



# Permissiveness in the learning and development of song syntax in swamp sparrows

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Vocal learning in swamp sparrows, *Melospiza georgiana*, is subject to a host of sensory and motor limitations. One such limitation is that young swamp sparrows almost invariably crystallize their songs with a simple trilled syntax, irrespective of the syntax of vocal models from which they learn. A striking exception to this pattern was recently identified by Podos (1996, *Animal Behaviour*, 51, 1061–1070), who found that large-scale organizational changes in vocal syntax, including the production of an intermittent or 'broken' syntax, were produced when birds faced limits on vocal performance capacities during motor ontogeny. Our goal in the present study was to determine whether song models with broken syntax could serve as suitable training models for young swamp sparrows, and, if so, if broken syntax could be faithfully reproduced. We hand-reared 10 male swamp sparrows and exposed them to control, rapid and broken song models. Control song models were copied with a high degree of accuracy, as in previous studies. Rapid song models were copied with deficiencies that suggested performance limits on vocal production; such deficiencies included the production of songs with broken syntax and the production of songs in which notes were dropped out as songs progressed. Broken songs proved suitable as training models. Furthermore, copies of broken song models were crystallized either with normal or with broken syntax. These data identify an unexpected direction of permissiveness in the types of songs swamp sparrows will memorize and accurately reproduce, and also point to a possible proximate basis for syntactical changes in the evolution of sparrow songs.

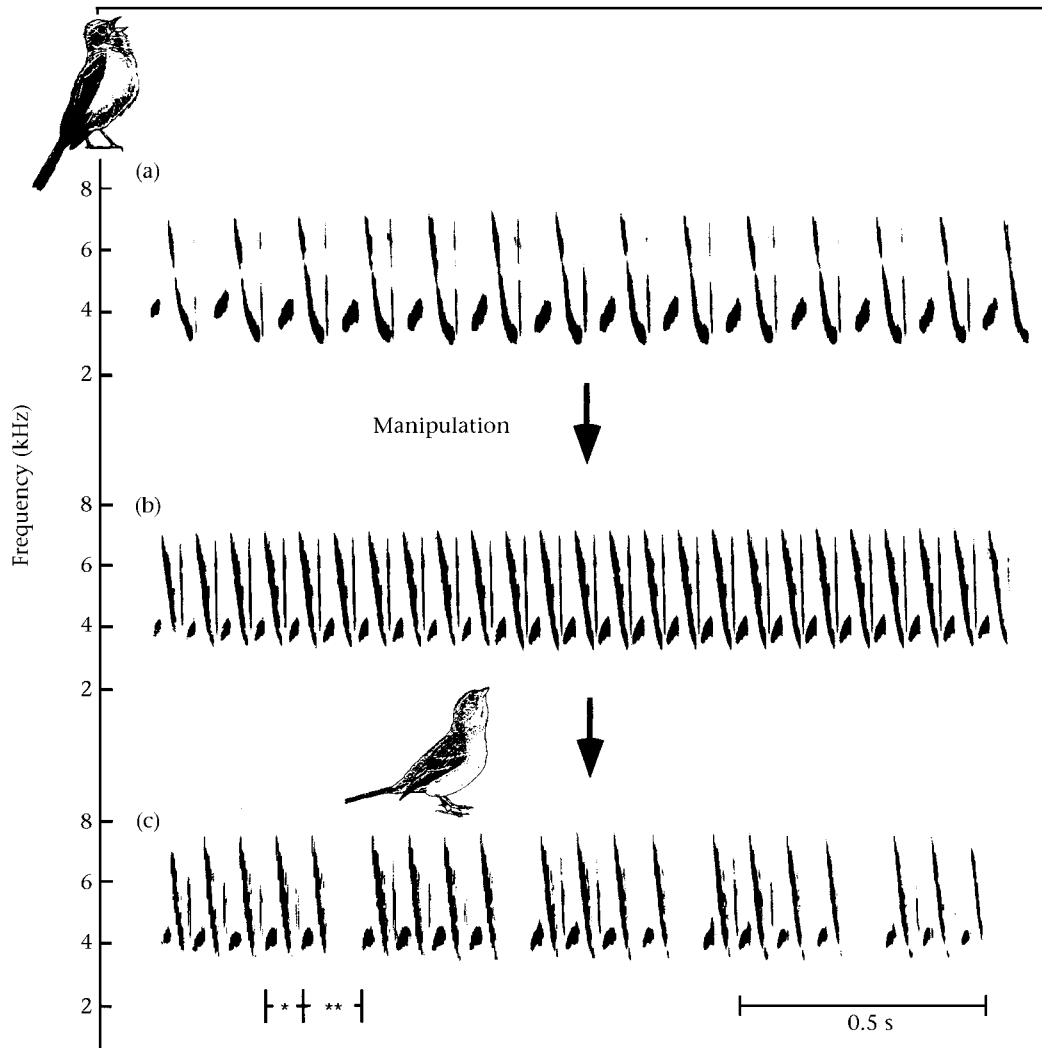
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Most songbirds learn their songs by imitation, through a process that includes an early 'sensory phase' when song models are committed to memory, and a subsequent 'sensorimotor phase' when stored representations of these models are accessed and reproduced (Slater 1989). Learning by imitation is inherently open-ended or 'permissive', insofar as sensory information directs the development of motor patterns (Marler 1976, 1984). In songbird vocal learning, permissiveness is illustrated by the fact that young birds are able to reproduce precisely the acoustic features of a broad range of models to which they are exposed. The range of acoustic stimuli that may be imitated includes not only widely divergent variants of conspecific song (e.g. Marler 1970) but even heterospecific songs under some rearing conditions (e.g. Baptista & Petrinovitch 1984; Marler & Peters 1989). Permissiveness also plays an important role in the sensorimotor phase of

song learning, during which time exposure to song patterns of other birds can help to determine the subset of previously memorized song models that an individual will eventually express (e.g. Nelson 1992; Nelson & Marler 1994).

Song learning is not completely permissive, however, despite the open-endedness associated with imitation. Instead, the range of songs a young bird may memorize and subsequently reproduce is restricted in some dimensions by both sensory and motor factors. For example, young birds typically display a strong predisposition to memorize conspecific songs in preference to heterospecific songs, as revealed by their greater attentiveness to conspecific models (e.g. Dooling & Searcy 1980; Nelson & Marler 1993) and by their eventual reproduction of conspecific song models (e.g. Marler & Peters 1977, 1989). Evidence for sensorimotor predispositions in song development comes from the observation that some species-typical motor patterns are produced even when young birds are deprived of all external song models (Marler & Sherman 1985). In addition, motor limitations on the performance capacities of the vocal apparatus may restrict

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**Figure 1.** Expression of broken syntax as an outcome of learning from rapid models (examples from Podos 1996). (a) Typical wild swamp sparrow song. (b) Digitally manipulated version of that wild song, used as a training model. The trill rate of this model was increased by 92%, compared with the trill rate of the original wild song. (c) Copy of model, produced with broken syntax. \*Syllable period within multisyllable segments; \*\*syllable period across gaps. Sonagrams were made using a Kay Elemetric Digital Sonograph (Model 5500) at 300-Hz filter bandwidth and a frequency range of 0–8 kHz.

a bird's ability to reproduce accurately songs that had been successfully memorized during the sensory phase (Podos 1996, 1997).

The swamp sparrow, *Melospiza georgiana*, is a species in which sensory and motor restrictions appear to play an especially strong role in the song-learning process. This species' song lasts about 2 s and is composed of a repeating sequence of one to five individual notes; the repeating sequence of notes is referred to as a 'syllable', and the repeated syllables form a 'trill' (Fig. 1a; Marler & Pickert 1984; Podos 1996). Although the species is widely distributed across eastern and central North America (Mowbrey 1997), all swamp sparrow songs show a relatively narrow range of structural characteristics. On the phonological level, all notes produced by individuals across the entire species range fall into only six categories of perceptually distinct note types (Marler & Pickert 1984; Clark et al. 1987; Nelson & Marler 1989). On the syntactical level, all

swamp sparrow songs are produced as continuous trills of identical syllables repeated at a relatively constant rates. In almost every case, these trills include only one type of syllable; much more rarely, songs begin with one syllable type and then switch to a second syllable type (i.e. to a different set of repeated notes) about halfway through the song, but in such cases the trill remains continuous with no obvious break between the repetitions of the first and second syllable type. In the laboratory, swamp sparrows show a strong preference for imitating conspecific songs and are especially resistant to learning phonology that deviates from the set of six species-typical note types, even when given no other choice of models (Marler & Peters 1977, 1980, 1989). When young birds learn from swamp sparrow phonology presented in a more complex syntactical structure, they typically reproduce this phonology as simple continuous trills (Marler & Peters 1980). Even birds raised in total isolation with no exposure at all

to song models produce songs as continuous trills (Marler & Sherman 1985). The fact that swamp sparrows rarely, if ever, deviate from production of continuous trills, irrespective of early experience, led Marler (1984) to suggest that an innate central motor programme underlies this species-typical feature of swamp sparrow song.

A striking exception to the tendency for swamp sparrows to develop songs with continuous trilled syntax was revealed in a laboratory study of song learning, in which young birds were tutored with song models that were digitally manipulated to have trill rates higher than species norms (Podos 1996; see e.g. Fig. 1a versus b). Birds were able to memorize these fast-trill models, but proved unable to reproduce them accurately. Instead, birds' reproductions of these models included several kinds of modifications in timing and syllable structure, all of which appeared to result from an inability of the vocal apparatus to produce the faster trill rates of the models. The most unusual of these modifications was the appearance of a 'broken' syntax (Fig. 1c), in which short bursts of syllables (reproduced accurately and at the fast rate of the model) were separated by silent gaps, as if the motor system could not sustain the high trill rate without breaks for the entire duration of the song. The appearance of broken syntax songs is of interest not only because it is consistent with the hypothesis that motor limitations constrain song expression (Podos 1996), but also because it represents a pronounced deviation from the restricted syntactical organization normally observed in swamp sparrow songs.

Our primary goal in the present study was to determine whether this novel broken syntax could be learned by other individuals. A first question to ask is whether young birds would attend to and memorize song models with broken syntax, particularly if models with normal syntax also were available. There is reason to suspect that such would not occur given that swamp sparrows are highly selective in their choice of song models, normally avoiding those that deviate from species-typical characteristics (Marler & Peters 1977, 1980, 1989). If birds indeed memorize song models with broken syntax, the question that follows is whether they themselves would reproduce these models with broken syntax. Earlier work again suggests that such an outcome also would be unlikely; in experiments in which young swamp sparrows acquired vocal material from models with more complex syntactical organization (as for example when they were not given a choice of species-typical models), they almost invariably reproduced the material they learned as continuous trills (Marler & Peters 1977; Marler 1984). We were drawn to ask these questions in spite of evidence suggesting the answers to both would be negative, because the broken syntax we studied is not an arbitrary deviation from species-typical song structure but rather a specific response of the swamp sparrows themselves to motor limitations on song development. Given evidence for the coupling of sensory and motor mechanisms involved in song learning and production (Nottebohm 1984; Margoliash & Konishi 1985; Williams & Nottebohm 1985; Nottebohm et al. 1990), it is possible that the inclination of the motor system to produce

broken syntax when faced with a performance limitation is mirrored by an unexpected permissiveness to learn and reproduce this novel vocal pattern.

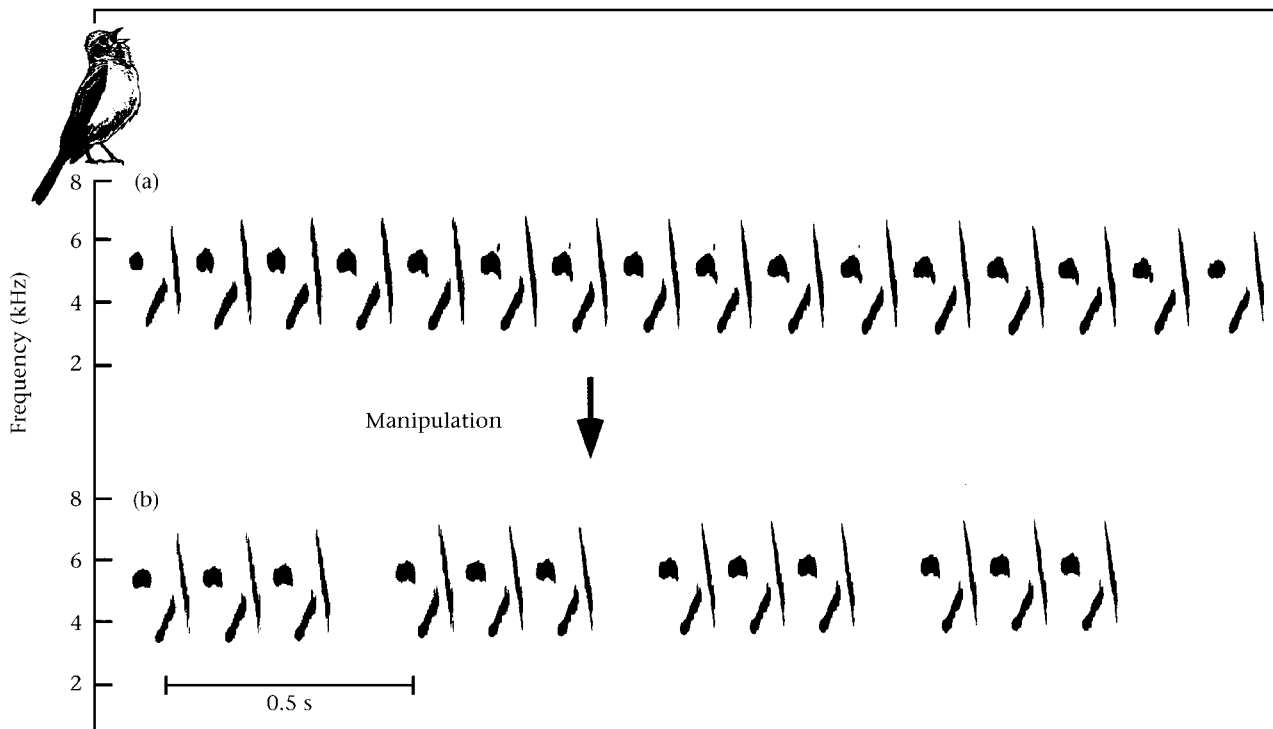
## METHODS

We collected 10 male swamp sparrows from eight nests, 4–7 days after hatching, on 25–26 May 1995, from a population in Crawford County, Pennsylvania. Birds were hand-reared (as in Marler & Peters 1988) and housed in individual cages inside two walk-in acoustic isolation chambers (5 birds/chamber). Cages were positioned inside these chambers so that birds could not see each other, although they were able to hear each other.

Using 'Signal' software (Engineering Design 1996), we constructed 10 songs to be used as learning models: two 'control' models, four 'rapid' models and four 'broken' models. Control and rapid models were constructed as in Podos (1996). Briefly, we digitized songs recorded in the wild at a sample rate of 25 kpt/s (Data Translation 2128G A/D board), after high-pass filtering to reduce low-frequency environmental noise (Krohn-Hite 3500, 1-kHz corner frequency) and low-pass filtering to prevent aliasing (Stanford Research Systems SR640, 10-kHz corner frequency; see Stoddard 1998 for explanation of sampling and aliasing). Individual syllables were selected from digitized songs, and copies of these syllables were concatenated to create model songs. Each model song was constructed using a different, unique syllable type. Control song models were constructed to have the same trill rates as the wild songs from which their syllables were sampled. To construct rapid song models, both internote and intersyllable silent intervals were shortened by a given ratio, to create song models having trill rates either 60, 70, 80, or 90% faster than the wild song from which the syllable was taken (e.g. Fig. 1b). To construct broken song models, syllables were concatenated as triplets, separated by silent gaps, with the trill rate within each multisyllable segment remaining the same as the wild song from which the syllable was taken (e.g. Fig. 2b). The duration of gaps introduced between multisyllable segments equalled the mean value for broken songs produced by birds in Podos (1996), in which the ratio of the syllable period within multisyllable segments (asterisk in Fig. 1c) to the syllable period across gaps (double asterisk in Fig. 1c) averaged 0.586.

We presented all 10 model songs to all birds. Birds were tutored twice daily, once in the morning and once in the afternoon, beginning at  $19 \pm 1$  days and continuing until  $103 \pm 1$  days posthatch, covering the sensitive phase for song acquisition reported for this species in the laboratory (Marler & Peters 1988). Each tutoring session lasted approximately 40 min, during which time each song type was played 24 times, at a rate of six songs/min, before the onset of the next song type (Marantz PMD 221 recorder, Paso 5000 amplifier, Realistic 40-1298 speakers).

The following spring, we recorded all birds once a week (Marantz PMD 221 recorder, Realistic 33-1070A microphone, and Digitech RDS 1900 digital delay to facilitate automatic recording), beginning with the onset of motor development at  $303 \pm 9$  days and continuing until



**Figure 2.** Construction of song models with broken syntax. (a) Wild swamp sparrow song. (b) Song model constructed with broken syntax. Note that the trill rate (within multisyllable segments) remains unchanged. Sonagrams produced as in Fig. 1.

377 ± 8 days of age when individuals had crystallized their adult song repertoires. A 1-kHz test tone (General Radio model 1567) was recorded at the beginning of each recording session to provide a reference for checking tape speed accuracy. We determined each bird's adult song repertoire by visual examination of spectrograms (e.g. Marler & Peters 1982). Song types that were copied from model songs were identified by assessing the similarity of song models and putative copies according to note structure and the sequence of notes within syllables (e.g. Marler & Peters 1988). Song types for which models could not be identified were excluded from further analysis (as in Marler & Peters 1977; Podos 1996).

Three to five renditions of each crystallized song type from each bird were digitized at 25 kpt/s; the accuracy of tape speed was checked using the recorded test tones as a standard. The copy accuracy of these songs was assessed both with respect to overall song organization (including timing and syntactical organization) and also with respect to the accuracy of note copying. For the former, we used oscillograms to measure temporal features including trill rate (as in Podos 1996, 1997) and gap duration in broken songs. We also used sonagrams to identify note omissions and other deviations from normal trilled syntax. To assess the accuracy of note copying, we used spectrogram cross-correlation analysis, which quantifies the similarity between model notes and corresponding copies in terms of their time-varying frequency and amplitude structure (Clark et al. 1987; Nowicki & Nelson 1990; Beeman 1998). This technique has been used successfully in prior studies of swamp sparrow phonology, and yields results which closely match intuitive

impressions of overall similarity based on visual examination of spectrograms (Clark et al. 1987; Podos 1996). We performed cross-correlations without frequency shifting (Engineering Design 1996; Beeman 1998), limited the analysis frequency range from 1 to 9 kHz, and calculated spectrograms using 256-point fast Fourier transformations (FFTs) and 150 time steps. Values for all measures were averaged according to song type or note type before statistical analysis (as in Podos 1996).

## RESULTS

We identified a total of 23 song copies produced by the 10 birds. All models were copied at least once, and all birds produced at least one copy ( $\bar{X} \pm SD = 2.3 \pm 1.06$  song type copies/bird). Five birds produced copies of songs from two different model classes, and two birds copied songs from all three model classes. A summary of the features of these song copies is presented in Table 1. The number of songs copied from the three model classes did not differ from values expected if birds copied randomly in proportion to the number of different model types they heard (observed: 4 control, 7 rapid, 12 broken; expected: 4.6 control, 9.2 rapid, 9.2 broken;  $\chi^2 = 1.41$ , NS). This result suggests that songs across the three model classes were equally acceptable as training models.

Across all three model classes, songs generally were reproduced with slower trill rates than the models from which they were copied (Table 1; paired *t* tests: control models,  $t_3 = 3.472$ ,  $P = 0.040$ ; rapid models,  $t_6 = 2.514$ ,  $P = 0.046$ ; broken syntax models,  $t_{11} = 2.455$ ,  $P = 0.032$ ).

**Table 1.** Features of songs copied from three model classes

	Model class		
	Control (2)*	Rapid (4)	Broken (4)
<i>N</i> song copies	4, from 4 birds	7, from 6 birds	12, from 9 birds
Syntax of copies	Normal	Normal or broken	Normal or broken
Trill rate reduction†	11.6±8.7%	20.4±20.8%	6.9±11.1%
Note omissions‡	0	0	0–1
Note drop-outs§	0	0–1	0

The values presented in the lower three rows refer to pairwise comparisons between song models and their copies.

\**N* training songs in each class.

†Mean (±SD) percentage by which trill rates of copies were lower compared with trill rates of their models (as in Podos 1996). Trill rates of copies with broken syntax were determined from within multisyllable segments.

‡Range of number of note types from song models not produced in copies (as in Podos 1996). Omissions of note type I (Marler & Pickert 1984), which occurs often in laboratory rearing of this species, were excluded from this definition.

§Range of number of note types from song models reproduced at the beginning of copies but dropped out over the course of song production (illustrated in Fig. 3c, e).

The syntax of copies of control songs accurately matched the models, with all model notes being accurately reproduced in a normal continuous syntax (Table 1). The only exception was an occasional failure to reproduce type I notes (sensu Marler & Pickert 1984) in a syllable, which is typical and consistent with previous studies (Marler & Peters 1988, 1989; Podos 1996).

Reproductions of rapid models expressed three distinct and mutually exclusive types of syntactical modifications in comparison to the model songs from which they were copied: (1) a pronounced decrease in trill rate; (2) broken syntax; and (3) the dropping out of notes as the song progressed. A pronounced reduction in trill rate occurred in four copies, each produced by a different bird, with an average (±SD) reduction in trill rate of 34.8 ± 12.7%. Broken syntax occurred in a single copy (Fig. 3a versus b) and, as was observed by Podos (1996), the trill rate within multisyllable segments achieved a control level of accuracy (7.5% reduction of the original rate). Two copies sung by two different birds were produced with notes omitted from syllables occurring later in the song (Fig. 3a versus c, d versus e), a pattern not observed in earlier work; the trill rates of these copies also achieved control levels of accuracy (a 6.5 ± 1.4% reduction). As was observed by Podos (1996), the type of deficiency expressed in a reproduced song corresponded to the degree to which the trill rates of model songs had been manipulated before presentation. Copies of model songs for which trill rates had been increased by 60 and 70% all expressed a pronounced trill rate reduction, while copies of model songs with trill rate increases of 80 and 90% expressed either broken syntax or note drop-outs.

Songs copied from broken syntax models were crystallized with either normal (*N*=9 song types from seven birds; e.g. Fig. 4a versus b) or broken syntax (*N*=3 song types from two birds; e.g. Fig. 4a versus c, d versus e). Both types of reproductions achieved control levels in trill rates (trill rate reductions for normal syntax reproductions=5.7 ± 11.1%, and for broken syntax reproductions=10.5 ± 12.3%). All copies also achieved control levels in the reproduction of other features, with the

exception of one copy (with broken syntax) in which a model song note failed to be incorporated into the copy ('note omissions' in Table 1). For those copies produced with broken syntax, the syllable period across gaps (see Fig. 1 for definition) was reproduced precisely, within 24.1 ± 17.3 ms of their models.

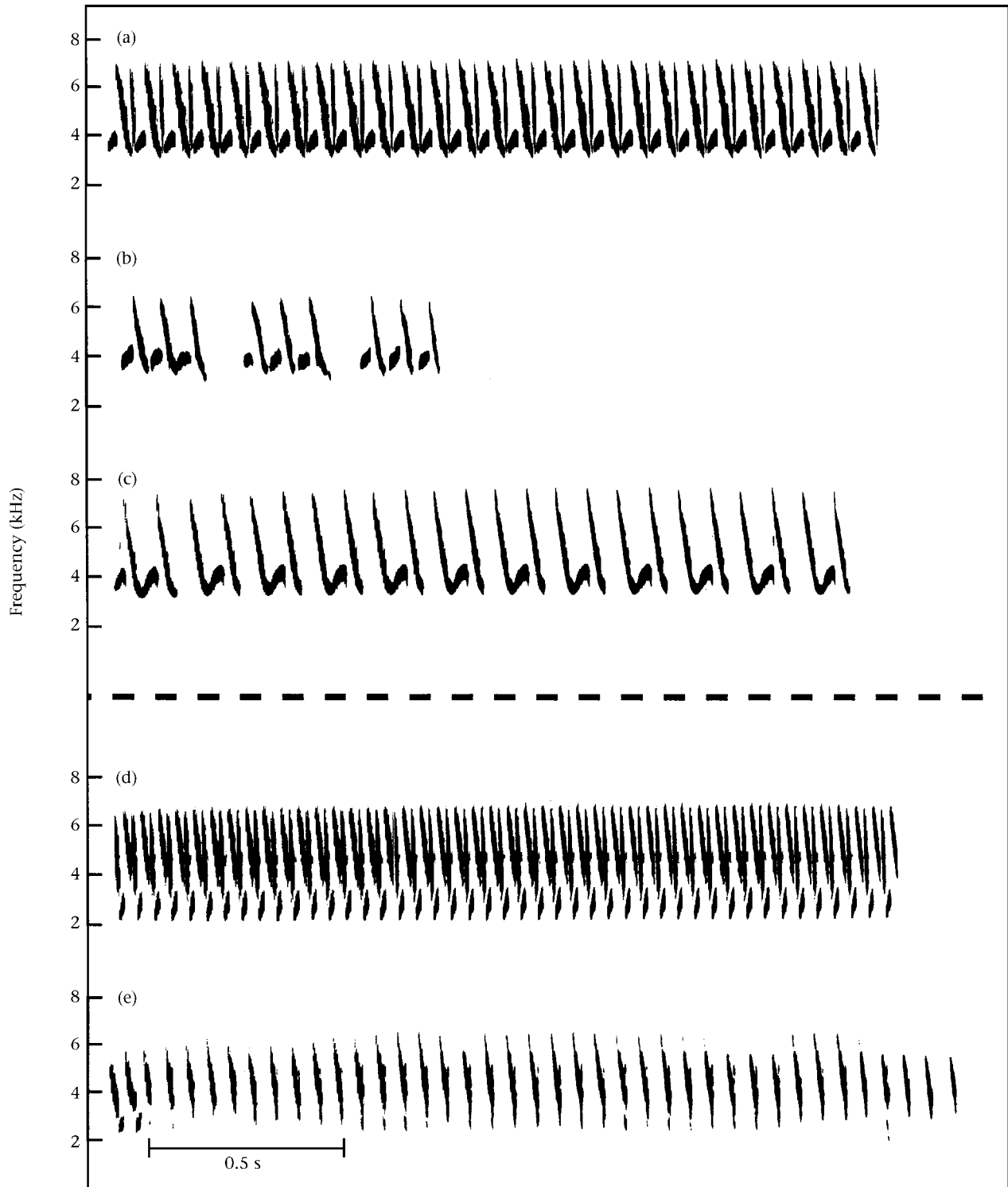
The accuracy of note copying, as measured by spectrogram cross-correlation, is summarized in Fig. 5. Analysis of variance (ANOVA) revealed significant heterogeneity among model conditions for cross-correlations (Fig. 5;  $F_{2,71}=3.381, P=0.043$ ). Post hoc Tukey tests, however, failed to reveal significant differences among condition pairs (control × rapid,  $P=0.057$ ; control × broken,  $P=0.818$ ; broken × rapid,  $P=0.091$ ), although the difference between the control and rapid song conditions approached significance.

## DISCUSSION

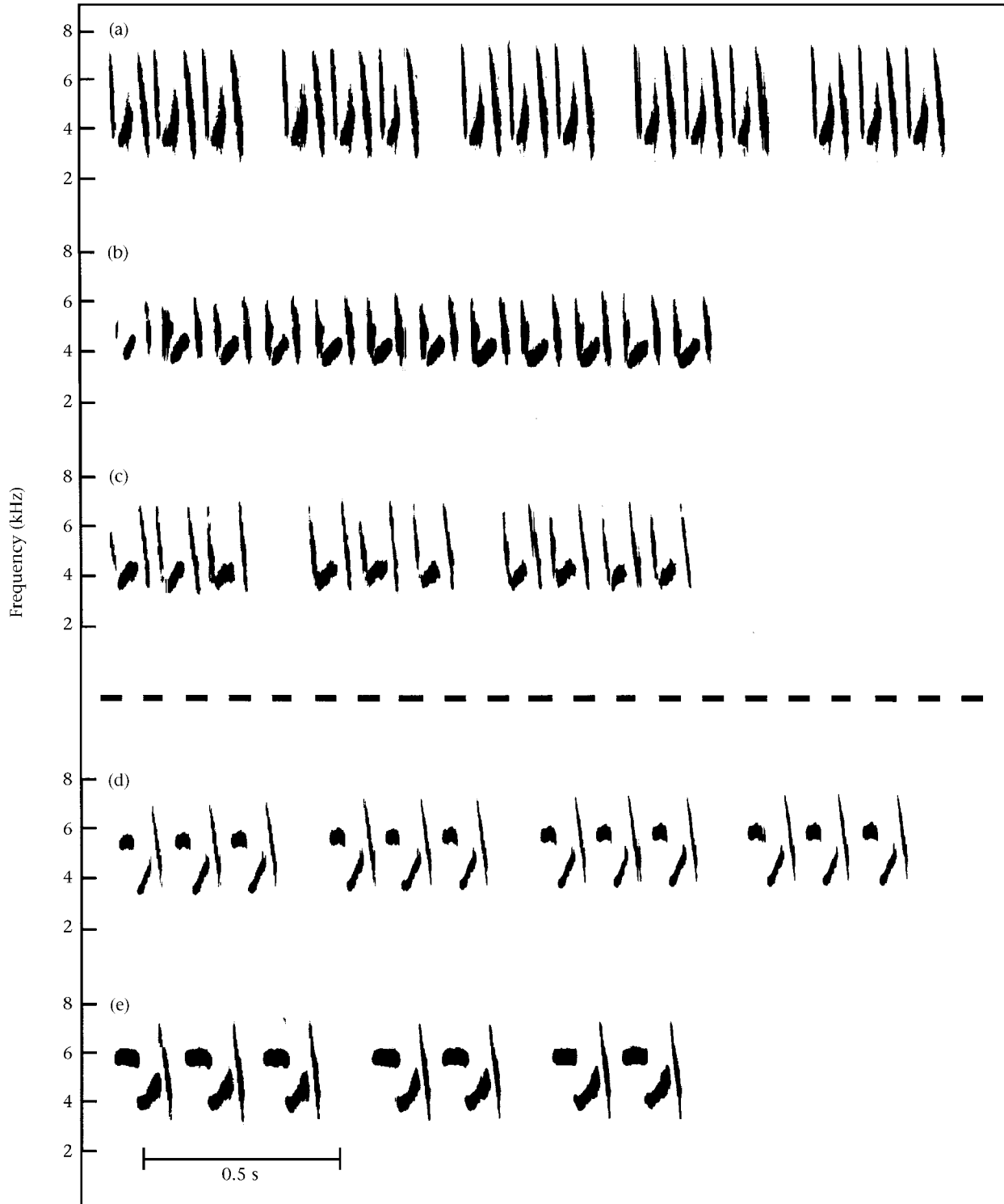
The birds in our experiment learned from broken syntax model songs in the same proportion as they heard these songs during training (Table 1), demonstrating that young swamp sparrows do not have a sensory bias against memorizing broken syntax songs during the sensory phase of learning. Furthermore, birds reproduced some of these songs with a broken syntax closely matching the syntax of the models they copied. This result demonstrates that the broken syntax song structure may be both memorized and reproduced faithfully, despite the fact that it is extremely atypical of wild swamp sparrow song. Before discussing the implications of this finding, we first examine how birds reproduced the control and rapid song models.

### Reproduction of Control Models

Our reason for including a control condition was to provide a baseline against which copying accuracy across the other conditions in our experiment could be compared. As expected, birds reproduced control songs with



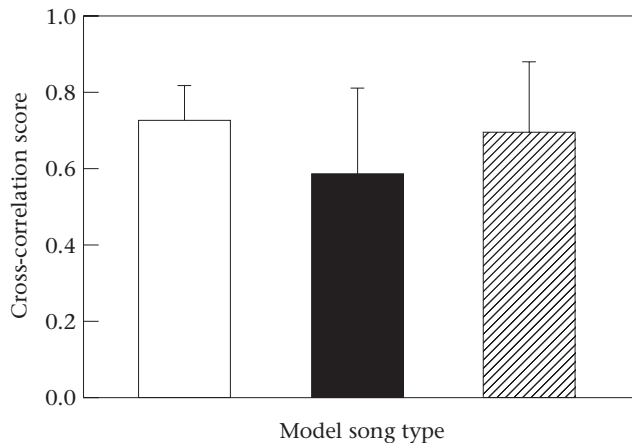
**Figure 3.** Song learning from rapid-trill models. Song (a) served as a model for copies (b) and (c), and song (d) served as a model for copy (e). The trill rates of the two models (a, d) were increased above natural rates by 80 and 90%, respectively. The repeating syllables in song model (a) are composed of, in order, note types II, VI and I (note classification follows [Marler & Pickert 1984](#)). The repeating syllables in song model (d) are composed of, in order, note types I, II and VI. In all three copies, model trill rates were reproduced with a baseline degree of accuracy, but other features of the copies were degraded. All copies were produced with the note type I of the model completely omitted. Copy (b) was reproduced with broken syntax. In both copies (c) and (e), the model was reproduced well except that one additional note of the repeating syllable was dropped out after the first two syllable repetitions (the omitted note is note type II sensu [Marler & Pickert 1984](#) in both cases); this omission occurs every other syllable in copy (c) and every syllable in copy (e). All of these deficiencies are consistent with a hypothesis of performance limits on vocal mechanics. Note that the first copy shown is from the second half of a two-trilled song, which occasionally occur in this species. Sonagrams produced as in [Fig. 1](#).



**Figure 4.** Song learning from broken models. Song (a) served as a model for copies (b) and (c), and song (d) served as a model for copy (e). Some song models, such as song model (a), were reproduced either with normal syntax or with broken syntax. Sonograms produced as in Fig. 1.

normal syntax. Notes learned from control songs also were copied with a high degree of accuracy; the cross-correlation algorithm yielded average scores exceeding 0.72, similar to the results of Clark et al. (1987) and Podos

(1996). Unexpectedly, trill rates of control copies were significantly slower than the trill rates of their models, by an average of 11.6% (Table 1). Podos (1996), the only other study we know of that quantitatively compared the



**Figure 5.** Note-copying accuracy across the three training conditions, as determined by spectrogram cross-correlation scores. Error bars are standard deviations. Sample sizes were 17 notes in the control condition (□), 21 notes in the rapid condition (■), and 36 notes in the broken condition (▨).

trill rates of model and copy songs, also found a decrease in the trill rates of songs copied from normal models, but only on the order of 3.3%. We recorded test tones of known frequency at the beginning of each recording session, allowing us to rule out mechanical problems with tape recorders used for recording and analysis as the cause of this systematic reduction in trill rate. It is conceivable that the recorder used to play tutor tapes began to run off-speed over the almost 3 months of training, but we deem this possibility unlikely, especially since we now have observed a trill rate reduction in two independent experiments in which different equipment was used. Another possible reason for the overall reduction in trill rate in our experiment is that birds that reproduced rapid models at slower trill rates may have similarly reproduced other models at slower speeds, through a carry-over effect. To test this idea, we compared the magnitude of reduction in trill rate for copies of nonrapid models (i.e. control and broken models) from (1) birds that also produced copies of rapid models ( $N=7$  copies) and (2) birds that did not copy any rapid models ( $N=4$  copies). No statistical difference between these groups was found (Mann–Whitney  $U=5$ , NS), arguing against the likelihood of a carry-over effect among different learned song types. At present, the significance of these trill rate reductions in our learning experiments remains unexplained.

### Reproduction of Rapid Models

Copies of rapid models were reproduced in three different ways, consistent with the patterns observed earlier by Podos (1996). Some copies were reproduced with normal syntax but at severely reduced trill rates. These reductions in trill rate ( $\bar{X}=34.8\%$ ) far exceeded the 11.6% reduction observed in control copies, and they account for the high average reduction in trill rate across the condition (20.4%; Table 1). The remaining copies were reproduced with baseline accuracy in trill rates, but either with broken syntax or with notes being dropped out over the

course of the song (Fig. 3). These copy inaccuracies are consistent with a vocal motor constraint hypothesis (Nowicki et al. 1992; Podos 1996, 1997), which argues that the inability to produce songs beyond particular trill rates, for given durations, reflects physical limits on respiratory, syringeal and/or vocal tract motor patterns (see also Suthers & Goller 1998; Podos & Nowicki, in press). The accuracy of note copying of rapid songs was statistically indistinguishable from that in the other conditions (Fig. 5), supporting the contention that increases in trill rate do not limit a bird's ability to hear, memorize and produce normal phonology (Podos 1996). That swamp sparrows can learn well from unusually rapid songs is not surprising, given their ability to discern note timing on an extremely fine scale (Kreutzer et al. 1991).

Our analysis of songs copied from rapid models also provides further evidence for a performance threshold in the types of deficiencies birds express, as suggested by Podos (1996). Combining data from the present experiment and from Podos (1996), those song models for which trill rates were increased 80% or more were always reproduced with a major organizational change, expressed either as broken syntax or as notes being dropped out of syllables as songs progressed (Fig. 3; see also Table II of Podos 1996). By comparison, almost all songs (16/17) copied from models with less extreme increases in trill rates (26–70%) were reproduced with normal trilled syntax and without note drop-outs over the course the song, although these songs expressed deficiencies in other features such as inaccuracies in trill rate.

### Reproduction of Broken Models

Our finding that swamp sparrows were able to learn from broken syntax models is not surprising in itself. Prior work had demonstrated that swamp sparrows, when deprived of conspecific song models, will learn from 'hybrid' songs composed of conspecific syllables presented in the context of a heterospecific syntax, such as the multisegmented structure characteristic of song sparrow, *M. melodia*, song (Marler & Peters 1977). The fact that the birds in our experiment learned from broken syntax models as readily as they did from normal models (Table 1) is less expected, given that young swamp sparrows strongly prefer to copy conspecific songs when tutored with both conspecific and heterospecific models (Marler & Peters 1977, 1989). Marler & Peters (1980) argued that this species' learning preference for conspecific songs depends on the recognition of species-typical phonology more than it does on recognition of species-typical syntax, based on experiments in which swamp sparrows learned equally from a selection of songs composed of either a single trill or of two trills presented continuously. The fact that the broken syntax of our models is even more atypical of wild swamp sparrow song than continuous two-parted trills (which do occur rarely in nature) lends further support to this hypothesis.

Much more unexpected is our finding that some broken syntax songs, when memorized, were subsequently reproduced with a broken syntax matching the model. In



earlier work, such as the ‘hybrid’ song model experiments mentioned above (Marler & Peters 1977), swamp sparrows invariably rearranged phonology they learned from songs having heterospecific syntax into the form of continuous trills. Even birds raised in complete isolation, having no models at all to copy, invariably produce their otherwise aberrant songs as continuous trills (Marler & Sherman 1985). This tendency for swamp sparrows to arrange learned syllables into continuous trilled syntax has been so consistent across experiments that Marler (1984) posited the presence of a central motor programme for the production of trilled syntax.

One might wonder whether the reproduction of broken syntax we observed is the result of motor performance limits, as was argued by Podos (1996) for birds learning from models with experimentally increased trill rates. This is not likely the case, however, because the broken song models used in the present experiment had normal trill rates (Fig. 2). Thus, the reproduction of broken syntax in this case must instead reflect a previously unidentified dimension of permissiveness in song learning, not only in what swamp sparrows will memorize but also in what they will subsequently reproduce.

One possibility is that swamp sparrows in our experiment more readily accepted and reproduced broken syntax models because this syntax, although completely atypical of normal swamp sparrow song, was not an entirely arbitrary novelty. The broken syntax we used in training songs emerged as the result of a motor challenge in production (Podos 1996). When faced with difficulty in reproducing a memorized song with a trill rate faster than the vocal production apparatus can manage, one stable ‘solution’ by the motor system appears to be the production of broken syntax. Because sensory and motor mechanisms underlying song learning and production are highly coupled in the songbird brain (Nottebohm 1984; Margoliash & Konishi 1985; Williams & Nottebohm 1985; Nottebohm et al. 1990), it is possible that the evident predisposition of the motor system to produce broken syntax is matched by a predisposition, or at least a tolerance, to learn and reproduce this particular behavioural novelty.

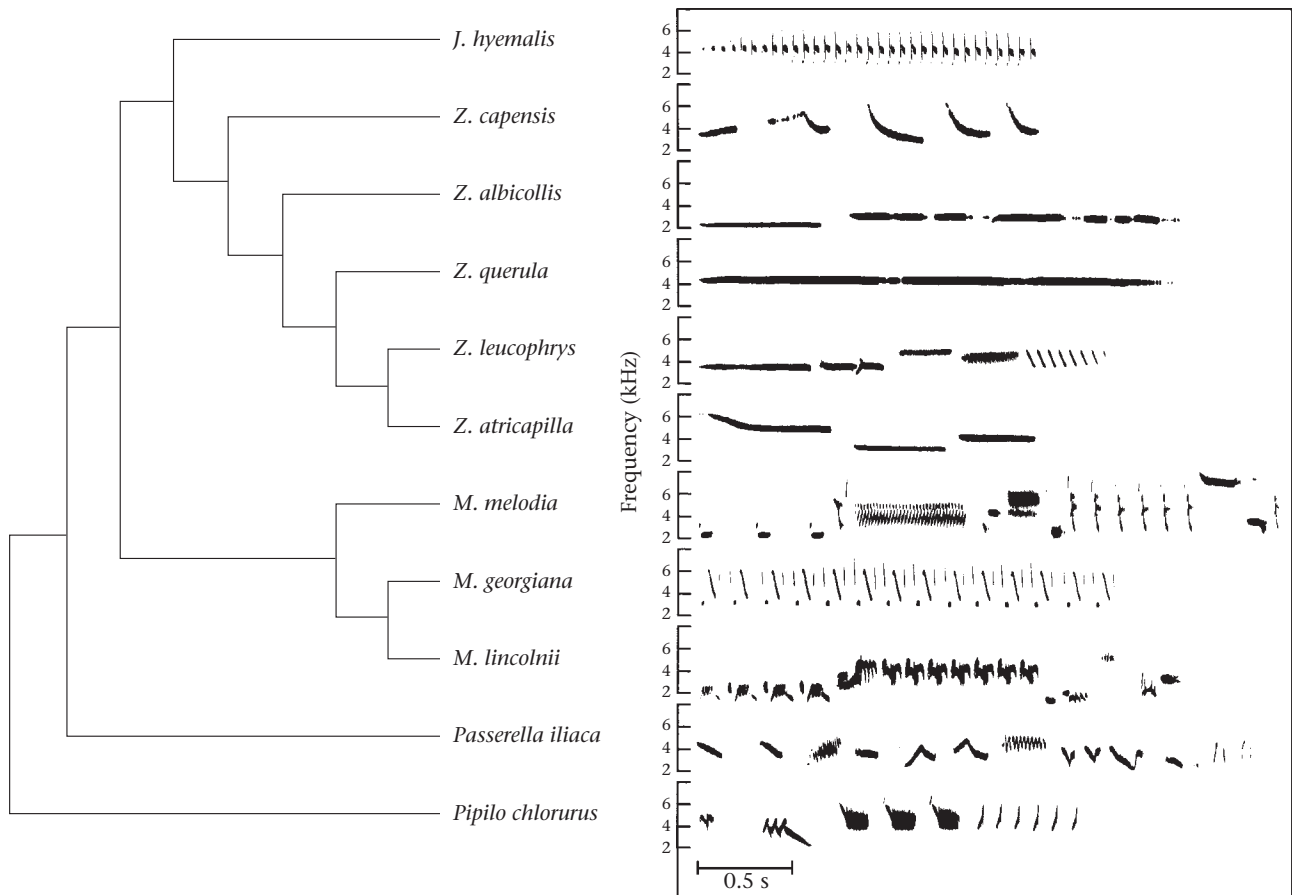
### Evolution of Vocal Syntax

Our demonstration of permissiveness in syntax learning suggests a mechanism that could account for the evolution of major organizational changes in the structure of bird song. The evolution of song has been described in longitudinal studies of wild populations for a number of bird species, and evolutionary changes have been documented for a variety of vocal features including the fine structure of notes (Jenkins 1978; Grant & Grant 1996), the addition or deletion of notes (Ince et al. 1980), changes in note or note type order (Payne 1996), and the blending of elements from multiple models (Slater 1989; Payne 1996). In general these changes represent relatively minor modifications of song structure falling within the range of species-typical songs, which is not surprising given that both cultural selection (related to how birds learn to sing) and biological selection (related to how

songs function in male–male and male–female interactions) tend to be stabilizing (see also Theilcke 1972; Slater 1986). Furthermore, observed changes have occurred primarily on the level of phonology; that is, they have involved changes in the structure, presence, or position of notes (e.g. Grant & Grant 1996). By contrast, large-scale evolutionary changes in the structural organization of song, including syntax, have not been described. Understanding how such structural changes might arise would be particularly informative because much of the apparent between-species diversity in song occurs at the level of syntax. For example, in the *Melospiza–Zonotrichia* clade, song has diverged most extensively in syntax, with some songs arranged as series of whistles, others as simple trills, and others as trills interspersed with groups of un-repeated notes (Fig. 6). How then might small-scale evolutionary changes in vocal features, thus far documented primarily on the level of phonology, accrue to the extent required to explain macroevolutionary diversity in syntax? This problem was well stated by Martens (1996, page 222), in a review of vocal diversity among several songbird groups: ‘Although learning processes routinely allow small variants, the basic parameters of the territorial song stay remarkably uniform in space, across large geographic regions and also through time (although we can only infer that indirectly). To grasp the principles of speciation from an acoustic–ethological viewpoint, then, we must understand how the stabilizing song tradition, which maintains the cohesion of all individuals of a species as a biological unit, can be breached.’

Our findings suggest that limitations on motor performance might provide one mechanism by which large-scale changes in vocal syntax originate, at least in sparrows. Female preferences for song features that potentially indicate male quality, such as faster trill rate, more notes per syllable, and so forth, may lead to selection on males to produce songs that challenge their motor performance capacities (Andersson 1994). It is not known whether female sparrows indeed prefer songs with enhanced trill rates, although Vallet & Kreutzer (1995) found that female canaries give higher rates of copulation solicitation displays to male songs with higher trill rates. If motorically challenging songs are indeed favoured by selection, then the motor systems involved in production should regularly face performance limits during song evolution, which in turn might lead to alternative modes of production such as broken syntax in the present case (Podos 1996, 1997). Consistent with this view, songs with broken syntax similar to that described here are observed in nature on rare occasions, for other species of the family Emberizidae that normally sing continuous trills including *Spizella passerina* (B. Lohr, unpublished recordings; see also Mathews 1921, page 102), *Pooectes gramineus* (Cornell LNS catalogue no. 15373), *Geospiza fortis* (R. I. Bowman recordings) and *Certhidae olivacea* (R. I. Bowman recordings).

Even if broken syntax songs can originate in this way, additional criteria need to be met for this novel song organization to be maintained in a population. First, young birds must be able to learn from and reproduce songs with broken syntax. The data we present here



**Figure 6.** Species-level diversity in songbird courtship song, across three sparrow genera (*Junco*, *Zonotrichia* and *Melospiza*) and two outgroup species. Songs of these species, for which typical examples are illustrated on the right as sound spectrograms, vary along many levels of organization including the fine structure of notes (phonology), the arrangement of notes into higher-order units, and the higher-level organization of song (syntax). The phylogenetic hypothesis of Zink & Blackwell (1996) on the left provides a framework for reconstructing evolutionary transformations in sparrow song structure. Some phylogenetic continuities in song features can be detected, such as in the structure of whistles in *Zonotrichia*, and in frequency–timing relationships within trills (Podos 1997). Still, song evolution appears to be strongly evolutionarily labile, given (1) large-scale differences in song features among closely related species, such as in song syntax among the *Melospiza*, and (2) multiple evolutionary origins of modes of higher-order song organization, such as the independent origin of trills (Podos 1997) in *Z. leucophrys* with reference to the other trilling species illustrated.

demonstrate that swamp sparrows are indeed capable of learning broken syntax models, and thus that these songs can be transmitted across generations. Another critical criterion required for broken syntax to be maintained over time is that songs with broken syntax would need to be functional in the contexts of territorial defence and mate attraction (Searcy & Andersson 1986; Kroodsmas & Byers 1991). Further work is needed to determine whether or not such is the case.

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