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FLIGHT SONGS OF SWAMP SPARROWS: ALTERNATIVE PHONOLOGY OF AN ALTERNATIVE SONG CATEGORY[1]

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Abstract. In addition to their simple trilled territorial song, normally sung while perched, male Swamp Sparrows (*Melospiza georgiana*) more rarely also sing a flight song with complex phonology and syntax. The typical trilled songs of Swamp Sparrows all can be broken down into only six simple constituent note types. Because these same note types, and no others, are found throughout the Swamp Sparrow's range, they are thought to represent a "species-universal phonology." Acoustic analysis of flight song notes from one population reveals no overlap at all with the phonology of trilled songs. One flight song note type ("B") appears similar to a trilled song note type ("VI"), but detailed analyses reveal these note types to be distinct. Thus, Swamp Sparrows appear to use independent phonologies in the production of two different types of song. These two phonologies may entail different mechanisms for processes of song acquisition and control.

Key words: Song; phonology; learning; song types; Swamp Sparrow; Melospiza georgiana.

INTRODUCTION

That songbirds learn to sing by listening to auditory models (Marler 1970, Nottebohm 1975, Kroodsma 1982) implies a significant potential for variability in the vocal behavior of a species. The common occurrence of local geographic dialects in many species' songs (Marler and Tamura 1964, Lemon 1979, Baker and Cunningham 1985) also suggests that song learning allows for plasticity in vocal behavior. An apparent contradiction to this idea, however, comes from the growing evidence that the minimal components of a species' song repertoire may be quite limited. That is, all the variations observed in a species' songs may be broken down into a circumscribed set of phonological elements that are universally shared among individuals, even across the entire geographic range of a species (Marler and Pickert 1984). We here describe a novel extension of this phenomenon, in which individuals of the same species use two independent sets of phonological elements in the production of two different types of songs.

The Swamp Sparrow (*Melospiza georgiana*) well illustrates the apparent contradictions between vocal learning and phonological constraints. Its typical song is a 2–3 sec trill of repeated "syllables," each syllable including 2–5 separate phonological units, termed "notes." As is typical for oscine birds, Swamp Sparrows develop abnormal songs if deprived of models during a sensitive phase (Marler and Sherman 1985), demonstrating that learning through imitation is required for normal vocal development (Kroodsma 1982). Swamp Sparrows are selective, however, in the stimuli they will accept as patterns for learning. In experiments with either live tutors or tape training, heterospecific song material

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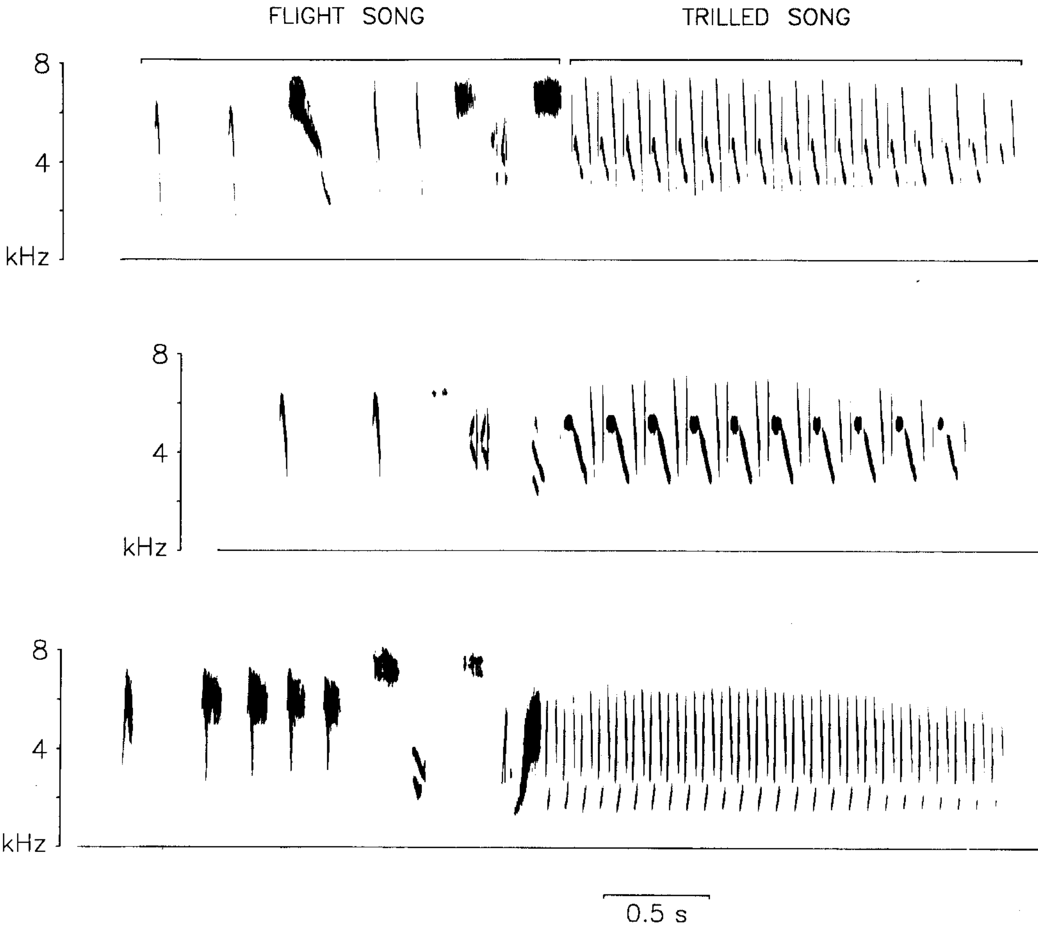

FIGURE 1. Sonagrams of typical flight songs of three Swamp Sparrows. Each song begins with a flight song and ends with a typical trilled song. (In our usage here "flight song" refers only to the series of notes preceding the trill, even though the large majority of flight songs are usually followed by a trilled song as one continuous vocalization; Table 1.) Shown at bottom are frequency and time scales (Kay 5500 DSP Sona-Graph, 0–8 kHz range, 100 pt FFT, 300Hz frequency resolution).

is almost universally rejected as a model (Marler and Peters 1977, 1988, 1989).

Consistent with this selectivity in learning is the discovery that Swamp Sparrow songs are composed of only a small number of basic note types. Acoustic analyses of songs recorded across the species' geographic range demonstrate that their constituent notes can be sorted into only four to six categories (Marler and Pickert 1984; Clark et al. 1987; D. A. Nelson, unpubl. data). Different song types arise from different combinations of notes comprising the trilled syllable. Geographic dialect differences, which are salient to both males and females (Balaban 1988b), result primarily from different typical ordering of these same note types within a syllable (Marler and Pickert 1984, Balaban 1988a). Finally, differences in Swamp Sparrow note types are in some cases perceived categorically by the birds, along the same boundaries that define notes acoustically, verifying that this phonology represents a set of meaningful natural categories of song production and perception (Nelson and Marler 1989).

In addition to this well-described trilled song, Swamp Sparrows also sing a flight song that differs not only in usually being delivered on the wing, but also in having a very different cadence and tonality (Fig. 1). First described over 100 years ago (Bicknell 1885), these flight songs are relatively rarely heard. We recorded nine Swamp Sparrows, including one laboratory-reared individual, that sang flight songs in captivity, permitting us to analyze their structure in detail. Given the conservative phonology of the trilled Swamp Sparrow song, we were surprised to discover that notes used in flight songs appeared to be different from those seen in trilled song. We here describe the phonology of the Swamp Sparrow flight song, evaluate the degree to which it represents a well-defined phonological set, and compare it to the previously described phonology of the trilled song.

METHODS

The songs of eight wild birds and one hand-reared bird were recorded in an anechoic room using a Realistic 33-1070 microphone, Shure FP 11 preamplifier, and Marantz PMD 221 cassette recorder. The frequency response of this system was flat in the range of interest (0.5–10 kHz). Wild birds were captured as adults from the Great Vly Swamp and the Cary Arboretum of the New York Botanical Garden, both in the Hudson Valley of New York State. Data on the subjects' recorded samples are presented in Table 1.

Sonagrams (Kay 7800 Sona-Graph, 0–8 kHz range, 300 Hz filter) were prepared of examples of each unique flight song type and trilled song type observed (see Fig. 1). The notes of each individual's flight songs were cut out and affixed to separate cards. "Notes" were operationally defined as elements clearly separated by about 8 msec (about 1 mm on the sonagram). All notes in an individual's repertoire that showed any apparent variation were included, and only notes that were repeated in more or less identical fashion within an individual's repertoire, usually from the same songs, were excluded from this sample. The 321 flight songs in our sample yielded 2,062 notes total, from which 658 different note examples were selected for our phonological classification.

Flight song phonology was categorized based on visual inspection of note structure from these sonagrams, following the methods of Marler and Pickert (1984). The note exemplars were independently sorted into categories by two of us

TABLE 1. Total numbers of songs recorded, numbers of flight songs recorded, and flight song note type repertoire sizes for eight wild, and one hand-reared, Swamp Sparrows.

Bird	Total songs recorded	Total flight songs	Flight songs sung alone[1]	Note type repertoire size
1	119	27	0	10
2	152	22	0	7
3	44	44	0	8
4	134	51	0	7
5	485	14	1	9
6	513	127	5	9
7	25	8	0	10
8	184	23	0	9
9[2]	457	5	0	3

[1] Flight songs that were not immediately followed by a trilled song.
[2] Hand-reared bird.

(MH and PM). Inter-observer agreement was good (see RESULTS) and there were few intermediate types, making a final classification easy to determine.

We used quantitative techniques to further examine the similarity between flight song note type "B" (see below) and trilled song note type "VI" (of Marler and Pickert 1984). Songs were digitized at 25 kHz (Compaq 386/25 computer; DT 2821-F A/D) and analyzed using the "SIGNAL" software package (Beeman 1989). Comparisons between note types were done using the "sound-comparative method" of Clark et al. (1987). This technique calculates the similarity of two digital sonagrams by determining the maximum 2-dimensional cross-correlation (frequency × time) between them. Multidimensional scaling (MDS) was used to evaluate clustering among notes based on matrices of similarity scores between all pairwise note comparisons (Kruskal and Wish 1978, Wilkinson 1988). This method provides a complement to multivariate approaches because it uses the overall structure of a sound to determine similarity scores (see Clark et al. 1987; and Nowicki and Nelson, in press, for further details).

Measurements from digital spectrograms of notes were also used in a multivariate analysis of variance, with post-hoc testing (Wilkinson 1988) to assess note differences. We measured duration (128 pt FFT, resolution = 2.5 msec) and high and low frequencies (256 pt FFT, resolution = 95 Hz), both at −21 dB *re* peak amplitude. Frequency slope was derived from these measurements. These four parameters efficiently

TABLE 2. Cross-tabulation of two independent note classifications based on visual inspection of sonagrams. Rows are the classification by MH; columns are the classification by PM. Zero values are indicated by a dash.

	1	2	3	4	5	6	7	8	9	10	11	12	Totals
A	—	—	—	—	—	—	—	—	—	—	31	—	31
B	—	53	—	—	—	—	—	—	—	—	—	—	53
C	—	2	79	—	—	—	—	—	—	—	—	—	81
D	—	2	—	—	—	—	—	—	63	1	—	—	66
E	—	—	—	—	—	28	—	11	—	—	—	—	39
E1	—	—	—	—	6	—	—	—	—	—	—	—	6
F	—	—	—	—	—	—	—	—	2	71	—	—	73
G	—	—	—	—	—	—	—	—	46	—	—	2	48
H	—	—	—	—	—	—	—	—	1	—	—	5	6
I	—	—	—	22	—	—	—	—	—	—	—	—	22
J	54	—	—	—	—	—	—	—	—	—	—	—	54
K	—	—	—	1	—	—	1	120	—	—	—	—	122
L	—	—	—	—	—	—	57	—	—	—	—	—	57
Totals	54	57	79	23	6	28	58	131	112	72	31	7	658

discriminate among the note types of trilled Swamp Sparrow songs (Marler and Pickert 1984, Nelson and Marler 1989). Equal variance among groups was tested using Levene's test (Schultz 1983).

Transition matrices of note sequences in flight songs, coded using the note typology determined above, were generated for each individual. Departures from randomly expected transitional frequencies were tested using a G-test for goodness-of-fit with Williams' correction (Everitt 1977, Sokal and Rohlf 1981). Only one bird (#6) had a large enough sample to warrant statistical assessment in this fashion; transition matrices from other birds were used only to aid in the identification of common note sequences.

RESULTS

DESCRIPTION OF SONGS

Flight songs are sung most often in the early spring, when males are first establishing territories (Roberts 1932; Nowicki, pers. obs.). As compared to the typical trilled song of Swamp Sparrows, flight songs differ radically in the cadence and syntax of their constituent notes (Fig. 1). After flying up, a bird will flutter down, delivering a halting, irregular series of notes. At the end of this flight song, the bird usually continues without a break directly into one of its trilled song types. In the laboratory, we recorded only a few occasions when a bird failed to follow a flight song with a trilled song (Table 1). Most flight songs observed in the field are sung while in flight, but some are delivered while perched. All of our laboratory recordings were sung while perched. Although we did not obtain a sufficient number of field recordings for a formal analysis, we could not detect any differences between our laboratory recordings and those flight songs observed in the field.

Based on a random subsample of 50 songs, 10 each from the five birds with the largest number of songs recorded, the duration of a typical flight song is 1.6 ± 0.5 s ($\bar{x}$ ± SD). The duration of the trilled song that immediately follows the flight song is 2.0 ± 0.4 sec, while the duration of a typical trilled song sung alone (i.e., not preceded by a flight song) is 2.5 ± 0.3 sec. The difference in duration between trilled songs alone and those preceded by flight songs is highly significant ($T = -6.946$, $P < 0.001$).

In six of the eight wild birds, we found every trilled song type in an individual's repertoire to occur both in association with flight songs and alone. In the remaining two birds, only one trilled song type out of a total repertoire of four each was not observed to occur at least once in association with a flight song.

Unlike trilled songs, flight songs are not easily assigned to discrete song types. Some flight songs are repeated identically in different renditions, but more often each rendition includes variable substitutions, deletions and repetitions of notes. It was thus impossible to generate a catalog of flight song types. The size of individuals' trilled song repertoires in our sample was 4.2 ± 1.1 song types. Considering exact repetitions of note sequences as our definition of flight song "types,"

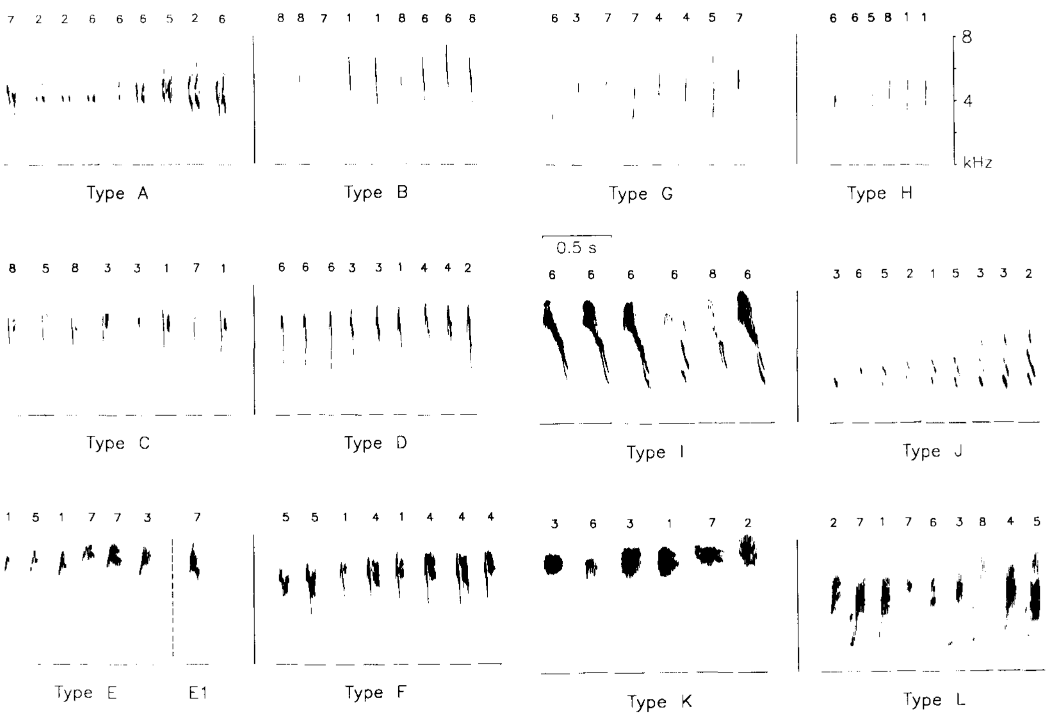

FIGURE 2. Ninety-four exemplars, from eight wild Swamp Sparrows, of the 13 flight song note categories, illustrating typical within-category variation. Numbers above notes identify the individual that sang that note (Table 1). Only one exemplar of category E1 is shown, as only one bird produced that note type. See Appendix for further descriptions. Sonagraphic analysis as in Fig. 1.

we recorded 23.0 ± 15.2 (range: 9–49) different variants per individual.

PHONOLOGICAL CLASSIFICATION

The process of sorting notes into categories was straight-forward, given the distinctive acoustic morphology of the categories that emerged, and the rarity of intermediate forms. One classification (by MH) resulted in 13 categories, while the other (by PM) resulted in only 12 categories. Despite this discrepancy, the inter-observer agreement in the placement of particular note exemplars into the same categories was 88.6% (Table 2). Most of the disagreement resulted from the PM classification cleanly lumping two categories that were split by the MH classification (Type 9 vs. Types D and G; Table 2). We decided on the conservative decision to keep these categories split, resulting in 13 final note types. Inter-observer agreement with this modification was 96.5%, illustrating the discrete nature of Swamp Sparrow flight song note types.

Examples of these 13 note types showing typical within-category variation are presented in Figure 2. Verbal descriptions of the types are found in the Appendix.

NOTE TYPE USAGE

We evaluated how often different note types occurred in the repertoires of the six birds that had the largest number of flight songs recorded (>20 songs and >100 notes from which to sample; note type E1 (Fig. 2) was rare, and only used by a single bird whose sample did not meet criteria, so it is excluded from further analyses). The proportion of songs that included at least one of a particular note type, averaged by bird, revealed some types to be relatively common (e.g., J and K; Fig. 3*A*) while others are rare (A, H, and I). Within a song, some note types are typically repeated in sequence two or more times (Fig. 3*B*) or are repeated several times, but not in sequence (Fig. 3*C*).

Five of 12 note types, D, G, J, K and L, were shared by all six birds meeting our sample criteria, while four notes, A, E, F and I, were found

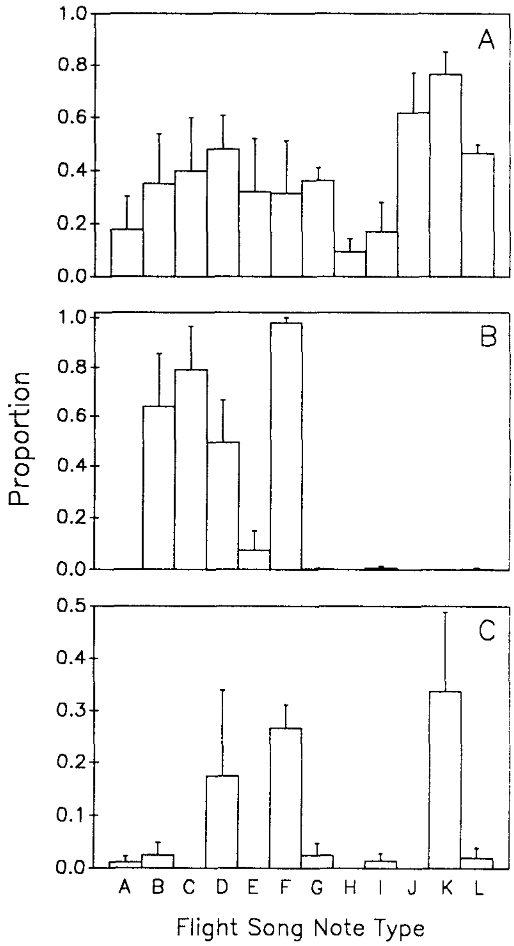

FIGURE 3. (*A*) Proportion of total songs including at least one of a particular note type; (*B*) Proportion of occurrences of each note type that are repeated sequentially in a song; (*C*) Proportion of occurrences of each note type that occur as non-sequential repeats in a song. Shown are means and standard errors for six individuals.

in only two birds. The remaining note types, B, C, and H, were sung by four, three, and five birds, respectively. Individuals also differed in the total number of note types they incorporated in their flight song repertoires (Table 1). For the wild birds, however, there was no correlation between total number of flight songs recorded and size of flight song note repertoire (Kendall's $\tau = -0.2758$, $P > 0.20$).

SEQUENTIAL ANALYSIS

The structure of flight songs is variable, but notes do not occur in completely random order. One bird (#6) had a sufficiently large number of songs in its sample to permit a statistical evaluation of the transition probabilities of its note sequences. With the exception of type J (which bird #6 sang only rarely), all note types differed significantly from random in terms of the note types that preceded and followed them ($P < 0.014$ in all cases, with α adjusted for the lack of independence between rows and columns; Everitt 1977). Thus, although this bird's flight songs did not follow a determinant note order, some transitions (e.g., D-I-B-K-A-K-G-L) occurred more frequently than expected by chance.

Transition matrices constructed for the other wild birds revealed no completely identical flight song note sequences shared between individuals. Some short sequences were held in common, however, such as K-A-K (birds #6 and #2), and D-I-B (birds #6 and #8). The most commonly shared combination of notes was K-G-L, appearing in 41% of all flight songs from all birds. (For reasons explained in the Appendix, we lumped type H with type G for this analysis.)

COMPARISON OF FLIGHT SONG AND TRILLED SONG PHONOLOGIES

All notes we observed in the trilled songs of our eight wild birds were easily classified using the phonological scheme of Marler and Pickert (1984). Typical examples of these note types drawn from our sample are shown in Fig. 4. Inspection of Figures 2 and 4 (see also Fig. 3 of Marler and Pickert 1984) shows that flight song phonology is quite distinct from the phonology of trilled songs, with one possible exception. Type B of the flight song (Fig. 2) and type VI of the trilled song (Fig. 4) are visually similar, and thus might represent a point of overlap between the two phonologies. To evaluate this similarity quantitatively, we digitized 12 examples of type B notes from each of three birds (#1, #6, and #8). Flight songs were chosen that also included a type VI in the associated trilled song, and we sampled one type VI from each of these songs as well. From the same birds, we also digitized 12 examples each of type VI notes taken from trilled songs that were not associated with flight songs.

Multidimensional scaling based on spectrogram cross-correlations of these notes (Clark et al. 1987) clearly segregated type B notes from both groups of type VI notes, which were themselves tightly clustered together (Fig. 5). This analysis was performed for each bird individu-

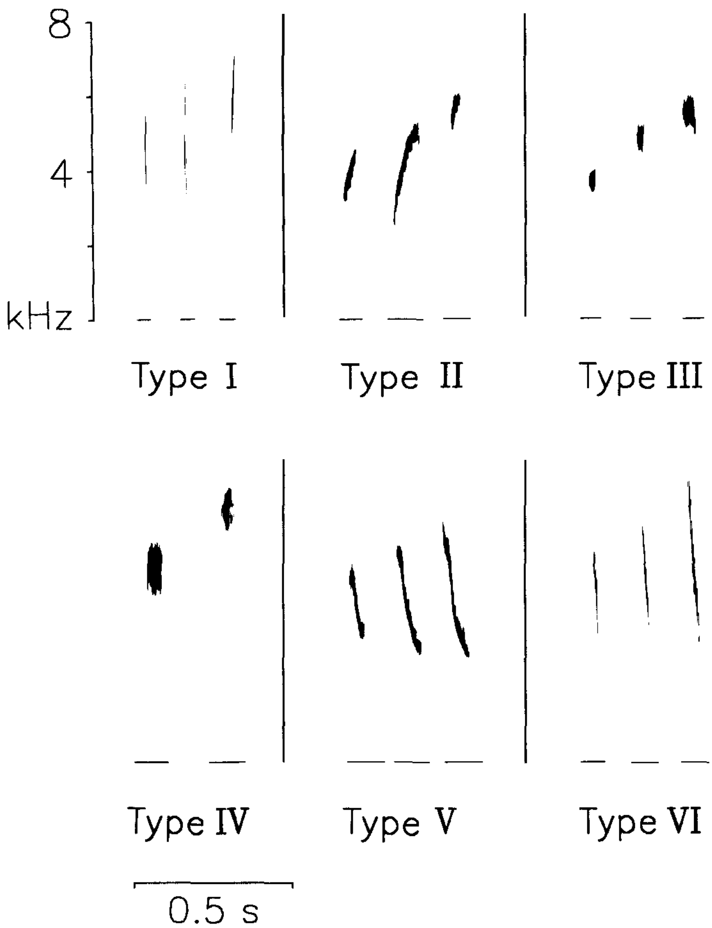

FIGURE 4. Seventeen exemplars, from eight wild birds, of the six normal song note types. Sonagraphic analysis as in Fig. 1.

ally. Figure 5 shows results for bird #1; data from birds #6 and #8 showed similar segregation of type B from type VI notes.

Multivariate analysis of variance of high frequency, low frequency, duration, and slope measurements also revealed significant variation among the three groups of notes (Wilk's Lambda $F[8, 192] = 3.18$, $P = 0.002$). There was a significant individual effect ($F[8, 190] = 17.57$, $P < 0.001$), however, and a relatively weak note-by-individual interaction ($F[16, 293] = 1.82$, $P = 0.028$), suggesting this significance value be interpreted with caution. Nonetheless, post-hoc testing revealed highly significant differences between type B notes and both groups of type VI notes ($F[4, 96] = 6.19$, $P < 0.001$), while the two groups of type VI notes did not differ from each other ($F[4, 96] = 0.50$, $P = 0.738$).

LABORATORY-REARED BIRD

Bird #9 was taken from the nest at six days of age and raised in the laboratory as part of a separate study (see Marler and Peters 1989). It was tape-tutored with normal trilled Swamp Sparrow song, and probably never heard examples of flight songs, certainly not after its age of capture. Nonetheless, five flight songs were recorded from this individual as an adult. The features of its flight songs were comparable to those of wild birds, although they were much shorter, including only 2.4 ± 1.4 notes per flight song, as compared to 7.5 ± 3.8 notes per flight song for the wild birds.

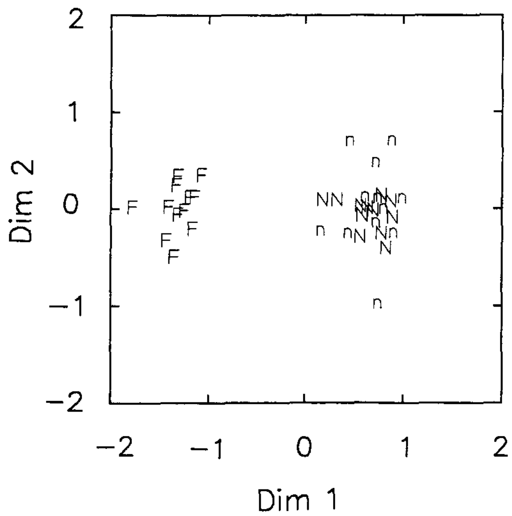

FIGURE 5. Spatial representation of multidimensional scaling results comparing flight song type B notes ("F"), trilled song type VI notes sampled from the trilled songs associated with these flight songs ("n"), and type VI notes sampled from trilled songs sung alone ("N"). Results are from bird #1. N = 12 notes/category.

This bird also stood out as having a disproportionately small flight song note type repertoire (compare, e.g., with bird #7, Table 1).

The three note types identified from bird #9's flight songs fit into types D, G, and K (Fig. 6). These notes could be matched to our classification, although they generally represented divergent examples (compare Figs. 6 and 2). Type D notes of bird #9 were the most similar to the wild birds' phonology, but there were insufficient examples to statistically assess this similarity.

DISCUSSION

The Swamp Sparrow flight song may be thought of as a complex preamble added onto the trill of the species' more familiar advertisement song (Fig. 1). Not enough is known of how these songs are used in the field to fully support the claim that they represent a unique song category in a functional sense (cf. Ficken and Ficken 1970; Kroodsma 1981; Nelson and Croner, in press). Nonetheless, flight songs are a distinctive vocal behavior. Both the aerial context in which they are most often sung, and the overall irregular syntax and spacing of their acoustic elements, unambiguously distinguish them from trilled song. The fact that flight songs are sung rarely and, as far as is known, under conditions of high motivation, further suggests that they provisionally can be considered a distinct category of vocal behavior.

The most distinctive feature of Swamp Sparrow flight songs is that their constituent notes form an independent phonological set, separate from the notes that comprise trilled songs. The distinctness of these two phonologies is immediately apparent from the visual dissimilarity between the two sets of notes (compare Figs. 2 and 5), and by the lack of a single example in our sample (or that of Marler and Pickert 1984) of a flight song note being found in a trilled song, or vice versa. The only possible case of overlap, between flight song note type B and trilled song type VI, was scrutinized using both multidimensional scaling of spectrogram cross-correlation scores (Clark et al. 1987) and multivariate analysis of acoustic measurements (Marler and Pickert 1984). The results of both techniques distinguish the two note types (e.g., Fig. 5), arguing that the phonological sets of the two song types are completely non-overlapping.

The complex acoustic structure of flight song notes makes it difficult to evaluate quantitatively the degree to which the types we defined represent discrete, as opposed to continuously varying, categories (Marler 1982; Nowicki and Nelson, in press). At the same time, the process of sorting notes into well-defined categories on the basis of sonagraphic structure was not difficult in this case. With the exception of one disagreement (whether or not to lump types D and G), two independent observers initially derived identical sets of categories. The final 96.5% agreement between observers demonstrates that very few notes could be considered intermediates between types.

Is the phonology we describe here complete? It is possible that an increased sample of individuals or more flight songs recorded per individual might reveal new phonological types. There is no correlation between the number of flight songs recorded from the wild birds and the size of their flight song note type repertoires (Table 1), suggesting that we obtained reasonably complete flight song note type repertoires, even for those individuals with few flight songs recorded. On the other hand, the fact that note types differ in the degree to which they are shared among birds suggests that adding new individuals to our sample could reveal new types. Re-

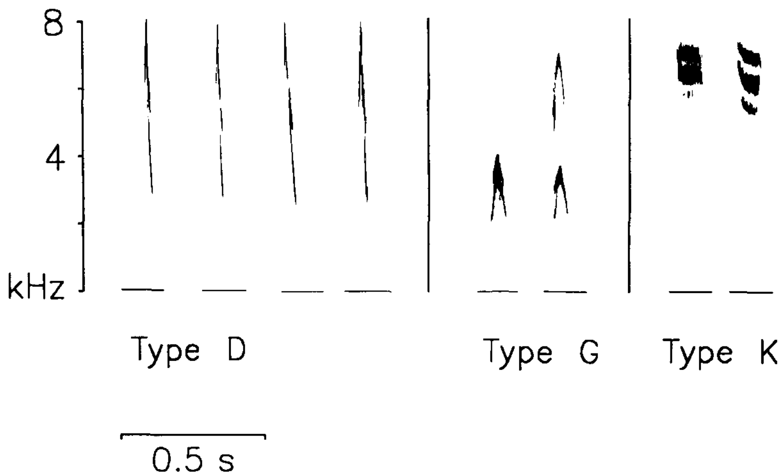

FIGURE 6. Eight exemplars of the three flight song note types produced by the hand-reared bird, #9. These exemplars and others were included, without reference to origin, in the initial sort of note exemplars and were classified as types D, G, and K of the wild flight song phonology. Sonagraphic analysis as in Fig. 1.

cordings of flight songs from different areas in the Swamp Sparrow's geographic range are needed to determine whether the phonology we outline here embodies species-typical "universals" in the same way as has been described for trilled song phonology. Our sample includes birds from two field sites separated by about 75 km. We see no evidence for differences between these groups in terms of the types or the proportions of note types used.

The discovery of two non-overlapping phonological sets, each occurring in a different vocal context and restricted to a small number of possible note types, raises interesting questions about mechanisms underlying the development and control of vocal behavior. First is whether the same learning processes involved in the acquisition of trilled song also account for the acquisition of flight songs. In the Hudson Valley of New York, flight songs are rarely if ever heard after the early spring, suggesting that they may not be acquired by young birds during the typical sensitive phase when trilled song is committed to memory (see, e.g., Marler and Peters 1988). Moreover, the hand-reared bird in our study (#9) was not trained with flight songs, but produced them as an adult anyway. These "isolate" flight songs were degenerate, in terms of length and the number of different notes employed, but their overall structure was relatively normal. Trilled songs of Swamp Sparrows who are deprived of appropriate models during their sensitive period also retain a relatively normal syntax (Marler and Sherman 1985).

Unlike isolate trilled song, however, in which typical note types rarely occur (Marler and Sherman 1985), all three note types in bird #9's flight songs could be placed easily into wild flight song note categories (Fig. 6). In an isolate bird's trilled song repertoire, note type VI is the only note type that can be fit into the wild song phonology (Marler and Sherman, unpubl. data). It may be that, like type VI of the trilled song, flight song note types D, K and G (at least) result from "active" features of the species' song template (sensu Marler 1984) that do not require exposure to external models to develop. Bird #9 did not produce note type B, the flight song note most similar to Type VI, but our sample is too small to attach significance to this fact.

Another question is whether flight song phonology appears in early stages of vocal ontogeny, especially during plastic song when Swamp Sparrows are known to "overproduce" many sounds that will later be dropped from the trilled song repertoire (Marler and Peters 1982). Some of these overproduced sounds are copies of trilled song models that do not appear in the final repertoire. It is possible that other, previously unidentified notes in plastic song are assignable to flight song note categories, and that one aspect of selective attrition during development involves the bird parsing phonological types into appropriate association with different song categories. Flight songs are unlikely simply to be remnants of plastic song in the early spring. The trilled songs with which they are associated are themselves completely crystallized, and the delivery of the flight song—trilled song pattern is unlike any observed in normal plastic song in Swamp Sparrows (S. Peters, pers. comm.).

A final question is why the underlying structure of a learned vocalization, such as birdsong, should be restricted to a limited set of species-universal phonological units. For Swamp Sparrow trilled song it is now well-demonstrated that this phonology includes a limited number of very simple note types. The existence of an independent phonology specific to the flight song rules out the suggestion that the vocal apparatus of Swamp Sparrows, either in the periphery or in the central nervous system, is simply incapable of producing a more varied set of sounds. It is thus even more striking that the normal vocal learning process displays such a high degree of selectivity and constraint.

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APPENDIX

Descriptions of Swamp Sparrow note types, corresponding to examples illustrated in Fig. 2: *Type A*—Complex, two-parted notes. Two tones, diverging in frequency, are followed by a sharp downsweep. This note almost always occurs as a rapidly repeated doublet, which we treat as a single note. *Type B*—Very short, tonal downsweep of narrow bandwidth and intermediate to wide frequency range. *Type C*—Like Type B, but followed by a short, mid-frequency buzz. The buzz can be constant frequency, or occasionally rising or falling. *Type D*—Hook-shaped note, usually comprising a short upsweep, from mid- to high frequency, followed by a longer downsweep. The lengths of these components can vary, and the upsweep is occasionally longer than the down. *Type E*—Short, high frequency, rising tone, merging into a buzz of medium duration. The buzz is usually constant in frequency. *Type E1*—Very similar to Type E, with a rising tonal portion consisting of 2–3 closely-spaced overtones. In contrast to Type E, the buzz is longer and falls sharply in frequency. This note type was observed only in one bird (seven occurrences in bird #7). The fact that bird #7 also sang an equal number of well-defined type E notes led to our decision to leave it as a separate category. *Type F*—Like a type D, but followed by a mid-frequency buzz of medium duration, usually without a measurable gap. The buzz is longer than that of type Cs, and may rise or fall in frequency. *Type G*—A low to mid-frequency upsweep followed by a downsweep of equal length, all of narrow bandwidth. This note tends to be very low amplitude, especially in the downsweep, and sometimes does not appear complete in spectrographic analysis (see Type H). Harmonics are often present as well. *Type H*—A low to mid-frequency, narrow-band upsweep, identical to the upsweep portion of Type G. Given that Type G tends to be low amplitude, and that the downsweeps of Gs appeared to be the portion of the note most susceptible to poor recording, it is possible that type H is a subset of, or even the same note, as type G. In the sequential analysis, above, we found that type G and type H often occur in the same relative positions. *Type I*—High frequency buzz of medium duration, leading to falling simultaneous elements (usually 2, but varies from 1–4) with fairly wide bandwidths. The buzz is sometimes reduced or absent. *Type J*—Tonal downsweeps of medium duration and wide bandwidth. The number of tonal elements varies from 2–5, although 2–3 are the most common. These downsweeps are similar to the downsweep portions of Type I, but are shorter and begin at a lower frequency. *Type K*—High frequency buzz, medium to long in duration. There are some cases of rising or falling buzzes, but for the most part, this type is quite homogeneous. *Type L*—A low frequency, narrow-band buzz, frequently double, rising and expanding to a mid-frequency buzz of short to medium duration, with a wider frequency range than type K. Sometimes the rizing buzz is not continuous. The final buzz may be reduced or absent.