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Calibration of song learning targets during vocal ontogeny in swamp sparrows, *Melospiza georgiana*

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Song learning in songbirds often includes an extended sensorimotor phase, in which birds gradually refine their vocal output to produce accurate copies of previously memorized song models. Increasing accuracy of song model reproduction during this phase occurs as birds refine the neural substrates that underlie vocal control, and as they develop proficiency with the vocal apparatus. We here test the hypothesis that sensorimotor learning also provides birds with an opportunity to calibrate their vocal learning targets, in the event that a bird's own vocal proficiency differs from that required to successfully reproduce song models to which it is exposed. We tutored hand-reared male swamp sparrows with song models that we manipulated to vary in how challenging they would be to reproduce, and then tracked patterns of song development. The calibration hypothesis was supported by two lines of evidence. First, we found that copies of manipulated models underwent comparatively large-scale modifications in syntax and note composition over development, in directions consistent with expectations about motor proficiency relative to the structure of learned models. Second, we found that birds tended to retain selectively, in their crystallized repertoires, song types that appeared to be comparatively easy to produce. Our results are consistent with an 'active' model of song learning, and also suggest a specific mechanism by which learning can act as a creative or a stabilizing force in song evolution.

Song development in songbirds typically is characterized by an early 'sensory' phase during which song models are memorized, followed by a 'sensorimotor' phase during which young birds retrieve and reproduce the song models they have stored in memory (Konishi 1965; Marler 1970, 1976; Slater 1989; Nelson & Marler 1993). During the sensory phase, model acquisition is guided by an innate neural mechanism (a 'template', Konishi 1965; Nottebohm 1968; Marler 1976) that normally restricts the range of models birds memorize to conspecific songs heard during a sensitive period for song acquisition (Marler & Peters 1977, 1987; Nelson & Marler 1993). The sensorimotor phase begins as birds produce highly variable, amorphous vocalizations that bear little resemblance to typical adult song (Nice 1943; Thorpe 1958; Marler & Peters 1982b). During an extended period of motor practice, sometimes lasting well over a month, young birds refine their vocal output and eventually produce stereotyped ('crystallized') copies of memorized models (Marler & Peters 1982d).

Two broad hypotheses have aimed to explain the proximate function of the sensorimotor phase of song learning. The first hypothesis is that birds require experience to develop and refine the neural substrates required for vocal control and accurate song model reproduction (Brainard & Doupe 2002). Sensorimotor learning depends on auditory feedback, as birds compare the auditory experiences of their own vocal output to memorized representations of song models (Konishi 1965; Nottebohm 1968). Such comparisons guide the production of subsequent renditions, and eventually enable birds to produce precise matches of training models (Nottebohm 1970; Marler 1976; Konishi 1985). Recent work has aimed

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to document cellular and synaptic modifications in auditory and vocal control pathways that occur during sensorimotor learning (e.g. Nordeen & Nordeen 1997; Mooney 1999). The development of the robust nucleus of the archistriatum (RA) vocal control nucleus, for example, appears to be shaped by patterns of neural activity in the anterior forebrain pathway, in a way that presumably helps to specify the structure of adult song (Akutagawa & Konishi 1994; Kittelberger & Mooney 1999; Brainard & Doupe 2002).

A second, related hypothesis to explain the proximate function of sensorimotor song learning focuses on the mechanics and proficiency of the vocal apparatus itself (Marler 1976; Marler & Peters 1982c; Konishi 1985). Successful vocal production in adult birds requires precise coordination of the two sides of the syrinx, as well as coordination of syringeal activity with the respiratory system and with movements of the suprasyringeal vocal tract (Nowicki & Marler 1988; Suthers 1990; Nowicki et al. 1992; Westneat et al. 1993; Fee et al. 1998; Hoese et al. 2000; Podos et al. 2004). Recent evidence suggests that adult songbirds often sing at or near their maximum vocal performance capacities (Lambrechts 1996; Podos 1997, 2001; ten Cate et al. 2002; reviewed by Podos & Nowicki, in press). Thus, young birds may require practice to achieve baseline levels of motor proficiency before they can successfully begin to reproduce song models. This process is analogous to the need for musicians to learn basic skills with an instrument before being able to learn and perform a particular piece of music. Some patterns in bird song development are consistent with this hypothesis. Young song sparrows, *Melospiza melodia*, for instance, produce vocal tract movements normally associated with singing only after the syringeal contribution to song has begun to stabilize in development (Podos et al. 1995). Neural and peripheral motor hypotheses for sensorimotor learning are not mutually exclusive; young songbirds may face constraints both in the development of vocal control pathways and in the development of basic motor coordination skills.

We here propose a third hypothesis to explain the proximate function of sensorimotor song learning. We suggest that sensorimotor learning provides a mechanism by which birds can calibrate their targets of song learning (i.e. their 'exact' templates, sensu Catchpole & Slater 1995) in the event of a mismatch between their vocal proficiency and the demands required for the reproduction of certain song models. This calibration hypothesis is suggested by recent studies that indicate female preferences for songs that are particularly challenging to produce. For example, females of some species appear to prefer rapid trills with wide frequency bandwidths (Vallet et al. 1998; Draganoiu et al. 2002; Ballentine et al. 2004), which are relatively difficult to produce because of physical constraints associated with rapid beak movements (Podos 1996, 1997; Hoese et al. 2000; Podos & Nowicki, in press). Sexual selection thus may drive young males to learn songs that are challenging to produce, and some models may fall outside of the range of a bird's vocal proficiency. Returning to our analogy to human music, a musician in a competition may benefit by choosing a piece that is difficult to perform, although there may be some pieces that are beyond his or her competency to perform well. Calibration of learning targets would allow birds to adjust the structure of particularly challenging song models so that they fall within the range of their vocal proficiency, or could allow individuals to selectively retain, among the many songs they might have acquired during the sensory phase, those they can reproduce most successfully.

Swamp sparrows produce trilled songs comprising multinote syllables repeated at steady rates (e.g. Marler & Peters 1977; Marler & Pickert 1984; Fig. 1). Hand-reared male swamp sparrows tutored with song recordings have been shown to accurately reproduce a wide range of model features including note structure, syllable composition, trilled syntax and trill rate (Marler & Peters 1977, 1981). In a study of proximate constraints on trill production, Podos (1996) tutored young male swamp sparrows with models that had been manipulated to increase trill rates above normal levels. Birds proved able to memorize these challenging 'rapid' models but were unable to reproduce them accurately. Some rapid models were reproduced with diminished trill rates, others with notes omitted, and others with a 'broken' syntax, in

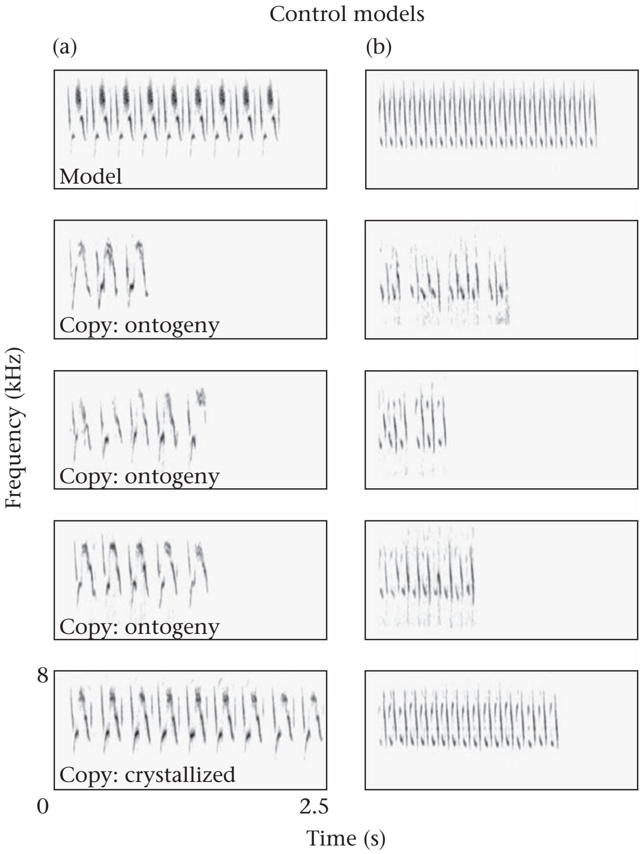

Figure 1. Representative examples of patterns of vocal development in this study, from control models. Here and in Figs 2 and 3, the upper spectrogram in each column illustrates the model that was copied, the middle three spectrograms illustrate developmental intermediates, and the lower spectrogram illustrates the crystallized song.

which song copies were produced as bursts of syllables interspersed with silent gaps. In a second experiment, Podos et al. (1999) reared young swamp sparrows with control models, 'rapid' models and models with normal trill rates but with broken syntax. The latter 'broken syntax' models were predicted to be especially easy to reproduce, given the presence of pauses between syllables with normal trill rates (Podos et al. 1999). Some copies of broken syntax were reproduced with broken syntax, although others were restructured towards the species-typical, continuous syntax.

These studies suggest that sparrows may compensate during learning for mismatches between their own vocal proficiency and that required for accurate model reproduction. It is not clear, however, when and how such compensation occurs. It may be that birds modify their learning targets during the sensory phase, as they memorize song models. Thus, for instance, birds tutored with rapid trill models (Podos 1996) might have adjusted templates of model songs during the memorization process, to encode broken syntax. Alternatively, young birds might calibrate their targets of learning during the sensorimotor phase. Swamp sparrows reared with rapid trill models, for instance, might have worked through a series of vocal trials and errors that led to motor solutions such as reductions in trill rate and broken syntax production (Podos 1996).

As a first test of the calibration hypothesis, we here analyse vocal ontogeny in a group of swamp sparrows that we tutored with three classes of song models (control, 'rapid' and 'broken syntax' models) that varied widely in the challenges they posed to birds with regards to accurate reproduction (Podos et al. 1999). The calibration hypothesis makes four predictions about how birds should learn from rapid and broken syntax models as compared to control models (Table 1). These predictions focus on two broad aspects of song development: structural transitions within song types and patterns of song type attrition (Marler & Peters 1981, 1982a; Nelson & Marler 1994). None of these patterns of song development are predicted by the two current hypotheses of sensorimotor learning (above), or by the hypothesis that birds calibrate song learning targets prior to sensorimotor development, during song model memorization.

METHODS

Sample

Our subjects were 10 hand-reared male swamp sparrows collected as nestlings in May 1995 from a population in Crawford County, Pennsylvania, U.S.A. These birds are the same as those described in Podos et al. (1999). Nestlings were fed a standard diet containing ground beef, hard-boiled eggs, tofu, monkey chow, pureed carrots, wheat germ, avian vitamin powder, and a powdered calcium supplement (see Searcy et al. 2004). Birds were transferred at 19 ± 1 days posthatch to individual cages ($46 \times 22 \times 26$ cm) placed inside two walk-in acoustic isolation chambers ($1 \times 1 \times 2$ m each, 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.

Birds were tutored with 10 song models: two 'control' models with normal trill rates and normal syntax, four 'rapid' models with rapid trill rates and normal syntax, and four 'broken syntax' models with normal trill rates and broken syntax. Models were constructed using Signal software (Engineering Design 1996). Details of model construction and song tutoring are provided in Podos et al. (1999). In brief, we digitized field recordings of 10 different swamp sparrow songs, at a sampling rate of 25 kilopoints per second. We selected a single syllable from each of the digitized songs, produced digital copies of each syllable, and arranged syllable copies in sequence so as to create model songs. For control models, we repeated syllables at the trill rates of the wild songs from which syllables were sampled (Fig. 1, top panels). To construct rapid models, we decreased the duration of internote and

Table 1. Predictions of the calibration hypothesis

Pattern in song ontogeny	Prediction	Example
Structural transitions within song types	Elevated levels of experimentation with song patterns, with potentially abrupt structural transitions.	Higher number of syntax forms over ontogeny; greater structural disparity among practiced forms.
	Specific adjustments during ontogeny that allow birds to better match their own levels of vocal proficiency.	Reductions in song trill rates, omission of notes, or insertion of gaps between song segments over ontogeny.
	Transitions in ontogeny away from the structure of models, for performance-related song features.	Accurate reproduction of model syntax during initial phases of vocal ontogeny, with eventual transitions to other forms of syntax.
Retention and attrition of different song types	Preferential retention of song types that are comparatively easy to reproduce.	Retention of songs with fewer notes per unit time, or with a more narrow frequency bandwidth.

Predictions refer to the expected patterns in song ontogeny in the event of a disparity between a bird's own vocal proficiency and that required to reproduce a memorized model.

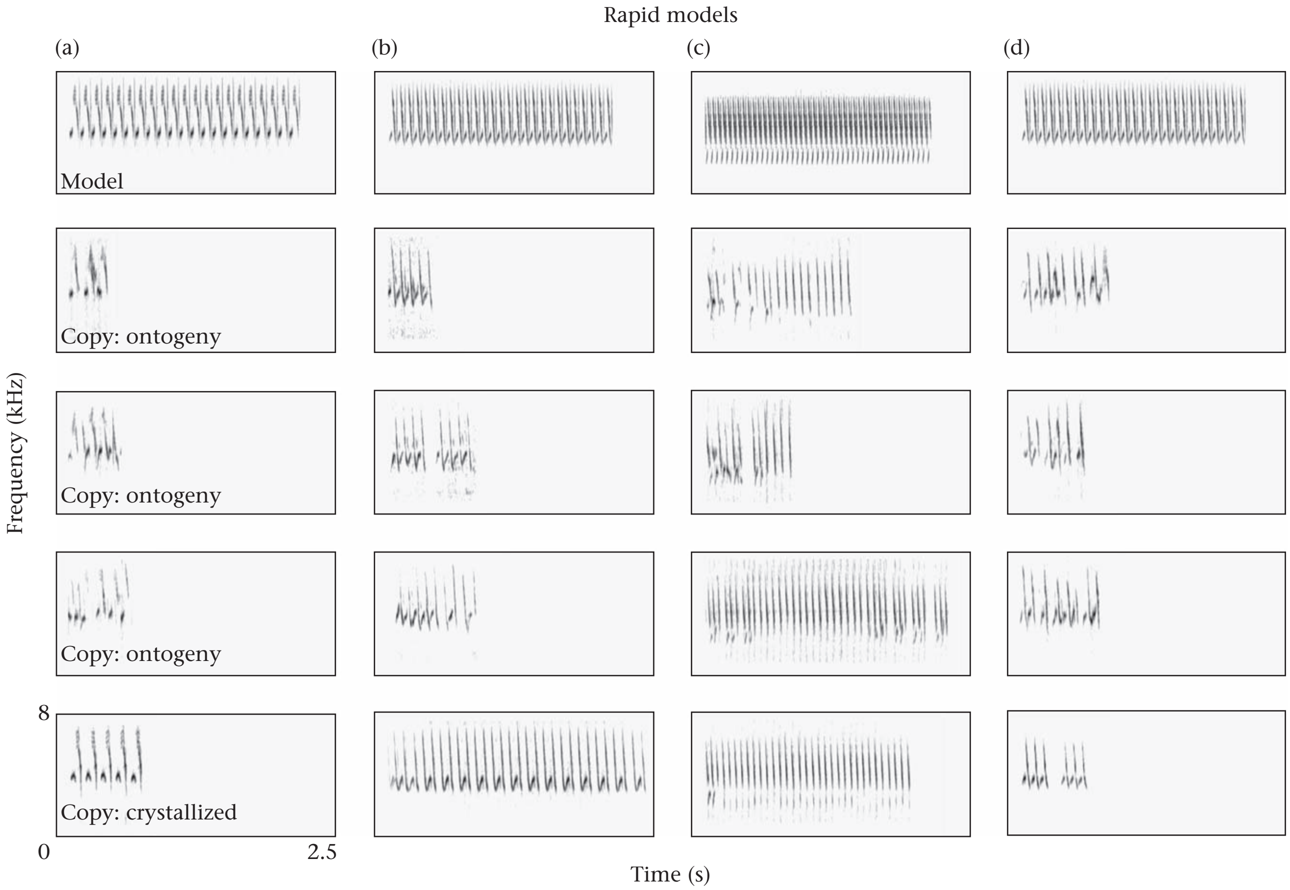

Figure 2. Patterns of vocal development for copies of rapid models.

intersyllable intervals by a single ratio, so that song models contained trill rates that were 60, 70, 80 or 90% faster that the wild songs from which syllables were sampled (Fig. 2, top panels). Broken models were constructed by arranging syllables as triplets separated by silent gaps (Fig. 3, top panels). All birds were trained with all 10 song models beginning at 19 ± 1 days and continuing until 103 ± 1 days posthatch, which encompasses the sensitive learning phase reported for this species in the laboratory (Marler & Peters 1988). We recorded the vocal behaviour of birds extensively the following spring. We began monitoring all birds for song once a week during the end of February 1996, when birds were about 280 days posthatch. On average, the first songs recorded for each bird occurred about 3 weeks later when birds were 303 ± 9 days of age. We continued to record birds on a weekly basis throughout their song development until 377 ± 8 days, at which time all individuals had crystallized their adult song repertoires.

We catalogued vocal exemplars from four stages of song development: subplastic, early plastic, plastic and crystallized song. Marler & Peters (1982c) provide illustrations of songs from these developmental stages. Subplastic song (a combination of stages V and VI of song development described in Marler & Peters 1982c) is defined as the earliest phase at which model phonology can be recognized, and at which model syllables are repeated in sets of two or more. Early plastic song (stage IV of Marler & Peters 1982c) is characterized by variable acoustic structure of syllables sung in trills, although here the number of repeated syllables in trilled segments increases and syllable structure is more developed and consistent within trilled segments. In plastic song (stages II and III of Marler & Peters 1982c), most songs take on the characteristic length of adult song and comprise a single trilled syllable, although with noticeable variations between repetitions of that syllable. Crystallized song (stage I of Marler & Peters 1982c) is characterized by highly stereotyped syllable phonology, trill rate and syntax. The birds in our study reached these four vocal stages at the following ages ($\overline{X} \pm$SD days posthatch): subplastic song, 318 ± 6.8; early plastic song, 327 ± 6.1; plastic song, 336 ± 8.9; and crystallized song, 378 ± 7.7.

Developmental Trajectories

The characteristic features of swamp sparrow songs emerge in a gradual manner during vocal ontogeny, with each stage of development presenting increasingly close matches to memorized model features (Marler & Peters 1982c; Clark et al. 1987). This gradual development of song features is consistent with neural and motor hypotheses of sensorimotor learning; as the mechanisms of song control and production develop, the song phenotype should become increasingly adult-like and closer in

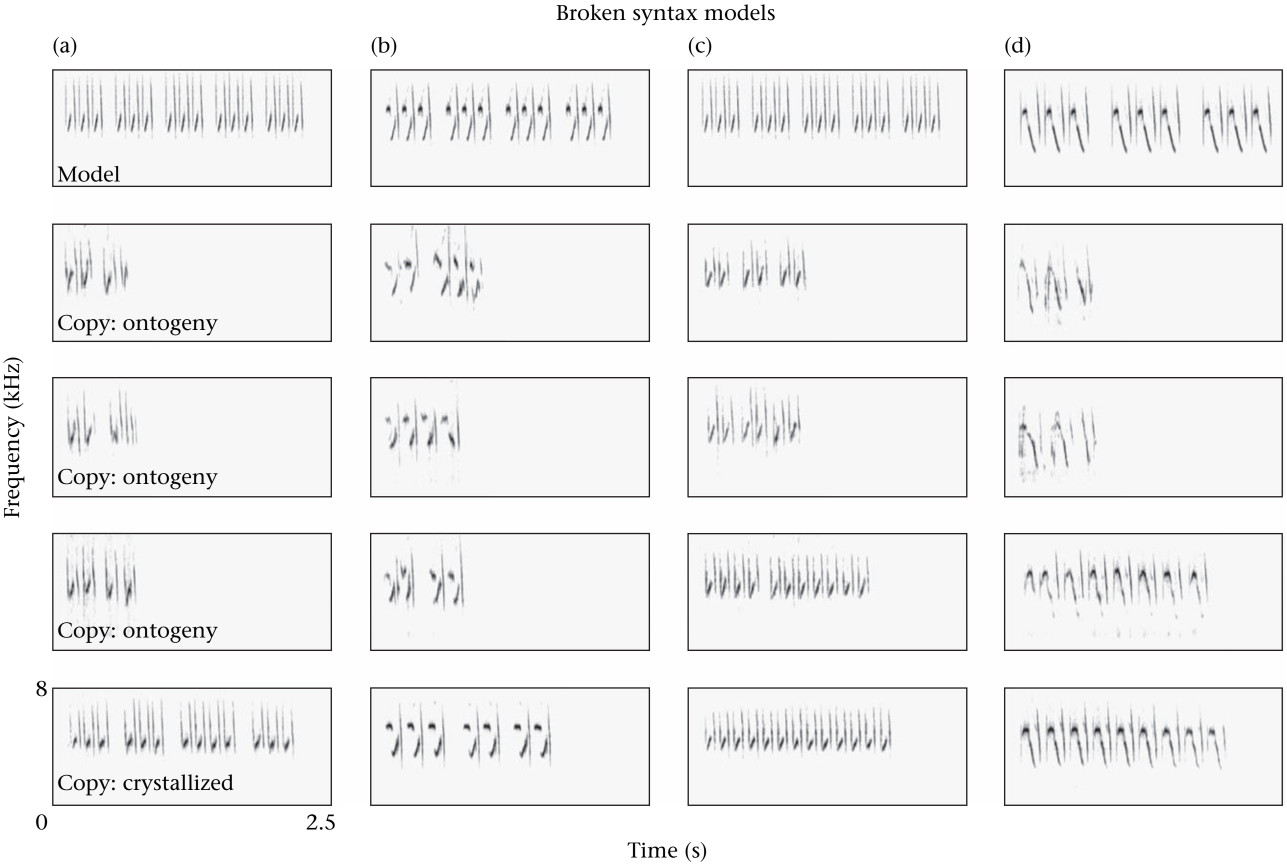

Figure 3. Patterns of vocal development for copies of broken syntax models.

structure to the previously memorized target. The calibration hypothesis makes several specific predictions about how song types should change over vocal ontogeny, when birds are confronted with atypical vocal performance challenges during sensorimotor development (Table 1). In contrast to patterns of normal song development, this process of adjustment is expected to include significant experimentation and specific adjustments that bring the template away from its original form and more in line with actual vocal performance capacities. Alternatively, if birds do not compensate for limits to their own vocal proficiency, or are somehow able to 'anticipate' their own levels of proficiency during model memorization, we would expect to observe only gradual modifications in vocal ontogeny without evidence of experimentation, leading to increasingly accurate renditions of the forms eventually crystallized.

We first used visual inspection of sonagrams to describe song ontogeny qualitatively for our study subjects. We focused in particular on three vocal features that we expected to be affected by birds' vocal performance abilities, and that were particularly divergent in some song copies with respect to their models: song syntax, trill rate and the presence or absence of notes in copies as compared to the original models (Podos 1996; Podos et al. 1999). The 'syntax' of a sparrow song refers broadly to the pattern by which elements (notes and syllables) are arranged in time (e.g. Marler & Peters 1977). Our use of the term syntax throughout this paper refers specifically to the rhythmic patterning of syllables. We digitally sampled vocal exemplars across the four stages of development for each bird, for subsequent analyses. Figures 1–3 illustrate models, crystallized copies and developmental intermediates for 10 of the 23 song copies that were eventually crystallized by birds. Our selection of these particular copies is intended to illustrate most broadly the range of developmental patterns observed.

Qualitative descriptions of development were supplemented with quantitative descriptions of developmental changes in syntax, trill rate and note composition. For each individual at each developmental stage, we selected as many as five song exemplars of each attempted copy of song models it produced. We were able to acquire trajectories with exemplars from all developmental stages for 14 of 23 song types that were eventually crystallized. For the remaining nine song types, at least one of the three precrystallization stages was not represented in our sample. Our analysis also included 258 song exemplars recorded during early stages of vocal development that were eventually dropped from the birds' vocal repertoires, in addition to those exemplars that were eventually crystallized. Our total sample size for analysis of syntax and trill rate was as follows: 147 subplastic song exemplars representing 33 song types from eight individuals, 234 early plastic song exemplars representing 50 song types from eight individuals, 147 plastic song exemplars representing 32 song types from eight individuals, and 110 crystallized song exemplars representing 23 song types from 10 individuals.

Syntax pattern is not always easily defined by visual inspection of sonagrams, especially in earlier developmental stages. We therefore developed an algorithm for categorizing the syntax of all exemplars as follows. First, we calculated from oscillograms the rates at which all successive syllable pairs were repeated. Rates (one syllable pair/period) were measured for all successive syllable pairs in each exemplar, irrespective of whether those pairs appeared to occur across gaps between adjacent multisyllable segments. We then calculated the stereotypy of syllable rates within all crystallized song copies as coefficients of variation for this measure across each exemplar ($CV_{\text{syllable rate}}$). The maximum $CV_{\text{syllable rate}}$ observed in crystallized song copies with normal syntax was 12.9, and we therefore classified all exemplars with a $CV_{\text{syllable rate}}$ less than or equal to 12.9 as having normal syntax. This classification corresponded well to our impressions from visual inspection of spectrograms.

The comparatively high degree of temporal variation ($CV_{\text{syllable rate}} \geq 12.9$) in the remaining exemplars resulted from the arrangement of syllables either in broken syntax, with one or more clearly defined breaks, or in irregular syntax in which syllable timing was erratic. For some exemplars, it was difficult to determine whether the syntax was broken or irregular. To distinguish between these cases, we applied two criteria that emerged from our observation that crystallized broken song copies comprised multisyllable segments with steady trill rates that were separated by obvious gaps. From crystallized copies produced with broken syntax, we calculated (1) trill rates of multisyllable segments divided by trill rates across breaks ('break ratios', see also Podos et al. 1999) and (2) coefficients of variation for syllable repetition rates, from within multisyllable segments only ($CV_{\text{syllable rate broken}}$). The minimum break ratio in our sample of crystallized broken syntax copies was 1.40, and the maximum $CV_{\text{syllable rate broken}}$ was 14.9. Thus, developmental exemplars in which the maximum observed break ratio reached or exceeded 1.40, and in which the $CV_{\text{syllable rate broken}}$ was below 14.9, were categorized as having broken syntax. Exemplars that did not meet both of these criteria were classified as having irregular syntax. The number of vocal exemplars assigned to the three syntax categories across development is presented in Table 2.

Table 2. Number of vocal exemplars assigned to three syntax categories across four developmental stages

Developmental stage	Normal syntax	Irregular syntax	Broken syntax
Subplastic	74	40	33
Early plastic	128	47	59
Plastic	85	21	41
Crystallized	92	0	18
Total	379	108	151

Trill rate was measured for exemplars with normal and irregular syntax as the average syllable rate in each exemplar. For exemplars with broken syntax, trill rate was measured in the same way but excluded syllable rates across breaks.

Patterns of Selective Attrition

Young sparrows normally produce much more song material during early ontogeny than they eventually crystallize (e.g. Marler & Peters 1982a; Nelson & Marler 1994). If birds calibrate their learning patterns according to their vocal performance abilities, then we predicted that they should exclude selectively those copies of song models attempted early on that presented particularly pronounced challenges in vocal performance, because of difficulties they experienced in reproducing these songs accurately. Alternatively, birds might not make any such distinction. If so, we expect patterns of selective attrition to occur independently of the performance challenges associated with given song models.

We identified 33 copies of models that were rehearsed during ontogeny but never crystallized. Features of these 'rehearsed-only' copies were compared to features of crystallized copies to determine whether certain types of copies were more likely to be crystallized, as opposed to being deleted from a bird's repertoire. First, we examined whether the type of syntax used in early stages of ontogeny predicted the likelihood that a copy would crystallize. Second, we examined whether syllables with different trill rates experienced different rates of attrition. We focused on trill rates during early ontogeny because this was the only parameter for which values were available for all noncrystallized exemplars.

RESULTS AND DISCUSSION

The overall pattern of song development we observed was generally consistent with that reported previously for swamp sparrows (Marler & Peters 1982c; Clark et al. 1987): song duration in most copies increased steadily over the course of development; syllables became increasingly stereotyped in their structure, and increasingly well matched to the model syllables on which copies were based; and birds produced more copies of models in early phases of vocal ontogeny than they eventually crystallized. To provide a baseline for testing and interpreting the calibration hypothesis, we first describe patterns of development in copies of control models.

Copies of Control Models

All copies of control songs were crystallized with normal syntax, as expected (Fig. 1). Syntax patterns expressed during the development of these control copies also were mostly consistent with our expectations based on prior studies (e.g. Marler & Peters 1982a). For three copies of control models, birds produced songs throughout development with normal syntax or, rarely, with irregular syntax. A fourth copy (Fig. 1b; Table 3, copy 2) was

Table 3. Syntax and trill rate (Hz) values across vocal ontogeny. Song types were copied from three classes of models (control, rapid, broken syntax) and reproduced following distinct syntactical strategies

					Number of exemplars in ontogeny containing:			Trill rates of:		
Copy	Fig.	Bird ID	Model	Copy syntax	Normal syntax	Irregular syntax	Broken syntax	Model	Copy, subplastic	Copy, crystallized
1	1a	1	Control	Normal	15	0	0	4.6	4.1	3.8
2	1b	2	Control	Normal	1	2	6	11.0	10.7	10.4
3		3	Control	Normal	11	2	0	4.6	4.3	3.7
4		4	Control	Normal	5	0	0	4.6	4.2	4.5
5	2a	5	Rapid	Normal	11	2	2	10.2	7.4	7.7
6		2	Rapid	Normal	2	1	4	10.2	9.5	7.8
7		6	Rapid	Normal	5	1	9	15.2	7.3	7.6
8		7	Rapid	Normal	14	1	0	10.2	5.5	6.1
9	2b	8	Rapid	Normal*	9	2	3	13.5	12.1	12.7
10	2c	5	Rapid	Normal*	1	5	8	22.2	18.0	24.5
11	2d	3	Rapid	Broken	2	4	7	13.5	12.9	12.5
12	3a	1	Broken	Broken	1	1	8	8.4	7.1	7.8
13	3b	6	Broken	Broken	3	2	10	7.0	6.2	5.3
14		1	Broken	Broken	2	1	12	11.4	11.0	11.4
15	3c	3	Broken	Normal†	4	6	5	8.4	9.4	7.7
16		8	Broken	Normal†	8	1	6	7.0	5.2	5.0
17		8	Broken	Normal†	8	3	4	4.6	4.1	4.2
18		3	Broken	Normal†	9	2	2	11.4	9.0	10.4
19	3d	4	Broken	Normal‡	9	1	0	4.6	4.5	4.7
20		2	Broken	Normal‡	3	5	1	4.6	3.7	4.5
21		5	Broken	Normal‡	12	2	1	4.6	4.1	4.0
22		9	Broken	Normal‡	1	2	0	4.6	4.2	4.9

Cross-references to Figs 1–3 are provided in the second column. We excluded one of our 10 test birds (and his single song copy) from these analyses because we failed to record a sufficient number of songs for this individual during ontogeny.

*Crystallized with notes omitted.

†Multiple broken syntax renditions during development.

‡Rarely or never produced with broken syntax.

produced in the subplastic stage with broken syntax. The occurrence of broken syntax in early developmental stages has been observed on rare occasions in prior studies of learning from normal swamp sparrow models, which suggests that broken syntax is a natural (if occasional) feature of trilled song learning (P. Marler & S. Peters, unpublished data). The broken syntax observed in this copy also may be a result of the broader training context; for example, the broken syntax may have been learned from another model and applied to this copy during ontogeny. This broken syntax was eventually replaced with the normal syntax of the model. We found no other evidence in control copies for experimentation during the course of ontogeny; all notes from control models were included during all developmental stages, and no model notes were excluded during ontogeny (Fig. 1).

We found in a previous study (Podos et al. 1999) that birds crystallize copies of control songs at trill rates slower than those of their respective models ($\overline{X} \pm \mathrm{SD}$ difference in trill rates of copies versus models $= -11.8 \pm 8.7\%$). Our present analysis revealed that, for three of four copies of control songs, the lower trill rates of copies resulted in part from a reduction in trill rate between early plastic song and crystallized song (Table 3, copies 1–3). To illustrate, the song shown in Fig. 1a (Table 3, copy 1) was copied from a control model that had a trill rate of 4.6 Hz. The first identifiable reproductions of this model during development, in subplastic song, were produced with a slightly lower trill rate, 4.1 Hz. Trill rate continued to decline until the song crystallized at 3.8 Hz. The trend was reversed in the fourth copy (Table 3, copy 4), for which trill rate increased over development, thus resulting in an improved match to the model trill rate. For all copies, changes in trill rates appeared to occur gradually over the course of vocal development.

Copies of Manipulated Models

Rapid models

Consistent with the calibration hypothesis, we found that copies of rapid models underwent comparatively pronounced modifications over the course of vocal development, especially in syntax and note composition, compared with the development of control model copies (Fig. 2). For six of seven copies of rapid models, multiple renditions in development were produced with broken syntax. This observation is particularly notable given that only one of these copies eventually crystallized with broken syntax (Table 3). The percentage of copies of rapid models that contained developmental intermediates with broken syntax (6 of 7, 85.7%) exceeded that for copies of control models (1 of 4, 25%), by a degree that approached statistical significance (Table 3; Fisher's exact probability test: $P = 0.088$). Furthermore, the single copy of a rapid model that was crystallized with broken syntax (Fig. 2d; Table 3, copy 11) showed not only broken syntax renditions during development, but normal and irregular syntax developmental renditions as well.

Developmental flexibility was particularly evident in the ontogeny of song copies that eventually crystallized with notes omitted (Fig. 2b, c; Table 3, copies 9 and 10). In both of these copies, birds experimented with broken syntax in earlier stages of vocal development before settling on note exclusion as a final production strategy. In the example shown in Fig. 2b, the bird came to exclude, midway through vocal development, a low-frequency note from every other syllable. Exclusion of this note apparently enabled the bird to switch from broken syntax to the normal continuous trill. In Fig. 2c, the bird came to exclude a low-frequency note from all syllables but the opening pair. The deletion of notes during ontogeny appears to reflect the bird's attempts to accurately reproduce the rapid trill rate and normal syntax of the song model, with the observed solution appearing only after vocal experimentation. These and other changes during ontogeny resulted in crystallized song copies that were highly distinct from their models, generally more so than in initial stages of ontogeny (e.g. Fig. 2b–d).

For copies of rapid models, developmental changes in trill rates were not statistically distinguishable from patterns of trill rate development in control copies (Mann–Whitney U test: $U = 6.5$, $N_1 = 4$, $N_2 = 7$, $P = 0.18$). One copy of a rapid model (Fig. 2c) was notable, however, for undergoing an unusually pronounced change in trill rate during ontogeny. This copy was based on a model with a trill rate of 22.2 Hz, and was initially produced with a trill rate of 18.0 Hz. During vocal development, however, the bird's eventual exclusion of low-frequency notes appears to have provided leeway for a substantial increase in the trill rate of this copy, to 24.5 Hz, a closer match to the original model.

Broken syntax models

Copies of broken syntax models showed additional evidence of experimentation with vocal forms during ontogeny, particularly in the development of syntax. The earliest renditions of these copies generally showed the broken syntax of the models (e.g. Fig. 3, second row), but more often, underwent a transition towards normal syntax. For those examples in which the broken syntax of models was retained in the crystallized copy (Table 3, copies 12–14, Fig. 3a, b), parsimony suggested that versions of these songs throughout development also would be produced with broken syntax. Indeed, in some cases, early renditions of songs copied from broken syntax models were produced throughout development in a broken syntax form (Fig. 3a). In a few cases, however, precursors of broken syntax copies were produced with normal or irregular syntax, even though they eventually crystallized with broken syntax (Table 3, copies 12–14; e.g. Fig. 3b). On the whole, birds appeared to make few adjustments to songs for these three copies (Table 3).

We did find evidence of substantial transitions in syntax, however, for copies of broken syntax models that eventually crystallized with a continuously trilled syntax (Table 3, copies 15–22). The syntax of developmental renditions of these copies was highly diverse, and as a group appear to have differed from control song copy renditions in their tendency to deviate from the syntax of their respective models (Table 3). This pattern can be attributed in particular to four song copies that were produced with multiple broken syntax renditions during development (Fig. 3c; Table 3, copies 15–18). The presence of broken syntax intermediates suggests that birds memorized the syntax of the original model, but then adjusted syntax during development to the more species-typical form of a continuous trill. The direction of this transition is consistent with the calibration hypothesis, which predicts that birds could increase the difficulty level of song copies (e.g. by removing pauses in this case) if the songs are easy to reproduce.

Such an adjustment was not observed for four additional copies of broken syntax models that were never, or with only a single exception per copy, produced in development with broken syntax (Table 3, copies 19–22; Fig. 3d). For these copies, it is possible that birds had encoded broken syntax models with normal, continuously trilled syntax during model memorization. Alternatively, these copies may have been encoded with broken syntax, but the uniformly short duration of renditions at intermediate stages of development for these song copies may have precluded the opportunity for birds to include, and for us to detect, pauses between multisyllable segments.

Developmental changes in trill rates did not differ between copies of broken syntax models and control models (Mann–Whitney U test: $U = 12$, $N_1 = 11$, $N_2 = 4$, $P = 0.21$). Copies of broken syntax models that crystallized with normal syntax (Table 3, copies 15–22) were notable, however, for maintaining constant trill rates across development. In four of eight cases, trill rates of crystallized songs were produced within 0.2 Hz of their first recognizable renditions during subplastic song. No other copies in our entire sample showed this degree of trill rate conservation (Table 3). This observation is consistent with our expectation that broken syntax models are comparatively easy to reproduce.

Patterns of Selective Attrition

All 10 of the model songs heard by young birds in our experiment were reproduced both as crystallized copies and as 'rehearsed-only' copies (i.e. copies observed early in development but eventually lost through attrition). We also found that rehearsed-only copies were produced in proportion to the number of training models per model class (observed: 5 control, 15 rapid, 13 broken; expected: 6.8 control, 13.6 rapid, 13.6 broken; chi-square test: $\chi^2_2 = 0.34$, NS). These data suggest that model class per se did not determine a model's likelihood of being copied or crystallized.

We did, however, identify several patterns of selective attrition suggesting that song copies that are easier to produce are more likely to be retained in the crystallized repertoire. For copies of manipulated models, those copies that eventually crystallized were particularly likely to include developmental intermediates with broken syntax: for copies of rapid models, six of seven copies (85.7%) that expressed broken syntax intermediates eventually crystallized, in contrast to only eight of 15 copies (53.3%) without broken syntax intermediates; and for copies of broken syntax models, nine of the 11 copies (81.8%) that contained broken syntax intermediates eventually crystallized, compared with six of 13 (46.2%) that did not contain broken syntax intermediates. These differences were not statistically significant (Fisher's exact probability test: $P = 0.193$ and $P = 0.213$, respectively), although this lack of significance is hard to interpret given the small sample sizes involved. Nevertheless, our results suggest that experimentation with model forms, defined here as the production of songs with broken syntax during earlier stages of vocal development, might be associated with the likelihood that a song will be retained in an individual's crystallized repertoire.

Next we compared trill rates between crystallized and rehearsed-only copies, to look for evidence of bias in the retention of models. For copies of control and broken syntax models, we found that initial trill rates did not differ between these copy classes (Mann–Whitney U test: control copies: $U = 13.5$, $N_1 = 4$, $N_2 = 5$, $P = 0.46$; broken copies: $U = 87.5$, $N_1 = 11$, $N_2 = 13$, $P = 0.37$). However, for copies of rapid models, we found that initial trill rates did indeed differ between crystallized and noncrystallized copies ($U = 87.5$, $N_1 = 7$, $N_2 = 15$, $P = 0.015$). Copies of rapid models that expressed slower trill rates early in development were more likely to be retained in the crystallized repertoire, as predicted by the calibration hypothesis. Thus, songs that appeared to be more difficult to produce and match, defined here in terms of absolute trill rate, were more likely to be deleted from the repertoire.

Consistent with this result, we also found that differences in trill rates between copies and models predicted probabilities of crystallization. Copies of rapid models that eventually crystallized were produced during subplastic song with trill rates substantially lower than those of their respective models ($\overline{X} \pm$SD difference in trill rate: 23.90 ± 19.0%). By contrast, for copies that were lost from the repertoire during attrition, initial trill rates were substantially more similar to trill rates of their respective models (a difference in trill rate of 1.05 ± 9.6 SD%; Mann–Whitney U test: $U = 95$, $N_1 = 7$, $N_2 = 15$, $P = 0.003$). No such pattern was observed for control copies ($U = 13$, $N_1 = 4$, $N_2 = 5$, $P = 0.54$) or for broken model copies ($U = 84$, $N_1 = 11$, $N_2 = 13$, $P = 0.49$).

GENERAL DISCUSSION

The calibration hypothesis posits that young birds may adjust their song learning targets (i.e. their 'exact' templates) during the extended sensorimotor phase of song learning in the event of a disparity between their own levels of vocal proficiency and the proficiency required for accurate song model reproduction. This hypothesis is not exclusive of neural and peripheral 'maturational' hypotheses concerning the proximate function of sensorimotor learning (Konishi 1965; Nottebohm 1970; Marler 1976; Brainard & Doupe 2002), but instead builds on these earlier ideas. In particular, the calibration hypothesis aims to account for variation between song models in their relative ease of reproduction, and for the possibility that not all individuals are equally good at reproducing all songs.

The main support for the calibration hypotheses comes from analysis of developmental changes in song structure. For those copies that crystallized with a syntax closely matching that of their respective models (Table 3, copies 1–4 and 12–14), we found little evidence for experimentation with alternative forms of syntax during development. The majority of developmental intermediates of these copies were produced with the syntax that eventually crystallized. By contrast, song copies that crystallized with a syntax distinct from that of their respective models (Table 3, copies 9–11 and 15–22) showed significant evidence of experimentation in development with forms of syntax that were not retained in crystallized copies. Copies of broken models that crystallized with normal syntax (Table 3, copies 15–22) regularly featured broken and irregular syntax during ontogeny, and copies of rapid models (Table 3, copies 5–11) regularly featured broken syntax during development, even for those copies that crystallized with normal syntax. Experimentation with syntax is particularly pronounced in the developmental trajectories of the copies shown in Figs 2b, c and 3c. For the copy in Fig. 2b, the bird produced one copy with broken syntax before settling on a novel solution, in which the normal syntax of the model was preserved but only through deletion of alternating low-frequency notes. The song exemplar in the fourth panel of Fig. 2b illustrates this transition from broken to normal syntax. For the copy in Fig. 2c, the bird followed a similar strategy during development, omitting a low-frequency note in selected syllables, leading to broken syntax, before settling on a solution that preserved normal syntax, but with a loss of notes. For the copy in Fig. 3c, a clear transition from broken to normal syntax is observed. Modifications made by birds during the development of all of these copies appeared directed towards the production of songs more consistent with expected levels of vocal proficiency. Furthermore, vocal forms generally appeared to make a developmental transition away from model song features and towards other forms of song organization.

Another line of evidence that provides support for the calibration hypothesis comes from patterns of selective attrition. As in prior experiments with swamp sparrows, we found that birds produced more song types during development than they eventually crystallized. The song types that were rehearsed during development but then excluded from crystallized repertoires ('rehearsed-only' songs) were copied from all models, and in proportion to the number of training models presented per model class. This suggests that birds did not encounter perceptual or other neural biases in the memorization and initial reproduction of songs with varying degrees of physical difficulty, which complements our previous finding that birds crystallized songs in proportion to the number of song types presented per model class (Podos et al. 1999). Analysis of patterns of selective attrition within the rapid model class did reveal a bias, however, in which songs were most likely to be retained or dropped from the developing repertoire. Those types that were produced during earlier developmental stages with broken syntax were more likely to be retained, even for those copies that ultimately crystallized without broken syntax. This bias is consistent with the calibration hypothesis: vocal experimentation apparently provided birds with a means to retain songs in their crystallized repertoires, albeit in modified forms. Furthermore, copies of rapid models that were produced with comparatively slow trill rates (both in absolute terms and relative to respective models) were more likely to be retained in the crystallized repertoire. This result suggests that birds were more likely to retain those copies that did not require the highest levels of vocal performance.

A third line of evidence examined here, the analysis of developmental changes in trill rate, offers additional although weaker support for the calibration hypothesis. Birds tended to modify the trill rates of their copies over the course of development, by an overall average of 10.1% (Table 3, compare trill rates during subplastic and crystallized exemplars). The direction of trill rate modifications over development was mixed, with developmental increases in trill rate for 13 copies and decreases for nine copies. There were no obvious biases in trill rate modifications with respect to given model types. Copies of broken and rapid models, for instance, showed similar tendencies for increases in trill rates over development (63.6% for copies of broken models, 71.4% for copies of rapid models). This is in spite of the expectation that trill rates would have tended to increase more often for copies of broken syntax songs, given their relative ease in reproduction. Nevertheless, we found that copies of broken syntax models were unusually likely to remain consistent in their trill rates throughout the course of development. The four copies that retained their initial (subplastic) trill rates with the greatest degree of precision were all copies of broken syntax songs reproduced with normal syntax. No other copies retained this degree of conservation in trill rates, perhaps because of the relative difficulty in accurate reproduction of other models.

Calibration and Models of Song Development

Evidence that swamp sparrows can calibrate their targets of vocal learning during the sensorimotor phase of song learning holds implications for models of vocal development. Our earlier work showed that male swamp sparrows are able to reproduce song models that deviate from normal performance levels, in part by introducing modifications that apparently compensate for the disparity between actual and required proficiency (Podos 1996; Podos et al. 1999). These results were consistent with the calibration hypothesis, but without a detailed analysis of vocal development, it was difficult to fully dismiss an alternative hypothesis, that birds compensate for vocal performance disparities when memorizing models during the earlier sensory phase of learning. The current analysis provides evidence that compensation indeed occurs during sensorimotor learning.

Our study thus supports and extends so-called 'active' models of song learning (Marler & Peters 1982a; Marler 1997). Discussion about the function of the sensorimotor phase of song learning has undergone a broad shift in recent decades (reviewed by Marler 1997). Early models of sensorimotor learning focused on the discovery that birds use auditory feedback to access and retrieve memorized song models (e.g. Konishi 1965; Nottebohm 1970). Templates in sensorimotor learning were viewed as inflexible, because there was no indication that birds could make any adjustments to template structure after closure of the memorization phase of song learning. More recent attention has focused on the formative role of additional experience during sensorimotor learning (Marler 1997). This discussion has been driven in particular by observations of developmental overproduction and attrition. It now seems clear that birds attend to additional song exposure that they experience during the sensorimotor phase, and use this additional input to guide patterns of template retention or attrition. For example, male sparrows retain those song types that allow them to match the songs or repertoires of neighbouring males (Nelson & Marler 1994; Nelson 2000; Nordby et al. 2000).

The data we present here suggest that the sensorimotor phase can guide a bird's patterns of song crystallization in two additional ways. First, a bird's experiences during sensorimotor development might lead him to retain those specific songs that are initially easier to produce (e.g. with comparatively slower trill rates), or for which they successfully identify a motor solution during development (e.g. through the production of broken syntax). By contrast, songs that are more difficult to produce either in their original form or in a modified form tend to be dropped from the repertoire. Second, our data suggest that feedback during sensorimotor learning can guide specific modifications that birds apply to song templates, in response to their success or failure in model matching during sensorimotor learning. In other words, feedback might actually drive changes in song type templates themselves in order to specify more appropriate motor output in crystallized songs. This would be analogous to a musician modifying a musical piece to match his or her particular skill level (e.g. by simplifying a particularly challenging score). Our study suggests that swamp sparrows have a specific tendency to produce broken syntax as an alternative motor pattern for model imitation during vocal ontogeny. This kind of process in bird song sensorimotor learning is distinct from other biases in selective attrition, as normally discussed, which centre on the retention or deletion of different song type templates as units. Feedback here would presumably occur through auditory pathways, but might involve somatosensory pathways as well (see Suthers et al. 2002). Confirmation of the mechanisms by which birds might modify their learning templates during the sensorimotor phase would require a deeper understanding of the neural bases of vocal control than is presently available.

Calibration and Song Evolution

Recent studies on song preferences in female songbirds suggest that sexual selection may drive males to produce increasingly complex, challenging, or accurately copied songs (e.g. Hasselquist et al. 1996; Vallet et al. 1998; Draganoiu et al. 2002; Nowicki et al. 2002; Ballentine et al. 2004). We therefore expect that over evolutionary time, birds will sometimes encounter disparities between their own vocal proficiency and proficiencies required for the accurate song model reproduction. For example, female preferences for songs with fast trill rates (Vallet et al. 1998) and wide frequency bandwidths (Ballentine et al. 2004), and the resulting directional selection on these song parameters, would elevate the general level of proficiency required for accurate model reproduction. The disparity in our study between actual and required vocal proficiency was probably greater than what birds would face in the wild. Nevertheless, our study illustrates that birds have the ability to calibrate their targets of song learning. The impact of sensorimotor constraints in shaping patterns of vocal evolution (Nowicki et al. 1992; Lambrechts 1996; Podos 1996, 1997; Suthers & Goller 1997) should be especially relevant for close-ended learners such as the swamp sparrow, for which vocal patterns determined in development are maintained precisely for the remainder of a bird's life.

In conclusion, we suggest that calibration during sensorimotor learning can, over the long term, act as both a stabilizing and a creative mechanism in song evolution. Consider again the possibility that sexual selection drives the evolution of increasingly rapid trills. The evolution of songs that require ever-increasing levels of vocal proficiency would be eventually counterbalanced by constraints imposed by the anatomy and function of the vocal apparatus. Some birds in some generations would thus find themselves unable to produce accurate reproductions of the song models that they had memorized. The ability to calibrate targets of song learning could lead birds to reduce the trill rates of song copies to facilitate the accurate reproduction of other song model features (Podos 1996). Such reductions in trill rate would act against the evolution of increasing trill rates in the population. Alternatively, calibration might drive the generation of novel song features or relationships between features. Accurate reproduction of rapid trill rates during sensorimotor learning might drive, for instance, corresponding reductions in syllable complexity and frequency bandwidth (Podos 1997) or the production of broken syntax (Podos 1996) as birds shift learning targets during sensorimotor development. Changes to song structure rendered by calibration could be translated into broader evolutionary patterns via cultural evolution (Slater 1986), at least to the extent that modified songs retain their efficacy as learning models and in the contexts of communication (Podos et al. 1999; Nowicki et al. 2001). Sensorimotor calibration during song learning might indeed be responsible for the evolution of diverse aspects of song structure between songbird populations and species.

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