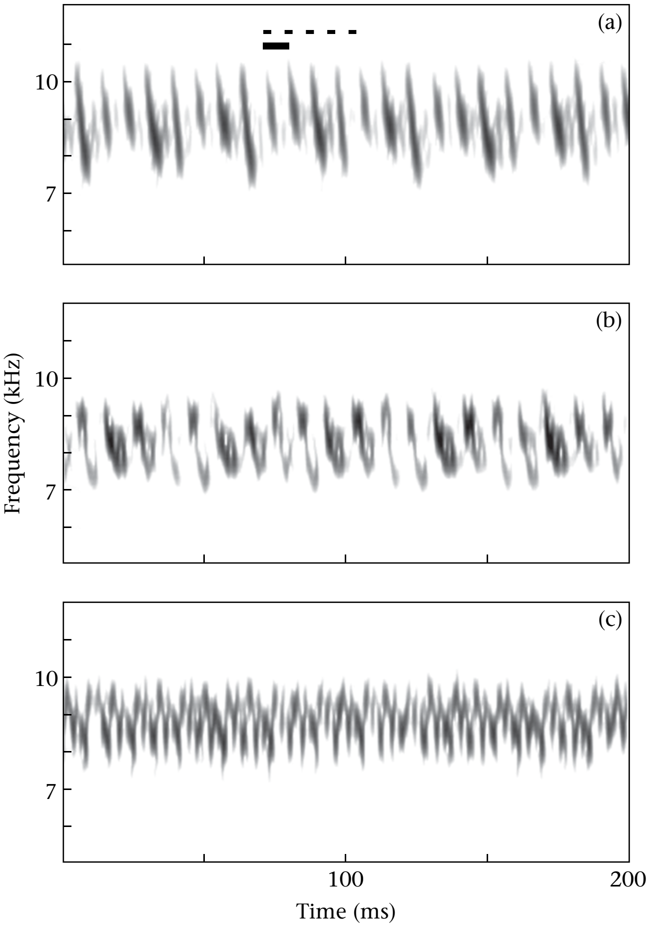

Figure 2. Segments (200 ms) of buzz songs, illustrating variation in buzz fine structure: (a) a tutor model, (b) a tape-tutored bird, (c) a bird reared with no tutor exposure. In panel (a), the solid bar indicates one minor cycle and the dashed line indicates one major cycle. For tutored birds, metrics of song learning were applied at the 200 ms scale as well as at the scale of the entire buzz segment.

chosen, and the song corresponding to that point was selected for printing. Spectrograms of each selected buzz song and each tutor buzz song were printed using Signal 3.1. The whole buzz song was graphed between 3 and 11 kHz, with silence appended as needed to make each file 2.5 s in duration. In addition, a 200 ms segment from the middle of each buzz was excerpted and graphed between 6 and 11 kHz. Both of these spectrograms were generated using 128-point FFTs ($N = 2000$). Printer resolution was 600 dpi, and the size of printed spectrograms was 8.4 cm high × 24.1 cm long.

Five judges familiar with spectrograms were presented with spectrograms of subject and tutor buzz songs. Judges identified the tutor song they thought most closely matched each subject song, and assigned a score to the match as follows: 1 = very poor, 2 = poor to fair, 3 = fair to good, 4 = very good. We used the highest agreement between judges on any one tutor song and the average score given to this match to calculate an 'imitation grade', % agreement × (average score/4), whereby 100% agreement and an average score of 4 gave an imitation grade of 100. This subjective analysis was done for both whole buzz songs and 200 ms segments.

Computerized spectrogram cross-correlations (SPCC) were run using the CORMAT command in SIGNAL 4.0. We analysed tutor buzz songs, and the same 10 buzz songs from each subject as above, at two levels: the whole buzz song (introductory notes were excluded) and 220 ms buzz segments. We hereafter refer to these segments as 200 ms segments. Prior to analysis, we multiplied the 200 ms segments by a ramp signal (20 ms ramp up, 180 ms full value, 20 ms ramp down) to exclude onset and offset artefacts. CORMAT settings were as follows: frequency range 3–12 kHz, FFT length 128, and number of FFTs 500 (whole buzzes) or 1000 (200 ms segments), no frequency shifting and no time normalization. Highest cross-correlation values were used to identify closest matching tutors and to compare imitation accuracy across treatments.

To verify that our analysis was not affected by tutor buzz degradation in the tape-tutor experiment, we played and re-recorded all 10 tutor buzz songs in one of the sound-attenuating chambers using the same equipment as in our study. SPCC values comparing original and re-recorded tutor buzzes (0.596 for whole buzzes, 0.795 for 200 ms segments) were similar to or better than the average within-bird SPCC values (i.e. self-correlation) for the tutored birds' crystallized buzz songs (0.569 for whole buzzes, 0.680 for 200 ms segments). Results of post hoc SPCC analysis comparing learned buzzes to re-recorded tutor buzzes did not differ substantively from those using original tutor buzzes, the results of which are presented below.

We saved and printed between four and eight renditions of the warble song of each subject for visual inspection. Only slight variation was observed across renditions, and we selected an exemplar with the typical phrase number and sequence for each bird. We defined phrase types as notes (individual traces) or groups of notes with distinct appearances on the spectrogram. We counted the phrase types and subjectively noted whether any phrases appeared atypical in comparison with the wild-type (tutor) phrases. We then saved individual notes and phrases from each song and used CORMAT for SPCC of these with individual notes and phrases saved from the tutor songs. CORMAT was run with frequency range 2–10 kHz, FFT length 128, number of FFTs 100, no frequency shifting and no time normalization.

Comparisons between treatment groups were made using Kolmogorov–Smirnov Z tests in SPSS 16.0 (SPSS Inc., Chicago, IL) with an alpha level of 0.05.

Post Hoc Analysis of Tutor Effect on Tape-tutored Birds

After finding that the buzz songs of tape-tutored birds did not closely match any of the tutor models, we further assessed whether the tutor songs influenced the buzz songs developed by the tape-tutored birds as follows. We compared the tape-tutored birds' learned songs to the set of tutor buzz songs (autumn tutor songs, spring tutor songs and songs used in the fledgling response experiment) and also to a set of 10 novel buzz songs that the tutored birds had never heard. We compared the values of the best song matches from each of these two comparisons (pupil–tutor and pupil–novel) using the three methods described above: Euclidean distance based on PCA of acoustic measurements, visual spectrogram analysis, and SPCC. We also analysed agreement among these methods in their identification of the closest match for each learned song. Finally, for each learned song, we compared the overall average Euclidean distances and SPCC values from pupil–tutor comparisons versus those from pupil–novel comparisons. For this last analysis, we used only the six tutor songs that each bird had heard during the autumn, to examine specifically whether autumn tutoring affected song development in this study. Wilcoxon signed-ranks tests were used to assess significance for all comparisons.

Song Recording and Analysis: Wild Birds

To explore whether our laboratory results were representative of grasshopper sparrow song development in nature, we recorded and analysed the buzz songs of eight yearling males in the field as well as songs of males that we considered to be their most likely tutors. Territorial songs of adult male grasshopper sparrows were recorded at the Chester River Field Research Center near Chestertown, Queen Anne's County, Maryland from 1 May to 8 August 2005. All males and most females at this site were colour-banded every year, and territories were mapped with handheld GPS units as part of an ongoing conservation project started in 1999 (Gill et al. 2006). Birds were recorded using TC-D5M cassette recorders (Sony, San Diego, CA, U.S.A.) and ME-67 shotgun microphone capsules mounted on K6U power modules (Sennheiser, Solrod Strand, Denmark). We digitized and analysed recordings using SIGNAL 4.0. For analysis, a single high-quality buzz song recording was selected from the recordings obtained from each of eight sons (F_1). These sons hatched between 7 June and 15 August 2004, were banded as nestlings, and returned to the site and defended territories in 2005. Recordings were also obtained from each of their social fathers (genetic parentage was not known), and their six closest territorial neighbours in 2005 (see Fig. 5). These buzz songs were analysed using the same set of techniques used for buzz songs in the laboratory, described above.

RESULTS

Fledgling Response to Playback

Of 15 birds tested with the six stimulus types, eight responded vocally to playback of buzz songs. Four of these birds also responded to trill calls and Savannah sparrow songs, three (a subset of the four) responded to warble songs, and two responded to tic–tillic calls. The seven birds that did not respond to buzz songs did not respond to any stimulus types, except for one bird, which vocalized once during playback of song sparrow song. All responding fledglings were female except one.

Average response rates to all six stimuli are shown in Fig. 3. Although overall response rate was somewhat low, comparisons between average responses to buzz song and other stimulus types were made. The response to buzz song was significantly higher than the response to either Savannah sparrow song (Wilcoxon signed-ranks test: $T = 1$, $N = 9$, $P = 0.008$) or song sparrow song ($T = 0$, $N = 8$, $P = 0.008$). The response to buzz song was also higher

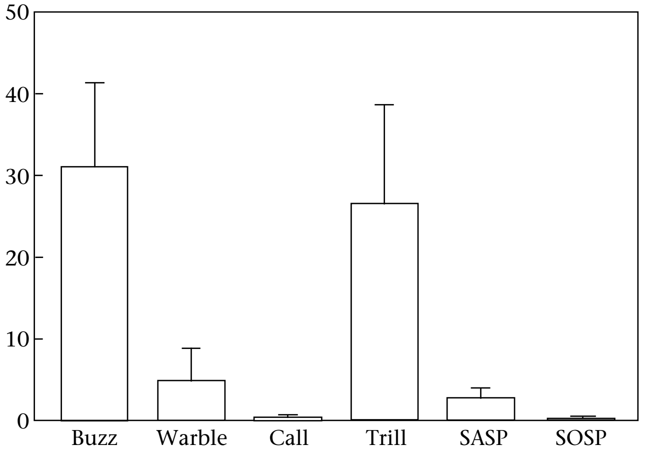

Figure 3. Mean + SE number of calls given by fledgling grasshopper sparrows in response to six stimulus types during a 2 min playback period. SASP: Savannah sparrow; SOSP: song sparrow.

than the response to warble song ($T = 0$, $N = 8$, $P = 0.008$). Too few birds responded to warble song to compare this response to that elicited by either heterospecific song. The response to buzz songs was significantly greater than that to the tic–tillic call stimulus ($T = 0$, $N = 8$, $P = 0.008$), and not different from the response to trill calls ($T = 15$, $N = 8$, $P = 0.74$).

Song Learning in Laboratory Tutor Conditions

All seven tape-tutored males produced buzz songs as adults. Six birds crystallized one buzz song each (an example is shown in Fig. 4a), and one crystallized two distinct buzz songs. The average imitation grades subjectively assigned to the learned buzz songs by the five judges were 42.4 (of a possible 100) for entire buzz segments and 31.9 for 200 ms buzz segments. Euclidean distances between learned and tutor buzz songs (based on PC1 and PC2 from the PCA on eight acoustic features) and SPCC values were also each used to assign a closest tutor match to each learned buzz song (Table 1). Average agreement between visual judging, Euclidean distances and SPCC in the assignment of tutors to each learned song was 40% (Table 1). One tutor song (t2) appeared more popular than the others as the assigned closest matching tutor song. In the PCA, this song lay closer to the centre on both the PC1 and PC2 axes than any other tutor song.

The three live-tutored males each crystallized one buzz song type as adults (Fig. 4b, for example). Tutor assignments made by each of the scoring methods are listed in Table 1. Assessments of imitation for live- and tape-tutored birds are compared in Table 2. Imitation grades assigned visually to buzz songs were significantly higher for live-tutored than for tape-tutored birds for entire buzz segments (one-tailed Kolmogorov–Smirnov Z test: $Z = 1.292$, $N_1 = 3$, $N_2 = 8$, $P = 0.024$) but not for 200 ms segments ($Z = 0.615$, $P = 0.355$). The smallest Euclidean distances between learned and tutor buzz songs were smaller for live-tutored birds than for tape-tutored birds, but not significantly so ($Z = 0.985$, $P = 0.097$). SPCC values were significantly higher in live-tutored birds than in tape-tutored birds for both entire buzz segments ($Z = 1.477$, $P = 0.003$) and 200 ms segments ($Z = 1.477$, $P = 0.006$). Finally, average agreement between scoring methods in the assignment of tutors to each learned song was twice as high for live-tutored as for tape-tutored birds (Table 1). One of the live tutors (t12) was most popular as the assigned closest matching tutor song. This bird might have sung more or interacted more with the young birds, and perhaps the young birds converged to some extent in their learned buzz songs.

All tape-tutored and live-tutored males developed a warble song type (Fig. 4d, e); one live-tutored bird crystallized two warble song types. Visual inspection revealed that none of the learned

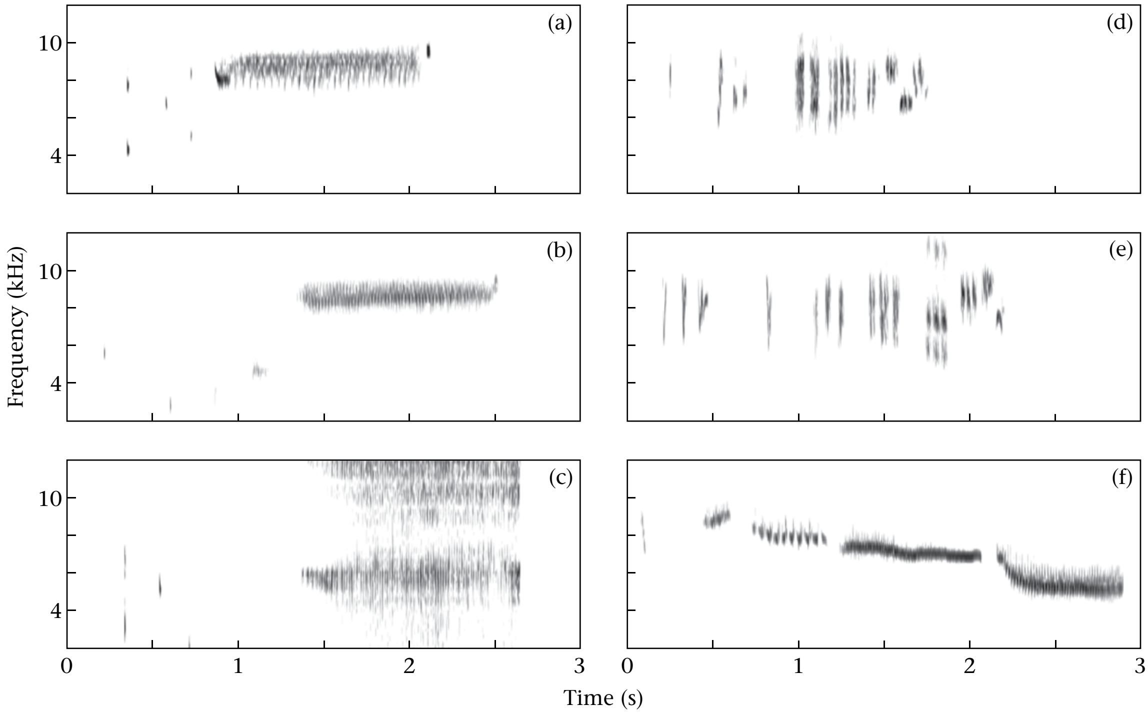

Figure 4. Examples of songs crystallized by birds in different tutor treatments: (a) buzz song of tape-tutored bird, (b) buzz song of live-tutored bird, (c) buzz song of isolate bird, (d) warble song of tape-tutored bird, (e) warble song of live-tutored bird, (f) closest equivalent to warble song of isolate bird. Songs (c) and (f) are from the same isolate male (Br21). Note that for buzz songs, introductory notes were not stereotyped and were not always produced as shown here.

Table 1
Tutor songs most closely matched by learned buzz songs according to three scoring methods

	Visual scoring		PCA	SPCC		% Agreement
	Whole buzz	200 ms	Whole buzz	Whole buzz	200 ms	
Tape-tutored birds						
Br5	t4	t4	t4	t6	t1	60
Br6	t10	t2	t4	t6	t1	0
Br7	t4	t2	t2	t1	t5	40
Br9	t2	t5	t2	t2	t2	80
Br13	t4	t2	t5	t6	t1	0
Br14a	t2	t2	t2	t2	t2	100
Br14b	t8	t1	t3	t6	t1	40
Br16	t4	—	t8	t6	t1	0
Average agreement						40
Live-tutored birds						
Br17	t12	t12	t12	t6	t12	80
Br18	t8	t12	t11	t12	t12	60
Br27	t12	t12	t12	t12	t12	100
Average agreement						80
Wild birds: subjects (sons) in first column						
BKM	PRM	PRM	BYM	PRM	BTB	60
BTM	GTM	WFM	GTM	GTM	GTM	80
BYM	RGY	RGY	RGY	RGY	RGY	100
GGM	**YRM**	GTB	YTM	YTM	GTB	40
GMM	YKM	YKM	GBM	YKM	YKM	80
RPM	RWM	TYM	YFT	YFT	YFT	60
RTM	TFM	TFM	YRM	TFM	TFM	80
TWM	YRT	TBM	**YPT**	TBM	**YPT**	40
Average agreement						68

In one case, visual scoring consensus was for no imitation of tutor models (dash). Tutor models t1–t6 represent the six autumn tutor songs, t7–t10 are the four songs used for both the fledgling vocal response test and spring tutoring, and t11 and t12 are the two live tutors. Br14a and Br14b represent two song types learned by the same bird. Wild bird identification codes reflect colour-band combinations, and boldface indicates social fathers of the sons in the first column.

warble songs were close imitations of tutor models, based on note composition and sequence. Table 2 lists comparisons between the warble songs of tape-tutored and live-tutored birds. The percentage of phrases in each song that appeared to be of normal, species-typical acoustic structure by our subjective judgement was equivalent (approximately 90%) in both groups. SPCC on individual warble song notes gave similar highest correlation values between learned and tutor notes in both groups (one-tailed Kolmogorov–Smirnov Z test: $Z = 0.513$, $N_1 = 4$, $N_2 = 7$, $P = 0.446$). Warble songs developed by live-tutored birds did not differ in phrase number from those of tape-tutored birds ($Z = 0.570$, $P = 0.309$). The warble songs developed by tape-tutored birds contained significantly fewer phrases than did the wild-type tutor songs that they heard ($Z = 1.498$, $N_1 = 6$, $N_2 = 7$, $P = 0.005$). Some of the tutor warble songs heard by live-tutored birds, namely those of the two live tutors, contained relatively few phrase types as well. As a consequence, phrase number did not differ significantly between learned and tutor warbles in the live-tutored group ($Z = 0.878$, $N_1 = 4$, $N_2 = 8$, $P = 0.168$).

None of the tape-tutored males developed Savannah sparrow or song sparrow song types despite having been tutored with equal numbers of heterospecific and conspecific song models.

Tutor Song Influence on Buzz Development

As described in the Methods, we compared buzz songs learned by the tape-tutored birds to both the set of tutor buzz songs and a set of novel buzz songs. Visual inspection yielded similar average grades for the pupil–tutor and the pupil–novel comparisons, at both the full buzz scale ($T = 5$, $N = 7$, $P = 0.156$) and the 200 ms segment scale ($T = 5$, $N = 5$, $P = 0.625$). Smallest Euclidean distances derived from the PCA analyses were also similar for the pupil–tutor and the pupil–novel comparisons ($T = 12$, $N = 8$, $P = 0.461$). Highest SPCC values were not significantly different between the two comparisons for either full buzzes ($T = 13.5$, $N = 8$, $P = 0.547$) or 200 ms segments ($T = 5$, $N = 8$, $P = 0.078$), although in this last comparison, 200 ms segments of learned buzzes approached better correlation to one of the tutor songs than to any of the novel songs. Finally, the level of agreement among methods in identifying which song most closely matched each

Table 2
Metrics of imitation derived by multiple scoring methods for both buzz and warble songs, for comparison of tape-tutored and live-tutored birds

	Tape-tutored	Live-tutored	*P*	Wild[†]
Buzz song types				
Visual judging: imitation grade				
Full buzz segment	42.4	75.0	0.024[*]	61.2
200 ms segment	31.9	50.8	0.355	52.7
PCA: smallest Euclidean distance	1.38	0.74	0.097	1.08
SPCC: highest value				
Full buzz segment	0.43	0.55	0.003[*]	0.42
200 ms segment	0.52	0.63	0.006[*]	0.46
Warble song types				
% Phrases appearing normal	91	89	0.409	
SPCC: highest value[‡]	0.62	0.61	0.446	
No. of phrases, absolute	5.6	7.8	0.309	
No. of phrases relative to tutors	−6.4	+2.3	0.003[*]	

[*] Kolmogorov–Smirnov Z test on values from tape-tutored versus live-tutored birds ($\alpha = 0.05$).

[†] Values of buzz measures for wild birds in our study population (see text for statistical results).

[‡] SPCC was performed on individual notes of learned and tutor warble songs.

learned song did not differ between the pupil–tutor and the pupil–novel comparisons ($T = 3$, $N = 4$, $P = 0.625$).

The above analyses compared only the best song matches. We also compared average Euclidean distance and SPCC values from the two comparisons (pupil–tutor and pupil–novel), including only the six tutor songs that the tutored birds heard during the autumn. Average Euclidean distances were closer between pupil songs and the autumn tutor songs than between pupil songs and the novel songs, but not significantly so ($T = 5$, $N = 8$, $P = 0.078$). Average SPCC values were significantly higher between pupil songs and the autumn tutor songs than between pupil songs and novel songs, for both full buzzes and 200 ms segments ($T = 0$, $N = 8$, $P = 0.008$ for both).

Song Development in Isolate Birds

Only two grasshopper sparrows were reared without exposure to song models. Therefore, no statistical tests were done on the songs developed by these birds, and the analysis presented here is descriptive.

We recorded three distinct crystallized song types from each bird. Each bird crystallized a buzz song consisting of a broadband but stable-frequency buzz segment following a string of short, variable-frequency introductory notes. The duration of the buzz segment fell near or within the normal range of duration for wild-type buzz segments. One of the two birds (Br22) produced a buzz segment that appeared normal in frequency and bandwidth, although fine structure of its buzz segment was atypically noisy (Fig. 2c). The other bird (Br21) produced a similarly noisy buzz segment over an atypically low, broadband frequency range (Fig. 4c). Br21 also crystallized another song containing short notes followed by a constant-frequency, longer note, but this longer note was considerably shorter and much narrower in bandwidth than a typical buzz segment.

In addition to buzz song types, both isolate birds developed at least one other song that contained multiple phrase types (stereotyped notes or note sequences). One of the two birds (Br22) crystallized two such songs. These ‘warble-type’ songs contained between five and eight distinct phrases. Many of these phrases (three or four per song) contained notes that were abnormally long compared to species-typical warble notes (see Fig. 4f).

Buzz Song Learning in the Wild

Buzz songs of eight males were compared to the buzz songs of their social fathers and their six closest territorial neighbours in their first breeding year (Fig. 5). Average imitation grades assigned by judges based on visual spectrogram inspection were 61.2 (of 100) for full buzz segments and 52.7 for 200 ms segments. These values did not differ significantly from those for either tape-tutored or live-tutored birds ($P > 0.1$ for all comparisons). The smallest Euclidean distance between sons’ songs and father or neighbour songs, calculated from PCA values, fell between the values obtained for tape-tutored and live-tutored laboratory birds and did not differ significantly from either ($P > 0.1$ for both). Highest SPCC values for wild birds were significantly lower than those for live-tutored birds in the laboratory for both full buzz segments and 200 ms segments ($Z = 1.477$, $N_1 = 3$, $N_2 = 8$, $P = 0.006$ for both), lower than those for tape-tutored birds for 200 ms segments ($Z = 1.250$, $N_1 = 7$, $N_2 = 8$, $P = 0.044$), and not different from those for tape-tutored birds for full buzz segments ($Z = 0.750$, $P = 0.311$). Finally, the average agreement between scoring methods in assignment of sons’ songs to potential tutor models, from among the social father’s song and neighbours’ songs, fell squarely between the agreement values for tape-tutored and live-tutored laboratory birds.

In all cases but one (see Table 1), each son’s song was more similar, although not identical, to the song of at least one of the son’s neighbours when compared with that of his social father, even when the social father subsequently became a neighbour (father YRM and son BYM; see Fig. 5). In addition, three sons that shared the same father (YRM), two of which were reared in the same brood, developed distinct songs from one another.

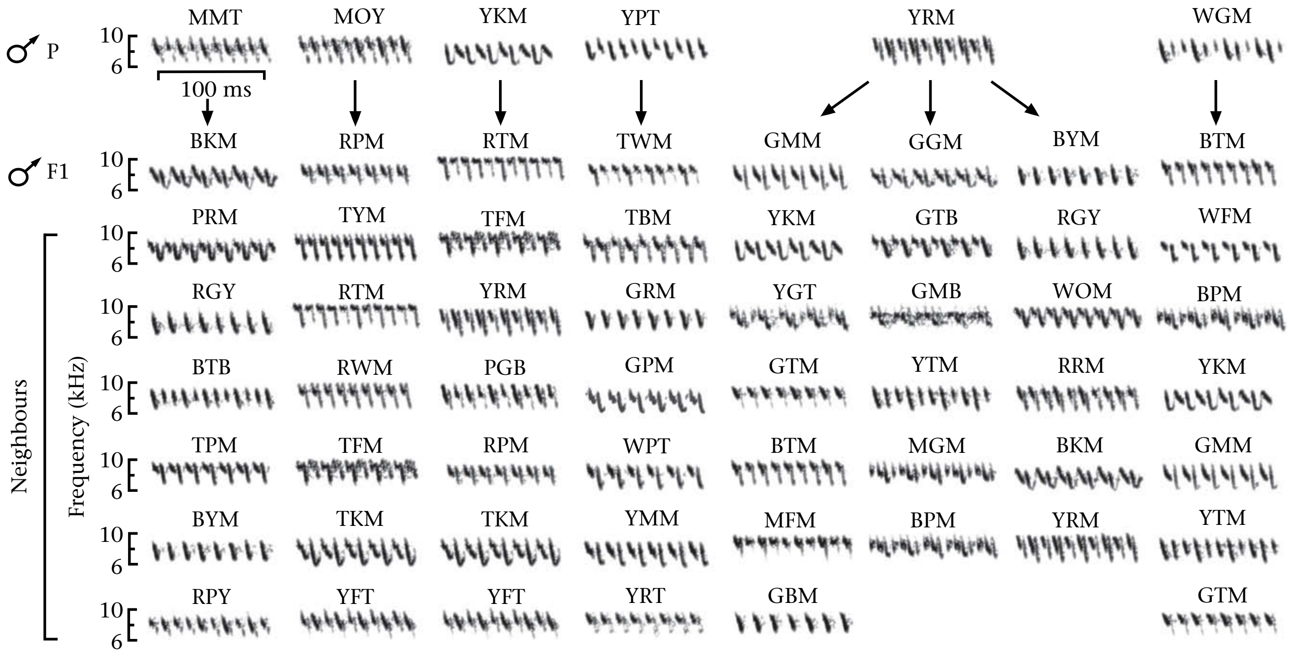

Figure 5. Buzz song segments (100 ms) of social fathers (P) of returning known F_1 males (sons), and of each son (arrows) and each son’s immediate territorial neighbours (the column under each F_1). Neighbours judged to be the closest match visually, at the 200 ms scale, are placed at the top of each column under the F_1’s song (e.g. in the first column, the song of bird PRM was considered to be the closest match to that of the F_1 bird BKM).

DISCUSSION

This study provides evidence that grasshopper sparrows are predisposed to learn two distinct song types and that accurate imitation of tutor models is not the normal mode of development for either type. While our fledgling response test showed early response to buzz songs and not warble songs, all birds in the laboratory developed both buzz and warble type songs by adulthood, regardless of acoustic experience with song models. The songs of the two isolate birds were abnormal, but showed distinctive characteristics of one song type or the other, and could still be categorized as buzz-like and warble-like. Tape-tutored birds developed more normal buzz and warble songs than did the isolates, but none of these closely matched any of the tutor models. Live-tutored birds all developed buzz songs that matched one of the live tutor models more closely, while the warble songs developed by live-tutored birds were each distinct and did not match any of the tutor models.

The tape-tutoring and live-tutoring experiments were done in two consecutive years. In this study, we believe treatment to be the most salient difference between years. The young birds used in the two experiments also came from different locations. While both locations are within the range of the same subspecies (*A. s. pratensis*), we do not know whether populations at the two locations differ naturally in song development. It could be that birds in eastern central Ohio (the source birds for the live-tutor experiment) normally imitate buzz songs more closely than birds in coastal Maryland (the source birds for the tape-tutor experiment). However, while we have not systematically investigated this possibility, we have not seen evidence in the field for greater buzz song similarity in Ohio than in Maryland.

In any case, the results of the tape-tutor study show that grasshopper sparrows can crystallize a buzz song that appears normal and yet does not precisely resemble any of several models heard earlier in life. The abnormal songs developed by the two isolate birds indicate that grasshopper sparrows must hear species-typical song models in order to develop normal songs. Thus, grasshopper sparrows appear to obtain and use some information from song models in normal buzz song development, but not to imitate a particular song model precisely. We do not yet know whether young birds of this species memorize a song model and crystallize a song that develops as a variation of this model (improvise, sensu Marler & Peters 1982) or whether normal exposure to song provides them with more general information about species-typical acoustic parameters, which they then use to invent their own song. Our comparison of learned buzz songs to both tape tutors and novel songs indicated that learned songs did not match any one particular tutor model more closely than they matched (by chance) one of a set of novel songs that the tutored birds had never before heard. This argues against improvisation based on only one of the tutor songs. However, average similarity between learned songs and the set of autumn tutor songs was higher than that between learned songs and the set of novel songs. This suggests that as a group, autumn tutor songs did influence buzz development in the tape-tutored birds. Acoustic analysis of buzz songs over their development from plastic to crystallized song might provide additional insight into whether improvisation contributes to this process.

Regardless of the extent to which buzz song development involves improvisation or invention, evidence from the field study suggests that the same non-imitative process also occurs in the wild, as first-year breeding males sang buzz songs that matched neither their father's nor their breeding neighbours' songs. Live-tutored birds in the laboratory crystallized buzz songs that resembled one of the live tutors' buzz songs, suggesting that imitation is possible in the development of this song type. This result also indicates that such imitation might occur in the male's first spring, as the live tutors that were imitated were heard to sing at that time and not during the previous autumn or winter. Our laboratory live-tutor protocol, however, involved an atypically sustained interaction between tutors and pupils in close proximity, and so does not replicate the situation in the wild. Based on the field results, we do not believe that precise buzz imitation necessarily occurs in the wild, as imitation accuracy in wild birds was similar to or worse than that in our laboratory-tutored birds. Of course, we cannot rule out the possibility that models for imitation in the field were provided by adults other than the social father or immediate breeding neighbours, although these individuals are known to provide the song models for many species studied to date (e.g. zebra finches, *Taeniopygia guttata*: Williams 1990; indigo buntings, *Passerina cyanea*: Payne & Payne 1993; Galapagos finches, *Geospiza* spp.: Grant & Grant 1996; song sparrows: Nordby et al. 1999; chipping sparrows, *Spizella passerina*: Liu & Kroodsma 2006). Males might also incorporate information from multiple tutor sources into their own songs, as was observed in a recent field study of song development in Savannah sparrows (Wheelwright et al. 2008). In the case of grasshopper sparrow buzz song (which consists primarily of one phrase, the buzz segment), however, this would have more subtle effects than in a song where different phrases might be imitated from different models.

In contrast to buzz song, warble song developed similarly in both tape-tutored and live-tutored birds. In both situations, warble song consisted of apparently normal notes, but contained fewer phrases than is typical in wild birds and did not resemble any of the tutor warble songs in their particular note sequence. Isolate birds, in contrast, developed warble songs containing unusually long notes (Fig. 4f). In combination, these results suggest two possibilities for normal warble song learning. First, individual warble notes might normally be imitated but their sequences improvised or invented. Sequence improvisation might include the recombination of partial sequences learned from multiple song models. Second, perhaps individual warble notes are also improvised or invented, but in order for this to occur, birds must experience some exposure to the normal range of variation in population-specific or conspecific song. In either case, warble song development does not appear to proceed by imitation alone.

Our finding that grasshopper sparrow song develops by means other than imitation might support the hypothesis that song improvisation or invention is correlated with low breeding site fidelity (Kroodsma et al. 2002). Breeding site fidelity in grasshopper sparrows varies among geographical regions, but in the most densely populated portion of its range (i.e. the grasslands of central North America, which might best reflect the ancestral habitat for this species), breeding site fidelity is low (Vickery 1996). In particular, Kaspari & O'Leary (1988) found no evidence of breeding phylopatry in a Nebraska population. In some eastern populations, such as our field site in Queen Anne's County, Maryland, the annual rate of adult return to the breeding grounds can be high (in our population, males: 53–88%, females: 31–62%). But if low breeding site fidelity observed in the midwest is the ancestral pattern, improvisation or invention may be favoured over imitation for a number of reasons. Compared with imitation of song types, the latter processes will maintain greater diversity and a finer gradient of acoustic variation in song within the species. In other words, the total 'acoustic space' of the species' songs will be more densely filled by different song exemplars. This might in turn facilitate general, noncategorical recognition of conspecific song, as well as more discrete distinctions between the songs of individual males. Similarly, Kroodsma et al. (1999a) have argued that improvisation reduces variation across geographical areas, which should also facilitate conspecific recognition regardless of where birds settle to breed. In the absence of precise song imitation, females might not obtain information about a male's natal site from his song. But in a species with low site fidelity, there is little chance for local adaptation to occur, and natal location might have little or no informational value anyway.

Song improvisation or invention might also be expected to occur if precise imitation of song is particularly difficult. Grasshopper sparrow songs are unusually high-pitched and the fine structure of the buzz is very rapid. These features do not present insurmountable obstacles to buzz song imitation, as evidenced by our live-tutored birds. However, even in these birds, human judges assigned lower imitation grades at a finer temporal scale, when comparing 200 ms segments, than at the scale of the full buzz segment. It could be that song imitation in general looks less accurate when examined at the fine scale, or it could be that precise imitation of fine buzz structure, which consists of high-frequency notes (often of more than one type, on the order of 10 ms in duration each; e.g. Fig. 2a), presents a special challenge. Podos (1997) reported an upper bound to the combination of trill rate and bandwidth within the family Embirizidae, suggesting a production constraint. However, grasshopper sparrow buzz song falls within the faster category of trills that Podos mentions, not the slower category of trills that he found to show this bounded relationship, and thus probably involves a different production mechanism.

Even without precise imitation, natural buzz song development may give rise to some degree of song similarity among neighbours if breeding site fidelity is sufficiently high. In a spectrogram scoring study, 10 judges sorted 30 buzz songs recorded in central Ohio correctly into their three populations of origin at above chance levels, while this was not true for warble songs from the same three populations (D. Nelson, unpublished data). This result suggests that at least in some cases, buzz songs may be more similar within than between populations. This is consistent with improvisation or invention of buzz songs if auditory experience of song models influences the acoustic features of improvised songs to any extent. Upon investigation, a similar result might be found in other eastern populations with relatively high site fidelity, including our study population in Maryland.

Our results suggest that warble song development proceeds by improvisation or invention of note sequence in a manner that maintains extensive variation between individuals in this song type. In contrast to buzz songs, the degree of imitation did not increase for warble songs in the presence of live tutors. We do not expect that the degree of imitation would have increased if live tutors singing more complex warble songs had been used in our study, but this is a possibility. In any case, improvisation or invention might be favoured for warble song development if a functional benefit to individual distinctiveness in warble songs exists. Warble song might be directed principally towards the female after pairing (Vickery 1996), and perhaps immediate recognition of the individual identity of the singer is beneficial to the reproductive success of the male, the female, or both. The more complex acoustic structure of warble song itself suggests that this song type may convey individual identity more saliently than buzz song. On a theoretical level, the number of ways in which a song is likely to vary across individuals (either within or across generations) is correlated with the number of parameters required to describe that song. More concretely, a song containing repeated notes of one type, such as the buzz segment of the buzz song, requires learning of a smaller set of features (note structure, repetition rate and total duration) than a song containing multiple note types, in which a larger set of note features and sequence information must be learned. In support of the idea that complexity and individual variation are correlated, more rapid cultural change in complex notes as compared to simpler notes has been observed within songs of the Puget Sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis* (Nelson et al. 2004). Within these white-crowned sparrow songs, the simpler syllables serve as a dialect marker while the complex syllables are thought to convey individual identity (Nelson & Poesel 2007). Similarly, the differences in both acoustic complexity and mode of development between grasshopper sparrow buzz and warble songs might be related to differences in the function of these two songs, in particular their potential function in conveying individual identity. The question of whether female preference drives cultural evolution of the two song types differently is an interesting topic for further research.

Our finding that buzz song elicits a vocal response from fledglings, while warble song does not, suggests that young birds recognize buzz song as conspecific song earlier in development. One possibility is that this results from greater exposure to buzz songs as nestlings prior to collection. However, the hearing system of songbirds is not fully developed at hatching (Khayutin 1985) and there is little evidence that nestling song exposure affects song learning (Catchpole & Slater 2008). Another possibility is that early recognition of conspecific song is at least in part genetically determined. If so, early recognition of buzz song but not warble song might have a functional explanation. Buzz songs may be a more reliable species indicator, as they are more uniform across birds than warble songs. A related possibility is that buzz songs may be easier to encode and recognize, as they can be described by fewer acoustic parameters than warble songs (see above). Both of these features, uniformity and simplicity, pertain to the trill call (Fig. 1f) as well, which also elicited a vocal response from fledglings. If the natural function of the fledgling's vocal response to conspecific adult song is to communicate location and hunger level to its parents, recognition of the buzz song and trill call may suffice, and fledglings may not gain sufficient additional advantage by also recognizing the more complex warble song. If early vocal response indicates the likelihood that a young bird will memorize the sound being presented (see Nelson & Marler 1993), one interpretation of our results is that the innate buzz template of young grasshopper sparrows might be more complete or available earlier than the innate warble template. In our experiment, almost all of the fledglings responding vocally to song playback were females, and while females might also memorize song (for recognition if not production), we cannot generalize our results to males. We did attempt to ascertain when males memorize buzz and warble songs during development, by presenting distinct tutor songs at different stages throughout the tape-tutoring period. However, because birds did not closely imitate tape-tutor models, we were unable to use our subjects' adult songs to identify when (or indeed whether) any particular buzz songs or warble songs were memorized.

We found that both categories of grasshopper sparrow song develop at least in part by a process other than imitation. In contrast, chestnut-sided warblers, which also have two song categories, develop their songs primarily by imitation (Byers & Kroodsma 1992). However, the major difference we observed in development of the two song categories in grasshopper sparrows parallels that seen in chestnut-sided warblers. In grasshopper sparrows, both song types developed more or less normally in a tape-tutor setting, but buzz songs were imitated more closely when live tutors were present. In chestnut-sided warblers, the putative territorial (UE type) song does not develop normally unless live tutors are present (Byers & Kroodsma 1992). In both species, therefore, social interaction with adult males appears to play a greater role in development of stereotypical territorial male song than in development of the second song type. In other respects, such as the geographical variation in each song type, these two species may differ, perhaps as a consequence of differences in overall learning strategy (improvisation versus imitation). In chestnut-sided warblers, one song type (UE) shows dialect-type clustering while the other (AE) does not (Byers 1996b). More complete work is needed on geographical variation in grasshopper sparrow song of both types before a thorough comparison can be made.

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