STRUCTURAL CHANGES IN SONG ONTOGENY IN THE SWAMP SPARROW *MELOSPIZA GEORGIANA*

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ABSTRACT.—Sixteen male Swamp Sparrows trained with recorded songs in infancy were recorded on a weekly basis throughout the process of song development. Analyses of the 15,000 songs recorded from them provided the basis for a seven-stage classification of the steps in song ontogeny, with the four major divisions of subsong, subplastic song, plastic song, and full song. The individually isolated males all followed a basically similar developmental progression through the seven stages of song development. Accounts of other species suggest that the pattern seen in the Swamp Sparrow is a rather general one, when one allows for species differences in song structure. The abrupt reduction of song duration and its variability was a marker for the crystallization of plastic song into full song. At this time there was also a reduction in the number of syllable types used and the number of parts per song. Swamp Sparrows produced considerably more syllable types in plastic song than necessary to generate the normal, species-specific song. *Received 10 June 1981, accepted 19 October 1981.*

A GENERAL picture is available of the overall structural properties of subsong and plastic song and the transformations to which they are subject prior to the emergence of full song (Nice 1943, Marler 1956, Thorpe and Pilcher 1958, Nottebohm 1972a). Despite the plethora of studies on mature birdsong, there has been little descriptive analysis of song ontogeny. The phenomenon of subsong is nevertheless of great potential interest because of its distribution in birds, which seems to coincide with the incidence of song learning (Nottebohm 1972a, 1975; Marler and Peters in press a). No one, however, has yet conducted a longitudinal study of song development in individual birds to determine the timing and manner of emergence of learned themes. As a first step, we present here the results of an investigation on the structure of subsong and plastic song in the Swamp Sparrow (*Melospiza georgiana*).

METHODS

Sixteen male Swamp Sparrows hatched in the wild between 30 May 1977 and 24 June 1977 were brought into the laboratory between 2 and 10 days of age and reared by hand to independence. Younger nestlings were brooded by canaries between feedings until about 10 days of age. The project on song development was grafted onto another study of possible effects of an anti-estrogen, CI628, on the development of song learning abilities. The experimental manipulations involved had no effect on singing behavior and will not be considered further in this paper beyond these details.

Four males, designated as the "prehatch treated" group, were injected with CI628 on 4 successive days between 8 days before hatching and two days after hatching. Three males, the "posthatch treated" group, were injected on 6 successive days between 3 and 8 days after hatching. A third group of five males, the "late treated" group, were injected on 4 to 6 successive days, between the ages of 9 and 24 days of age. Four males were not treated at all. There were no losses as a consequence of the treatments, and no differences in song could be detected between treatment groups and controls.

All birds were trained for 40 days between 24 June 1977 and 26 August 1977 starting between the ages of 16 and 26 days of age and ending when the birds were between 55 and 67 days of age. The birds were trained with one of two sets of tape-recorded songs, A and B, designed to explore some of the species differences in song learning in Swamp and Song (*Melospiza melodia*) sparrows. The details of this experiment will be presented elsewhere, but we describe the training songs briefly here.

Wild male Swamp Sparrow songs typically consist of identical repetitions of one distinctive syllable type at a steady tempo. This pattern and the rarely-occurring (<5%) two-parted trill served as the basis for our training songs (for examples of natural Swamp Sparrow song, see Marler and Peters 1977, Peters et al. 1980). Schedule A, used for training six males, contained 16 one-parted trills composed of either normal Swamp Sparrow syllables or artificial syllables created from notes of Swamp and Song sparrow syllables (see Zoloth et al. 1980 for procedural details). The remaining 10 males were trained with Schedule B, which contained 11 different songs, 6 one-parted trills, and 5 two-parted trills. These

TABLE 1. Criteria for a seven-state classification of stages of song development in the Swamp Sparrow.

		Syllables		Songs	
	Stage	Morphology	Repetitions	Morphology	Duration
Crystallized song	I	Stereotyped	Clear trills	Stable order	Short
	II	Stereotyped	Clear trills	Variable order	Short
Plastic song	III	Minor variations	Clear trills	Stable order	Longer
	IV	Variable	Clear trills	Variable order	Long and
	V	Rudiments	Some	Variable order	variable
Subplastic song	VI	Rudiments	None	Variable order	Variable
Subsong	VII	None	None	None	Variable

songs were composed of a total of 16 different intact Song and Swamp sparrow syllables. Songs for both schedules were organized into 3-min bouts by repeating a single song type once every 10 s, a normal song delivery rate for Swamp Sparrows. These were played to subjects twice per day, morning and evening, during the periods already indicated.

After song training was completed, each male was housed in a sound-proof chamber, with the lights kept on a normal photoperiod by a time-clock changed every week. We first determined the peak singing period during the day. A Crown International 800 series tape deck was set up with a time delay and reset system. Once per week from 8 August 1977 to 2 September 1977, we sampled a subset of 3–7 birds from each training schedule, starting at about 50 days of age and selecting 1 out of every 5 min for 24 h. Most singing occurred just after dawn, when the lights were switched on in the chambers. This information provided the basis for the recorded sampling of singing of all 16 males. Beginning at an average of 99 days of age and continuing until about 380 days of age, we recorded each male for 1 h once per week. Tandberg Series 15 tape recorders on time clocks were used, with a tape speed of 3¾ inches per second. From 593 recording sessions for all birds, 235 h of recordings were obtained that contained song.

All recordings were monitored and then edited for analysis. The editing procedure differed slightly for early and later stages of singing. With early singing, we edited out up to 15 min of continuous singing and estimated the remaining amount in the 1-h recording. In later stages, song occurred in more discrete units, and all songs were edited out, with two exceptions. Occasionally, recording quality was poor because of microphone or tape-recorder malfunction. In a few of these cases a small sample of song was edited out to document the stage of singing. Late in song development we occasionally edited only alternate songs, when it was clear that a large sample of the male's crystallized songs had already been obtained.

The edited tapes were run on a Princeton Applied Research Spectrum Analyzer, which provides a photographed, sound-spectrographic analysis of songs with the frequency spectrum displayed against time. In early stages we analyzed a 5–10-min sample for each recording date for each bird. With later singing all edited material was analyzed.

For detailed analysis of the songs, we adopted a definition of a "song unit" suitable for all stages. Songs of adult Swamp Sparrows in nature are about 2.3 s in duration with a typical intersong interval of more than 5 s. The average intersyllable interval for full song is 40 ms and the average internote interval is 12 ms. The timing of early singing behavior is very different, however. Songs separated by intervals of more than 5 s often contain within them intervals greater than 80 ms. Some of the note sequences bounded by 5-s intervals are extremely short. After some experimentation, we adopted the following criteria for song-like units. Any sequence of notes qualified as a song if it lasted more than 0.5 s with no intervals of silence longer than 0.25 s between notes. Thus, a 1.3-s sequence of notes that contained an interval of 0.3 s occurring after the first 0.5 s would be analyzed as two songs. Applying these criteria to the output of all 16 subjects, we defined a total of 15,062 songs for all song stages. Song durations were measured on a Summagraphics tablet and a PdP 11/10 DEC computer, programmed to register time durations to the nearest 12.8 ms.

RESULTS

PATTERNS OF SONG ONTOGENY

As a first step in the interpretation of song development, we created a seven-stage classification, based primarily on the presence or absence of syllabic structure and on the relative stability of syllable morphology and the sequences in which syllables were delivered (Table 1). Figure 1 represents samples of song production from one male Swamp Sparrow, illustrating the seven stages in the emergence of one of this male's two crystallized syllable

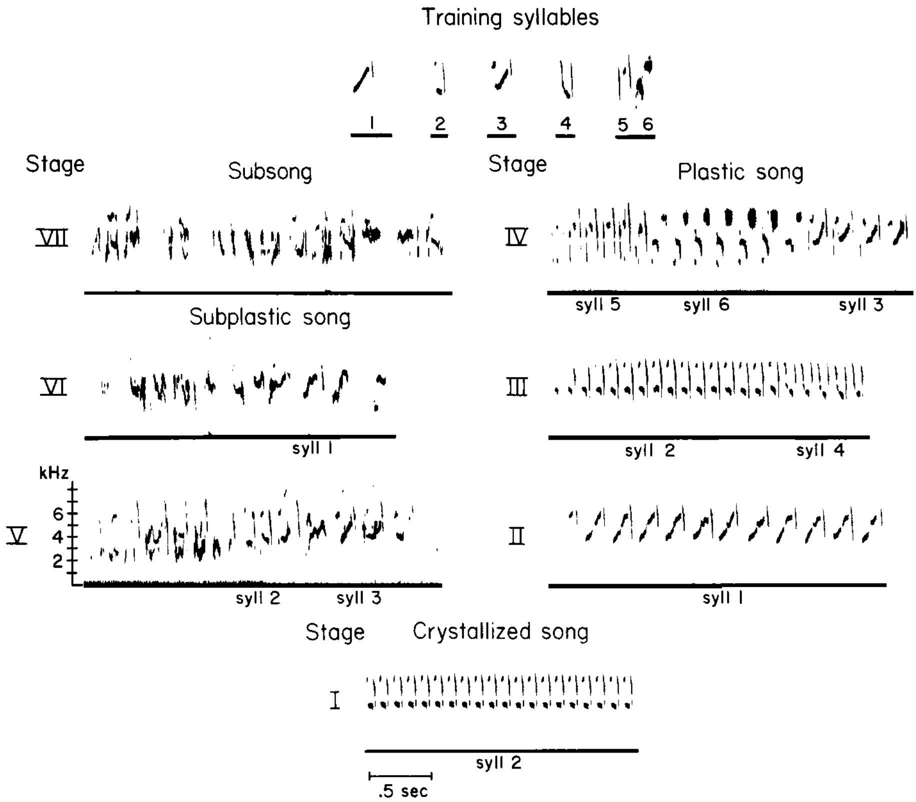

Fig. 1. Song development in a Swamp Sparrow. Samples of each of the seven stages of developing song in a male Swamp Sparrow that was trained with Schedule B. The stage is indicated at the left and major stages above. Imitations of the six training syllables portrayed at the top of the figure are identified by number. Training syllable 6 is a Song Sparrow syllable; the remainder are from Swamp Sparrows. Syllables were presented in one-parted songs, except for syllables 5 and 6, which appeared together in the same "hybrid" song. In nature, Swamp Sparrows typically have a repertoire of three to four song types, and, although there is some syllable-sharing in local populations, most individual repertoires are unique. The experimental male shown here had a final repertoire of two song types, shown in stages I and II. This crystallized song is virtually identical to the song of the local wild male that served as the original source of the training syllable.

types. The upper row of the figure illustrates syllables from some of the training songs imitated by this male. It is convenient for most purposes to collapse this classification into four stages, crystallized song (stage 1), plastic song (stages 2–4), subplastic song (stages 5–6), and subsong (stage 7).

Using this classification, we inspected the internal structure of each sound-spectrographed song unit. We developed a catalogue of syllable types for each male by working back from crystallized song into earlier stages. The organization of syllable types within songs was also recorded. By this procedure we were able to trace syllables present in a bird's crystallized repertoire back to more rudimentary syllabic forms. We also identified additional syllable types not present in the mature repertoire but common at earlier stages.

In the very earliest stages, song units contained sequences of unclassifiable notes, identified as subsong. Subplastic song is composed of unidentifiable note sequences as well as syllables in a very rudimentary form. Thus, it is the stage at which we can detect a bird making his very first attempts at recalling memorized material. Because the syllable morphology is only incipient, however, and because unidentifiable note sequences predominate, we have combined subsong and subplastic song for

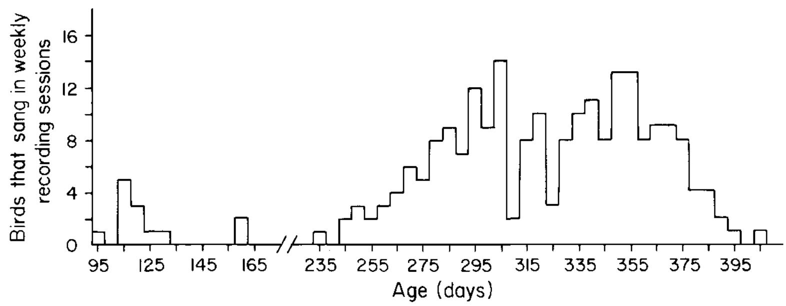

Fig. 2. Numbers of male Swamp Sparrows singing during weekly recording sessions from about 95 to about 405 days of age. Note the midwinter break from 165 to 235 days. The 16 males were individually isolated in sound-insulated chambers.

many of our analyses. For stages later than subplastic song, each song unit was analyzed for the syllable types present, their order, and the number of consecutive repetitions within the phrase.

This analysis provided us with a basis for describing the stages of song development and relating them to other parameters, such as age and the emergence of imitations.

Numbers of birds singing.—Figure 2, a graph of the numbers of birds represented in each of the weekly recording sessions from 95 to 400 days of age, is one index of the incidence of singing behavior at various ages under our experimental conditions. Note that the scale is broken between 165 and 235 days of age. During this interval no singing was recorded. Previous to this there was sporadic singing, but, as can be seen from Fig. 2, only two or three birds were likely to be represented in any given week. This was also true of singing prior to 95 days of age. Because birds were not systematically recorded prior to 95 days, we cannot make a quantitative statement on the early incidence of singing, but it was heard sporadically from all males beginning at 20–30 days of age. After about 240 days, the number of individuals represented began to climb, until, by 280 days of age, between 50 and 75% of the males were represented in each recording session. For the next 100 days all of the 16 males remained in full song until singing waned at about 400 days.

Developmental changes in song duration.—Mean song lengths were calculated for each of the major stages of song development. For subsong and subplastic song, represented in 64 of the total of 234 recordings, 2,422 songs yielded a mean song duration of 2.53 s (SD = 1.82). For plastic song, 56 recordings yielded 2,826 songs with a mean duration of 2.50 s (SD = 1.29). For crystallized song, represented in 114 recordings, 9,814 songs gave a mean duration of 1.96 s (SD = 0.38). There are thus indications of a decrease in song duration as development pro-

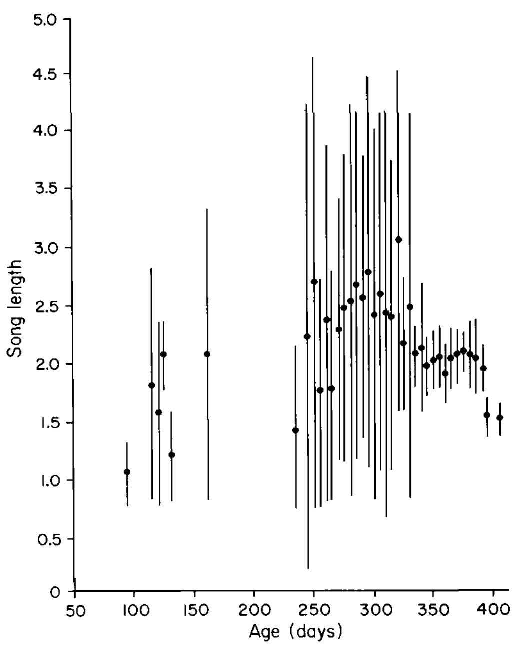

Fig. 3. Changes in average song duration in developing Swamp Sparrows. Vertical lines indicate standard deviations around the means. Song crystallization occurred, on average, at 334 days of age. The two final points represent mean recordings for one late-season singer, which happened to have shorter songs than average.

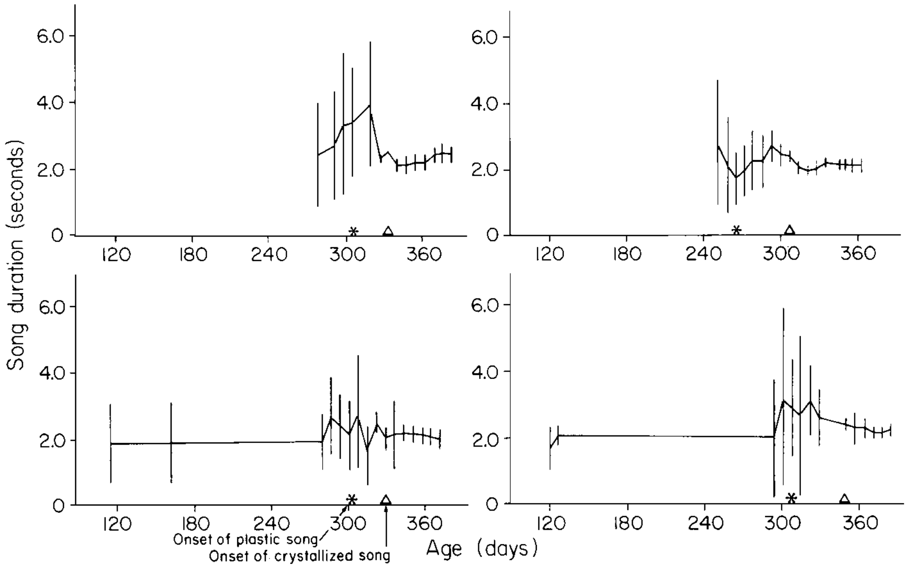

Fig. 4. Average song duration/recording day during the song development of four individuals. Vertical lines indicate standard deviations around the means. Onset dates of plastic and crystallized song are shown. Numbers of songs sampled per day for these four birds ranged from 1 to 190. Average samples per bird were 67.1 ± SD 52.1 songs per hour of recording.

ceeds and a striking reduction in the variability of song duration as crystallization occurs. These trends are seen more clearly if song duration is simply plotted against age (Fig. 3). There are signs of a drastic change in song organization occurring at about 330 days of age, with the mean duration dropping to a very stable value of 1.5–2.0 s. As shown below, this sudden change in the temporal characteristics of song is accompanied by a number of other transformations.

Song duration data for individual males revealed a change equally dramatic to that in the averaged data in song duration and its variability. Mean song durations during development for four individuals are shown in Fig. 4. Mean song durations for subsong, plastic song, and crystallized song were calculated for each bird. Table 2 summarizes the results. Each of the 16 birds averaged longer songs in both subsong and in plastic song than in crystallized song, and for 12 birds these differences were significant. For two birds only plastic songs were significantly longer than crystallized song, and one bird only had significantly longer subsongs (t-tests, see Table 3).

The order of stages in song.—As shown in Fig. 5, there was considerable individual variation in the age at which singing began after the mid-winter hiatus. Despite the variation in time of onset, each bird went through a regular progression. Crystallized song emerged at an average age of 334 days, preceded by a period of plastic song, comprising stages 2–4. Plastic song was in turn preceded by subplastic song with an average age of 299 days for the changeover. The average onset age of subplastic song was 285 days.

It was not uncommon for more than one stage to be recorded on a given day, although, once crystallized song began, a male rarely reverted to an earlier stage. Thus, in only 7 out of the 114 samples containing stage 1 crystallized song were any stage 2 or 3 songs represented. Crystallization appears to constitute a stepwise change in development, tending to be irreversible for that reason. Thus, if one considers the onset dates for crystallized song indicated in Fig. 5, for 14 out of the 16 birds this was the first record of stage 1 song.

The onset of plastic song was designated as the first occurrence of stage 4 and was the first date on which the majority of songs were composed of syllable types that could be reliably identified. Songs of all classes occurred during the plastic song periods designated in Fig. 5.

TABLE 2. Durations of subsong, plastic, and crystallized song in 16 male Swamp Sparrows.

	Song duration								
	Subsong			Plastic song			Crystallized song		
Bird	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1	103	2.48	2.17	210	2.81	1.53	585	2.21	0.26
2	213	2.42	1.84	219	1.84	0.79	418	1.52	0.21
3	227	2.43	1.66	52	3.42	2.63	396	2.10	0.24
4	184	2.77	1.79	118	3.71	1.78	379	2.28	0.26
5	44	2.39	1.49	140	2.18	1.07	622	1.90	0.19
6	198	2.47	1.86	149	2.54	1.62	949	1.85	0.22
7	156	3.34	2.93	53	3.40	1.44	479	1.88	0.14
8	125	2.49	0.99	421	2.21	0.53	474	1.95	0.17
9	204	2.66	1.86	56	2.33	1.24	535	1.78	0.13
10	156	2.43	1.71	375	2.33	0.77	754	2.11	0.20
11	353	1.99	1.21	199	2.19	1.11	203	1.86	0.33
12	64	3.14	1.75	181	2.22	1.10	1,032	2.19	0.17
13	41	2.52	1.35	366	2.51	0.92	1,054	1.91	0.18
14	138	2.17	1.17	59	2.28	1.09	1,032	2.08	0.29
15	128	2.47	1.64	24	3.78	1.56	377	1.76	0.17
16	88	3.80	2.39	204	3.32	1.84	525	1.89	0.24

The most common was plastic song, occurring in 42 of the 56 samples representing this stage.

Stage 6 was the criterion for the onset of subplastic song. Thirty-two recording dates were designated as subplastic song, and all contained stage 6 songs, 23 contained stage 7, and 18 contained stage 5. All 32 recording dates prior to the onset of subplastic song consisted almost entirely of stage 7 songs. Thirteen of these occured in the prewinter singing period, and two of them contained songs of one male that were classified as subplastic song. All other prewinter song was stage 7 subsong. Note that the first hints of syllabic structure appear in subplastic song. Thus, a considerable period elapses between training and the explicit rehearsal of learned song syllables, as analyzed in detail elsewhere (Marler and Peters in press b).

With the onset of spring song, 7 of the 16 males sang stage 7 subsong exclusively. The first records of spring singing of the nine remaining birds qualified as subplastic song, included with subsong in Fig. 4. The onset date of spring song was significantly later for these nine birds by an average of about 2 weeks (Mann-Whitney U-test, $P < 0.05$). There is evidence that the later a bird starts to sing, the more rapidly he develops. The onset date of subsong is negatively correlated with the duration of the subsong period ($P < 0.05$, Spearman rank correlation coefficient $r_s = -0.453$ for $n = 16$). Likewise, the onset date of plastic song is negatively correlated with the duration of the plastic song period ($P < 0.05$, Spearman rank correlation coefficient $r_s = -0.535$ for $n = 16$).

Occasionally, though rarely, birds reverted from one developmental stage to an earlier one. The progressive nature of development is displayed more clearly in Fig. 6, which shows the

TABLE 3. Statistical comparisons of song durations in three stages of development in individual birds. Asterisks indicate significant differences (t-test).

	Subsong vs. crystallized song		Plastic song vs. crystallized song	
Bird	t	P	t	P
1	1.26	$P > 0.2$	5.65	$P < 0.001$*
2	7.10	$P < 0.001$*	5.89	$P < 0.001$*
3	2.98	$P < 0.01$*	3.62	$P < 0.001$*
4	3.69	$P < 0.001$*	8.70	$P < 0.001$*
5	2.18	$P < 0.05$*	3.09	$P < 0.01$*
6	4.68	$P < 0.001$*	5.19	$P < 0.001$*
7	6.22	$P < 0.001$*	7.68	$P < 0.001$*
8	6.07	$P < 0.001$*	9.63	$P < 0.001$*
9	6.75	$P < 0.001$*	3.32	$P < 0.001$*
10	2.33	$P < 0.05$*	5.44	$P < 0.001$*
11	1.90	$P > 0.05$	4.02	$P < 0.001$*
12	4.34	$P < 0.001$*	0.37	$P > 0.2$
13	2.89	$P < 0.01$*	12.39	$P < 0.001$*
14	0.90	$P > 0.2$	1.41	$P > 0.1$
15	4.89	$P < 0.001$*	6.34	$P < 0.001$*
16	7.49	$P < 0.001$*	11.06	$P < 0.001$*

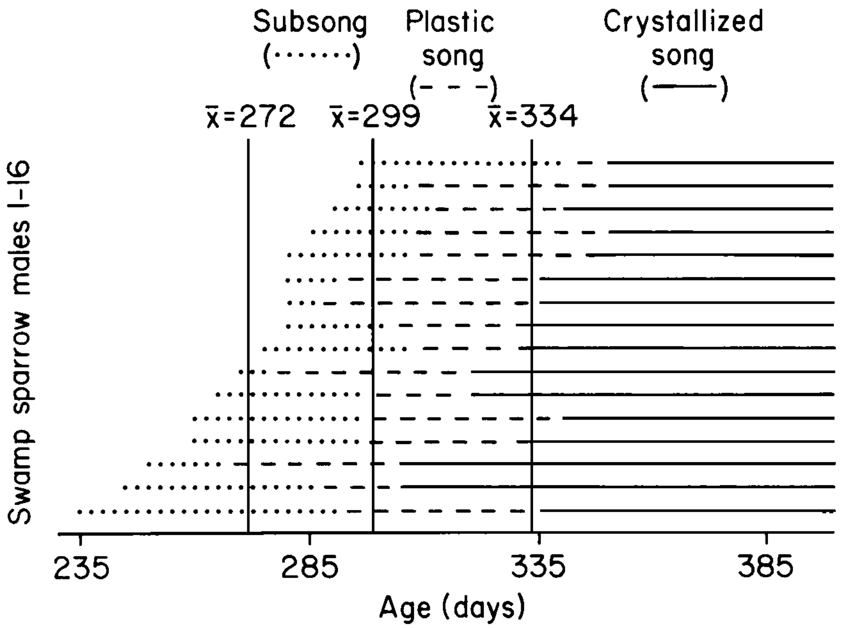

Fig. 5. A diagram of song development in the spring in 16 male Swamp Sparrows. Birds are arranged with the earliest to start at the bottom. Subplastic song is included with subsong (dotted line). The mean ages for the onset of subsong, plastic song and crystallized song are indicated by vertical lines.

least advanced of the seven developmental stages represented on a given recording date. Despite occasional regressions through one stage, each male tends to progress through the series in the same order. In only 6 out of 234 samples did a bird revert to an earlier stage of development. The seven stages represent a relatively smooth progression, except for stages 2 and 3 (Table 1). As can be seen in Fig. 6, males vary in how they proceed from stage 4 to stage 1, and it may be that stages 2 and 3 are alternative pathways to crystallization.

Thus, despite the great variability of the developmental stages of song, Swamp Sparrows kept in captivity under these conditions display a regular and repeatable pattern of ontogeny leading up to the emergence of full song.

Song development in relation to season and age.—With the exception of one bird, all fall singing recorded (from 50 to 165 days) consisted of stage 7 subsong. Although not tape-recorded, subsong was noted as early as 20 days in some birds. After the silent mid-winter period, vigorous subsong and subplastic song began, with a median onset date of 9 March 1978. The earliest bird began on 14 February and the latest on 28 March. Plastic song typically started during the first week of April (median starting date 4 April), with the earliest on 10 March and the latest on 9 May. The first delivery of crystallized song was recorded on 21 April. The last bird crystallized 36 days later, and the median date of onset was 10 May. These dates indicate that the singing programs for these caged and individually isolated males did not depart too greatly from those of wild birds in the area.

As can be seen in Fig. 5, a bird that starts spring subsong and subplastic song early also tends to be ahead with the transitions to plastic song and crystallized song. The onset of later developmental stages is no more synchronous with regard either to age or to time of year than is the onset of subsong. On the other hand, the duration of the subsong and subplastic song periods combined was negatively correlated with duration of the plastic song period, hinting at a possible compensatory relationship between these two developmental stages ($P < 0.05$, Spearman rank correlation coefficient $r_s = -0.511$ for $n = 16$). A search for possible correlations between age and development also revealed a negative relationship between hatching date and the ages of onset

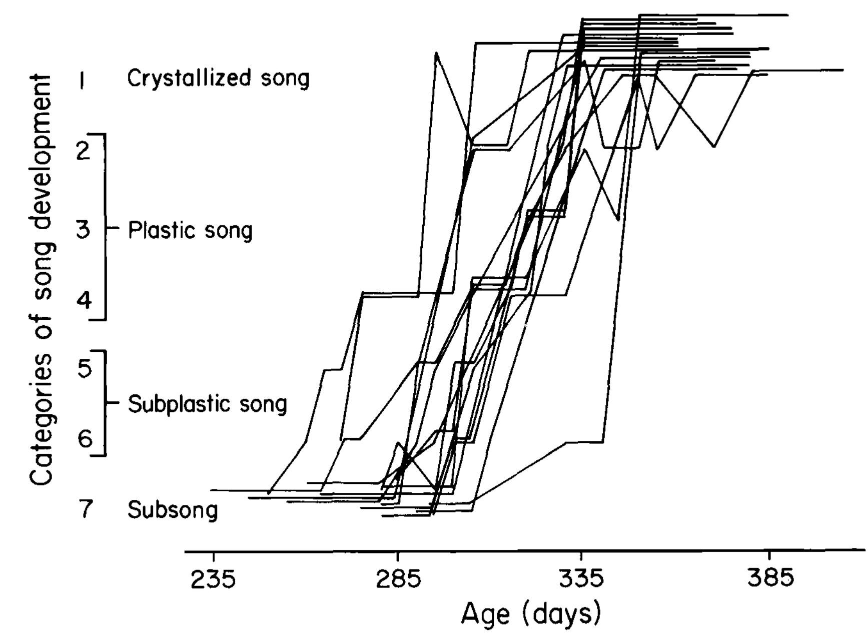

Fig. 6. Song development in the Swamp Sparrow as revealed by plotting the least advanced stage represented in any given sample. Sixteen birds are represented. The categories of song development are as defined in Table 1.

of three major stages of song development ($r_s = -0.672$ for subsong and subplastic song, -0.737 for plastic song, -0.680 for crystallized song). Thus, the earlier in the season a bird was hatched, the later the age at which subsong or subplastic song, plastic song, and full song began. The differences become amplified in the process, so that one bird hatched 24 days before another started spring subsong or subplastic song 65 days later. The functional significance of this correlate of early- and late-season hatching is unclear and merits further investigation.

Changes in Song Structure During Ontogeny

Syllable structure.—We have yet to attempt a comprehensive analysis of the structure of subsong. As indicated in the sample in Fig. 1, it is exceedingly variable, with a wide range of frequencies represented and virtually no repeated elements. Only with the birds' attainment of stage 6 subplastic song do we occasionally see the first hints of syllabic structure. By stage 4, most note sequences could be identified, and all plastic song syllables were then classified on the basis of their acoustic structure. We identified 199 different plastic song syllable types for the 16 males. A comparison with the training songs revealed that 59 of these were imitations (29.6%). The remaining 140 were classified as inventions or improvisations (70.3%). A detailed analysis of these will be presented elsewhere (Marler and Peters in prep.). Evidently, nonimitated syllables make up an appreciable part of the plastic song repertoire. Twelve sang a combination of imitated and nonimitated syllables, and four sang the latter only.

Despite this large syllable vocabulary employed during plastic song, the males only crystallized a small part of their potential repertoire (22.6%). As a group, they crystallized 45 syllable types, of which 19 (42%) were imitations. Four of the 16 birds produced no imitations in either plastic or full song, and two of the 12 males that sang imitated syllables in plastic song failed to include them in their final repertoire. No bird produced a syllable in crystallized song that was not represented in some form in plastic song. Excluding the four without imitations in plastic song, there was some tendency to favor imitated syllables in the crystallization process [39.6% in plastic song,

TABLE 4. Numbers of syllable types used by male Swamp Sparrows up to the time of song crystallization.

Number of birds	1	8	10	12	10	9	6	16
Average syllables per bird	13	12	11.6	10.1	7.3	8.3	5.8	3.1
Range	13	8–15	3–16	5–18	1–12	2–19	3–10	1–5
Standard deviation	—	±2.4	±4.3	±3.8	±3.9	±3.9	±3.1	±1.3
Days from song crystallization	−49	−42	−35	−28	−21	−14	−7	0

57.6% in crystallized song, but the difference is not significant (χ^2 test: $\chi^2 = 2.87$, $0.05 < P < 0.1$)].

The 45 crystallized syllable types were represented in 35 songs, with an average repertoire of 2.2 song types per bird. Of these crystallized songs, 25% of them were two-parted. Wild males, with a repertoire of 3–4 typically sing one-parted songs. Two-parted songs do occur in nature, although rarely. Three out of 58 (5%) of the song types recorded from 25 wild males were composed of more than one part. In the laboratory-reared birds, one-parted songs still predominated, although less so than in nature.

There is a decline in the number of syllable types uttered by a bird as it proceeds from the first stages of plastic song through to crystallization. The mean number of syllable types per bird per recording session during plastic song was 9.5 (SD = 4.25: 56 recording sessions). In crystallized song, the mean number of syllable types per bird was 2.9 (SD = 1.22: 114 recording sessions), a highly significant difference (t-test, $P < 0.001$, $t = 11.4$). Early in plastic song the average number of syllable types per male went up to 12–13, and one male peaked at 19 (Table 4). It is thus clear that the male Swamp Sparrows develop many more syllables in plastic song than are needed to generate species-specific song. The process of developmental attrition that accompanies the progression through plastic song is discussed in more detail elsewhere (Marler and Peters in prep).

Phrase structure.—If we use the term "phrase" for structural units within the song larger than individual syllables, the typical crystallized song of a male Swamp Sparrow consists of a single phrase (e.g. Fig. 1). Although two-phrase songs do occur both in nature and in our captive birds, songs with more than two phrases have never been recorded from Swamp Sparrows after crystallization. By contrast, plastic song often incorporates more than two phrases. Figure 7 presents the mean number of phrases per song for all 16 birds, plotted in relation to the day of song crystallization. In addition, the average minimum and maximum number of phrases are also indicated. It is clear that, just as the number of syllable types used by each bird decreases in plastic song as the time for crystallization approaches, so the same is true of the number of phrases per song. In early plastic song there may be as many as eight phrases per song, with a maximum averaging 3.5, decreasing to an average of 1.2 with crystallization. Both phrase structure and syllable type number undergo progressive reduction as mature song emerges.

Further developmental trends.—One might hypothesize that the complexity of mature singing relates to the time spent in certain developmental stages, such as plastic song. We could find no correlation between the duration of any phase and the number of plastic or crystallized syllable types developed. There is, however, a positive correlation between the number of syllable types used in plastic song and the number of songs crystallized in the final repertoire ($P < 0.05$, Spearman rank correlation coefficient $r_s = 0.463$ for $n = 16$). The different training schedules had no effect on the number of plastic or crystallized syllable types, whether imitated or not.

To what extent does knowledge of the structure of plastic song permit prediction of the syllables destined to be crystallized? For each bird's plastic song recordings we counted the number of songs containing each syllable type, then grouped the syllable types and combined the numbers of songs in which they occurred under the following four categories: imitated and nonimitated syllables, syllables eventually included in the final repertoire, and syllables excluded from the final repertoire. For an absolute measure of syllable usage, we calculated the average number of songs per hour in which a copy or noncopy syllable and a final repertoire syllable or a discontinued syllable oc-

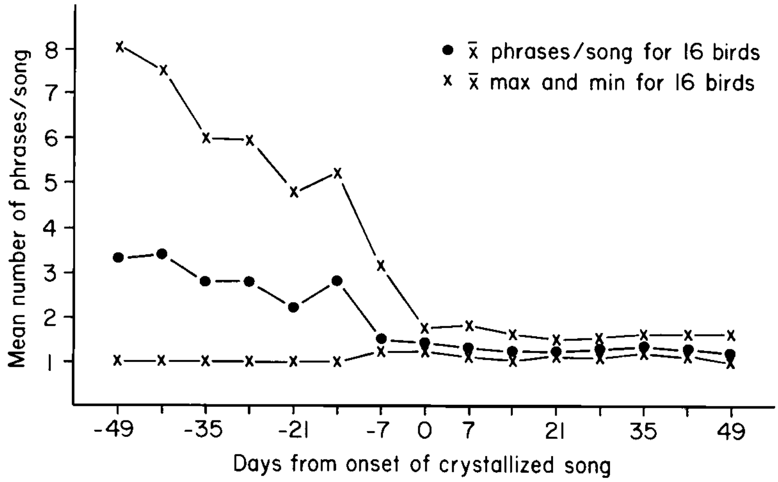

Fig. 7. Developmental changes in Swamp Sparrow song structure. The mean numbers of phrases per song are plotted in relation to the day of song crystallization. Average maxima and minima are also shown.

curred in each of the recording dates during the plastic song period. The results were as follows.

For the group of 16 birds, the average number of songs per hour in which an imitated syllable occurred during plastic song was 9.3 (SD = 10.6) and for a nonimitated syllable 7.4 (SD = 4.7). We had 39 plastic song recordings for the 12 birds that used imitations. An imitated syllable occurred in an average of 13.3 (SD = 10.4) plastic songs and a nonimitated syllable in 7.2 (SD = 4.9), a significant difference (t-test, $P < 0.01$). A comparison of the average frequency of occurrence of a final repertoire syllable (12.5, SD = 10.8) and a discarded syllable (7.6, SD = 5.3) in plastic song revealed that the birds sang those syllables destined for the final repertoire significantly more often (t-test, $P < 0.01$).

DISCUSSION

The term subsong seems to have originated with Nicholson (1927, Nicholson and Koch 1936). Its use was extended by various other ornithologists (e.g. Lister 1953), but Thorpe was most responsible for formalizing use of the term and defining the basic properties of subsong (Thorpe 1955, Thorpe and Pilcher 1958). An apparently equivalent term, "warbling," was coined by Nice (1943) but has been displaced by the earlier term. Analyses of subsong in the Chaffinch (*Fringilla coelebs*) led to a further division of ontogenetic stages of song development, in which the term "subsong" was restricted to the very earliest stages, as with Nice's "warbling" definition, and the term "plastic song" was coined for a more highly structured, intermediate stage, distinct both from subsong and from the fully crystallized adult song (Marler 1956). This classification, or others equivalent to it, has been applied and extended by others (e.g. Lanyon 1960; Nottebohm 1968, 1972a, b, 1975). To judge from published descriptions, it is applicable to a wide variety of songbirds (e.g. Lanyon 1957, 1960; Poulsen 1959; Armstrong 1963; Lemon and Scott 1966; Kroodsma 1974). We have found it instructive to add a further stage of subplastic song, transitional between subsong and plastic song. It has many of the qualities of subsong discussed below but also contains some suggestions of syllabic structure.

Given the great variation in the structure and complexity of the full, primary song of different species, there appears to be a surprising degree of conformity to a general pattern of development. Singing tends to begin with an amorphous, highly variable and unstructured subsong.

The subsong of the Swamp Sparrow illustrates several of the general features outlined by Thorpe and Pilcher (1958) for the subsong of thrushes, finches, and some other species. The differences between subsong and full song that recur include the volume, with subsong quieter than full song; patterning, with subsong having a very different structure; duration, which tends to be longer in subsong; frequency range, inclined to be greater in subsong; and seasonal timing, with subsong occurring earlier in the season.

There are some striking parallels between the Swamp Sparrow and the Song Sparrow as reported by Nice (1943). She listed five stages, beginning with "continuous warbling" and culminating in "adult song." After stage 1, continuous warbling, stage 2 included some short songs and much warbling, with intervals between songs much shorter than the song length. Stage 3 included some warbling but consisted predominantly of short songs, not yet crystallized into adult form but with interval lengths about equal to those of songs. Stage 4 songs were practically adult in form, with intervals usually twice as long as the songs themselves. This was described as a period of trying out songs, adding some, and deleting others. With Stage 5, fully adult song was achieved, stereotyped except for some variation in endings, restricted to the final repertoire.

It is notable that variations in song duration served as useful markers for the five Song Sparrow stages. We have shown that an abrupt decrease in song duration and a dramatic contraction of the variability are striking accompaniments of the process of song crystallization in the Swamp Sparrow, coinciding with the first emergence of the full song.

Nice also described in the Song Sparrow a process that may correspond to the syllable attrition we have described in the Swamp Sparrow in its progression through the plastic song period. She describes young males as they establish territories replying to rivals with similar songs, even though many of these were subsequently dropped from the repertoire. She concluded that "each young song sparrow has a large fund of potential songs, as is clear from listening to the rambling warblings of juveniles." She suggests that what may appear to be a process of imitation occurring during early territorial establishment may actually be "a calling forth of songs already in the potential repertoire, most of them being later lost through disuse" (Nice 1943:139). A loss of song material toward the end of ontogeny has been noted in other species, such as the White-crowned Sparrow (*Zonotrichia leucophrys*) and the Red-winged Blackbird (*Agelaius phoeniceus*) (Marler 1970, Marler et al. 1972), indicating that this may be a rather general phenomenon.

There are indications that the classification of ontogenetic stages of Swamp Sparrow song presented here may be applicable to a variety of other songbirds, with adjustments for differences in species-specific song structure. Despite these similarities, it would probably be a mistake to conclude that subsong and plastic song serve a similar function in all songbirds. Although we can do little more than speculate at this stage, it seems likely that there are multiple functions even within a species.

One further finding in the Swamp Sparrow that complicates functional interpretation concerns the occurrence of plastic song in older birds. In four males we followed the process of song development through a second year. There was virtually no subsong or subplastic song, but plastic song did occur, though for a shorter period than in the first year. Without exception, all of the second-year plastic song syllables could be matched from the first year of that individual. Fewer were used, however. The four birds used 51 syllable types in first-year plastic song and only 25 in the second year. Although there were no additions, some shifts of emphasis occurred, favoring different syllables from those in year 1. The four birds crystallized the same 12 syllable types as in year 1, all well rehearsed in plastic song. The 13 plastic song syllables that were rejected in second-year crystallization had also been rejected in the first year.

Thus, in Swamp Sparrows the excess of syllable production does not provide a bank for generating new songs in the future. In fact, Swamp Sparrow song remains virtually unchanged from year to year. In our 16 captive males, for example, 31 of the 33 song types produced in the first year persisted unchanged in the second. One song was dropped, and in another some high frequency components were lost, as though perhaps from a syringeal abnormality. Indications from field data are that no new songs are added to the adult repertoire after the first year (D. Kroodsma and R. Pickert, in litt.).

In species that change the song repertoire from year to year, such as the canary (*Serinus canarius*) (Marler et al. 1973, Nottebohm and Nottebohm 1978), the Red-winged Blackbird

(Marler et al. 1972, Yasukawa et al. 1980), the Saddleback (*Philesturnus carunculatus*) (Jenkins 1977), the Indigo Bunting (*Passerina cyanea*) (Rice and Thompson 1968), and the indigo bird [*Vidua* (= *Hypocherina*) spp.] (Payne 1973), an excess of plastic song material, if it occurs, might provide a source for additions to the full song repertoire in subsequent years. This is one of many questions raised by this study that deserves further investigation.

Perhaps the most surprising result is the high incidence of song invention in our captive Swamp Sparrows. This occurred despite the large set of training songs used, though it is hard to be sure what would constitute a surfeit of acceptable models. A comparison with the simple syllables of innate Swamp Sparrow songs (Marler 1981) suggests that exposure to song actually stimulates vocal invention in this species. It remains to be determined whether the use of live tutors rather than tape recordings affects the amount of song invention. Unlike some emberizines, such as the White-crowned Sparrow, local Swamp Sparrow populations exhibit considerable heterogeneity in their songs, with a high incidence of rare song types. A high invention rate is one means by which male Swamp Sparrows may generate this trend toward song diversity in local populations.

ACKNOWLEDGMENTS

This research was supported by PHS research grant S07 RR-076512 to the Rockefeller University and MH 14651 to Peter Marler. Valuable contributions to the project were made by P. Price, C. Marler, J. Marler, M. Searcy, and G. Sherman. L. Baptista and D. Heinemann made useful comments on the manuscript.

LITERATURE CITED

ARMSTRONG, E. A. 1963. A study of bird song. London, Oxford Univ. Press.

JENKINS, P. F. 1977. Cultural transmission of song patterns and dialect development in a free-living bird population. Anim. Behav. 25: 50–78.

KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's wren. Z. Tierpsychol. 35: 352–380.

LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publ. Nuttall Ornithol. Club No. 1: 1–67.

———. 1960. The ontogeny of vocalizations in birds. Pp. 321–347 *in* Animal sounds and communication (W. E. Lanyon and W. N. Tavolga, Eds.). Washington, D. C., Amer. Inst. Biol. Sci.

LEMON, R. E., & D. M. SCOTT. 1966. On the development of song in young Cardinals. Can. J. Zool. 44: 191–199.

LISTER, M. D. 1953. Secondary song; a tentative classification. Brit. Birds 46: 139–143.

MARLER, P. 1956. Behaviour of the chaffinch. Behaviour Suppl. 6: 1–186.

———. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. J. Comp. Physiol. Psych. 71: (2, Part 2) 1–25.

———. 1981. Birdsong: the acquisition of a learned motor skill. Trends in NeuroSciences 4: 88–94.

———, & S. PETERS. 1977. Selective vocal learning in a sparrow. Science 198: 519–521.

———, & ———. In press a. Subsong and plastic song: their role in the vocal learning process. *In* Ecology and evolution of acoustic communication in birds (D. Kroodsma and T. Miller, Eds.). Bloomington, Indiana Univ. Press.

———, & ———. In press b. Long-term storage of learned birdsongs prior to production. Anim. Behav.

———, M. KONISHI, A. LUTJEN, & M. S. WASER. 1973. Effects of continuous noise on avian hearing and vocal development. Proc. Natl. Acad. Sci. USA 70: 1393–1396.

———, P. MUNDINGER, M. S. WASER, & A. LUTJEN. 1972. Effects of acoustical stimulation and deprivation on song development in the Red-winged Blackbird (*Agelaius phoeniceus*). Anim. Behav. 20: 586–606.

NICE, M. 1943. Studies in the life history of the song sparrow. II. Trans. Linnaean Soc. New York, Vol. VI.

NICHOLSON, E. M. 1927. How birds live. London, Williams and Norgate.

———, & L. KOCH. 1936. Songs of wild birds. London, H. F. & G. Witherby.

NOTTEBOHM, F. 1968. Auditory experience and song development in the chaffinch *Fringilla coelebs*. Ibis 110: 549–568.

———. 1972a. Neural lateralization of vocal control in a passerine bird. II. Subsong, calls and a theory of vocal learning. J. Exp. Zool. 179: 35–49.

———. 1972b. The origins of vocal learning. Amer. Natur. 106: 116–140.

———. 1975. Vocal behavior in birds. Pp. 287–332 *in* Avian biology, vol. 5 (D. Farner, Ed.). New York, Academic Press.

———, & M. NOTTEBOHM. 1978. Relationship between song repertoire and age in the canary, *Serinus canarius*. Z. Tierpsychol. 46: 298–305.

PAYNE, R. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. Ornithol. Monogr. 11: 1–33.

PETERS, S., W. A. SEARCY, & P. MARLER. 1980. Species song discrimination in choice experiments with territorial male Swamp and Song sparrows. Anim. Behav. 28: 393–404.

POULSEN, H. 1959. Song-learning in the domestic canary. Z. Tierpsychol. 16: 173–178.

RICE, J. O., & W. L. THOMPSON. 1968. Song development in the Indigo Bunting. Anim. Behav. 16: 462–469.

THORPE, W. H. 1955. Comments on "The bird fancyer's delight," together with notes on imitation in the subsong of the chaffinch. Ibis 97: 247–251.

———, & P. M. PILCHER. 1958. The nature and characteristics of subsong. Brit. Birds 51: 509–514.

YASUKAWA, K., J. L. BLANK, C. B. PETERSON. 1980. Song repertoires and sexual selection in the Red-winged Blackbird. Behav. Ecol. Sociobiol. 7: 233–238.

ZOLOTH, S., R. J. DOOLING, R. MILLER, & S. PETERS. 1980. A minicomputer system for the synthesis of animal vocalizations. Z. Tierpsychol. 54: 151–162.

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