

SONGS OF THE FOX SPARROW. III. ORDERING OF SONG

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ABSTRACT.—I studied organization of singing in Fox Sparrows (*Passerella iliaca*) breeding in northern Utah and southern Idaho during 1973 and 1974. Fox Sparrows possessed a variety of songs that, due to their uniformity in structure within and among individuals, could be categorized into five major types. Each song of an individual tended to be presented with equal frequency. Fox Sparrows presented their songs in particular sequences, singing each song once, until the entire repertoire was exhausted. The sequences in which individuals presented the songs in their repertoire did not change between successive utterances of a particular song, whether separated by singing sessions, days, or years. Markov chain analyses of the sequences of the songs accounted for the behavior of 53 of 56 birds by a first-order model, while the organization of singing of the remaining three birds was accounted for by a higher-order model. Neighboring territorial Fox Sparrows that shared similar song repertoires showed no preference for singing the same sequence of songs. Neighboring males which shared similar song-type repertoires showed no preference for sequencing their songs similarly. Matching of song-types among counter-singing neighbors did not occur and basically was precluded by each individual's rigid organization of singing. Functional and causal explanations for the style of singing in Fox Sparrows are discussed. The manner in which Fox Sparrows organize their singing suggests that the pattern of song presentation may simply crystallize at random during the first spring. *Received 21 Nov. 1989, accepted 10 Feb. 1990.*

There is great variation in the structure of primary song, size of the song repertoire and manner of sequencing songs in male passerines (Hartshorne 1973, Kroodsma 1982). Individuals of species characterized by one song-type generally do not vary the structure of song or, of course, the order of song presentation during singing. Individuals of species that tend toward large song-type repertoires are generally more variable. Some have songs that are structured similarly between individuals and the order of presentation is somewhat variable (e.g., Northern Cardinal [*Cardinalis cardinalis*] Lemon 1965, Lemon and Chatfield 1971), while others possess more individualistic song-types in which the structure of a major song-type may be considerably altered between successive utterances (e.g., Song Sparrow [*Melospiza melodia*] Mulligan 1966). In some species both styles may be used in different populations and the ordering of songs may be varied both within and among singing sessions. For a general review of the definition and use of song repertoires see Kroodsma (1982).

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Often as not, species with moderate-sized repertoires sing in bouts, wherein a single song-type is repeated a number of times prior to switching to a different type (eventual variety e.g., CCCCBBB . . .). Those species with large repertoires often sequence their songs in a more random manner, using "favorite" songs more frequently than others (more immediate variety e.g., LMQLLAMLZ . . .). There has been a concerted effort by researchers to fathom the significance of variation in repertoire size and the permutations of song ordering resulting in numerous functional (Whitney 1981, 1985; Catchpole 1982, 1989; Kroodsmma 1982; Shy and Morton 1986; Stoddard et al. 1988) and causal (Hartshorne 1973, Lambrechts and Dhondt 1988) explanations. These studies have considered only those species which sing a single song repertoire or multi-song repertoire as described above.

Herein I describe the ordering of song-types during singing sessions in Fox Sparrows (*Passerella iliaca*). Fox Sparrows of North America are of interest because the structure and complexity of their song and the size of individual song repertoires in western races are intermediate in comparison with most other species and, in particular, with their close relatives in *Melospiza* and *Zonotrichia* (Martin 1977, 1979). It will be shown that the ordering of song presentation by Fox Sparrows is quite unlike that of their closest relatives and of emberizids in general. Particular attention will be paid to hypotheses that may explain the observed form of singing organization.

METHODS

Fox Sparrows in northern Utah and southern Idaho were recorded during the breeding seasons of 1973 and 1974 at 19 cm/sec on a Uher 4000 IC tape recorder equipped with a Uher 516 microphone mounted in a 60 cm parabolic reflector. Songs of all individuals were identified after their visual display on a Kay Electric Company Sona-graph (6061-B) at a wide band-pass setting. Although 153 males were recorded, only the 56 for which I had extensive data were analyzed in detail. Totals of 8, 15, and 7 males in 1973 and 9, 12, and 5 from 1974, with repertoires of two, three and four songs, respectively, were analyzed. Numerous recordings from more than 50% of the birds were gathered during singing sessions which occurred at various times of the day and various stages of the breeding season. Six individuals color marked in 1973 were also recorded in 1974. Because results indicated that individuals did not vary the frequency of occurrence of song-types sung between bouts, all recordings of an individual were pooled.

For all Markov chain analyses, the behavior of song presentation was considered to be stationary. This was assumed because the probabilities of events (song-types) at the beginning and at the end of behavioral sequences (singing bouts) were not significantly different at the $P > 0.05$ level in those sequences for which the entire bout was recorded. That is, no individual appeared to have a preferred song-type with which it began or terminated a bout of singing. Analysis of variance tests (Sokal and Rohlf 1969), with α at 0.05, were used to determine if the differences in the various parameters of song and singing were statistically significant.

Normal singing.—All analyses of the organization of singing in Fox Sparrows used recordings collected from territorial birds singing normally. The term “normal singing” (Hinde 1958:212) “signified singing when no recorded . . . conspecific . . . songs were played back . . .” However, playback of conspecific songs may have been used prior to the recording session to elicit an individual’s singing, or other conspecifics may have been singing within hearing range. Recordings were also used from singing sessions that were already in progress before I arrived and began recording.

The term “bouts” and “singing sessions” will be used interchangeably: both refer to the behavioral unit from the onset of singing until its termination, denoted by an interval of silence considerably longer than the mean interval between songs, which averaged 7.1 ± 2.9 [SD] ($N = 29$ birds and 725 inter-song intervals, at least 20 songs/bird).

Structure of song.—Fox Sparrow songs are composed of sequences of temporally discrete sounds, termed syllable-types, which may or may not be repeated within a song but by definition never occur in an abbreviated form. In all, I recognized 49 syllable-types (Martin 1977). Although the syllable-types and their sequences, which compose the introductory portions of songs, vary considerably among individuals, the terminal sequence of syllables of songs of many individuals tends to be similar. This structural similarity among renditions of song permits them to be categorized into one of five major song-types: A, B, C, D, and E (Table 1). Thus the main feature used to categorize songs as to their type, except song-type D, is the terminal flourish of syllable-types. Song-type D may be most easily characterized by syllable-types nearer the middle of the song (Martin 1977).

Because of the considerable variation in the syllable-type structure of the initial portion of individuals’ particular song-types, those songs of individuals that are designated as being of the same major song-type are not generally identical in overall structure (Table 1). All five major song-types were represented by a large number of versions in which the introductory syllable-types and/or sequence varied among birds but the syllable-types and sequence of the ending among birds were nearly identical (Table 1). During 1973 and 1974, 13 versions were recorded for song-type A, 67 for B, 31 for C, 22 for D, and 13 for E. Distinguishing among song-types and song-versions is important in that many individuals (48 of 133) possessed more than one version of some major song-type, usually B or C. However, the overriding emphases should be on the fact that songs are easily classified to type and that a great percentage of birds have songs that are structurally very similar to each other (Table 1). Even birds with multiple versions of one particular song-type used their versions as functionally independent units during singing bouts. This emphasizes that the birds, as well as I, recognize and treat each of their renditions as discrete entities.

Units of analysis.—Fentress (1973:163) noted that “. . . the investigator of behavior is faced with a potential paradox in that categories of behavior must be formed . . .,” even though the categories may not be divisible or functionally independent, and that “. . . categories are necessary abstractions convenient for summarizing data and suggesting subsequent analysis.” The syllable-types and sequences of syllable-types in particular song-types of individual Fox Sparrows were consistent between successive utterances, both seasonally and yearly (Martin 1977). The structure of each of the several songs of an individual, then, was rigidly deterministic. Each song-type uttered by an individual, however, is likely to be followed by a different song-type and the ordering of different songs within bouts is non-random (Table 2). This latter phenomenon is easily visualized by observing portions of the raw field data of singing sessions, upon which some of these analyses are based, as shown in Table 3. Therefore, the units of behavior that were chosen for analysis of repertoire organization were the song-types presented by individuals during singing sessions. Recent work by Falls et al. (1988) presents data that support such an approach and categorization of vocal behavior. Their data indicate that in Western Meadowlarks (*Sturnella neglecta*)

TABLE 1
 MOST COMMONLY SUNG SYLLABLE-TYPE SEQUENCES OF THOSE BIRDS WHICH POSSESSED A PARTICULAR SONG-TYPE IN 1973 AND 1974

Percent of birds possessing pattern				Syllable-type sequence
1973	N	1974	N	
Song-type A				
38	17	48	16	1, 2 or 3, 4, 5, 6, 7, 8, 9 ^a
49	22	33	11	1, 2 or 3, 5, 6, 7, 8, 9
Song-type B				
38	24	28	15	1, 10, 17, 12, 22, 49, 25, 26, 27
25	16	16.6	9	1, 4, 14, 5 or 16, 20, 22, 49, 25, 26, 27
Song-type C				
39	27	31	20	1, 11, 34, 35, 29, 37, 38, (39) ^b
20	14	20	13	1, 36, 11, 28, 29, 37, 38, (39)
34	24	8	5	1, 3, 36, 11, 28, 29, 37, 38, (39)
Song-type D				
17	3	5	1	1, 10, 41, 42, 28, 24, 25, 49, 43
22	4	28	5	1, 10, 40, 41, 27, 28, 24, 25, 49, 43
Song-type E				
71	5	0		1, 3, 44, 31, 30, 45, 32, 25, 46
0		42	5	1, 2, 44, 17, 45, 32, 25, 26

^a Syllable-types are designated numerically 1-49.

^b Parentheses indicate syllable-types an individual may add or delete from its song between successive utterances. A complete list of the syllable-type sequences used may be found in Martin (1977).

those song-types long recognized by human observers are also the units recognized by the birds.

RESULTS

Frequencies of song-types within singing bouts.—Birds with repertoires containing two, three, and four songs tended to present each song with equal frequency (see Table 2). Aberrations (i.e., unequal frequencies of song presentation), however, were observed (e.g., see B32-73 and B62-74 in Table 3). Although there was no significant difference ($F = 2.16$, $df = 2, 27$, $P = 0.135$) in the percent of aberrations committed among birds with repertoires of two ($\bar{x} = 7.1 \pm 6.2$ [SD], $N = 10$), three ($\bar{x} = 12.6 \pm 13.7$, $N = 10$) and four ($\bar{x} = 17.4 \pm 12.0$, $N = 10$) songs; the trend was for those birds with larger repertoires to have a higher percentage of deviations in song ordering.

Ordering of song-types within singing bouts.—The sequences of song presentation of individual Fox Sparrows were analyzed to determine the

TABLE 2
 REPRESENTATIVE FIRST- AND SECOND-ORDER MATRICES OF THE FREQUENCIES OF TRANSITIONS BETWEEN SONGS IN FOX SPARROWS WITH
 REPERTOIRES OF TWO, THREE AND FOUR SONGS

From song	To song																
	B28-74-BC			B29-73-BC			B21-74-BCC*			B4-73							
	A	B	C	A	B	C	A	B	C	A	B	C					
A	0	11	B	6	32	B	0	66	BB	0	0	0	B'B'	0	0	0	0
B	10	0	C	41	0	C	66	0	BC	0	0	65	B'A	0	0	31	0
									BC'	2	0	0	B'C	0	4	0	0
									CB	0	0	0	B'B	1	0	0	0
									CC	0	0	0	AB'	0	0	0	0
									CC'	66	0	1	AA	0	0	0	0
									C'B	0	67	2	AC	0	0	0	0
									C'C	0	0	0	AB	3	0	0	0
									C'C'	1	0	0	CB'	0	0	0	0
													CA	0	0	1	3
													CC	0	0	0	0
													CB	32	0	0	0
													BB'	0	32	4	0
													BA	0	0	0	0
													BC	0	0	0	0
													BB	0	0	0	0

From song	B62-74-BCB' or A						B21-75-BCC'						B4-73-B'ACB											
	A			B			C			A			B			C			A			B		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C			
A	12	2	12	B	0	69	2	B'	0	34	4	1												
B	10	0	16	C	0	0	68	A	0	0	33	3												
C	6	24	3	C'	69	0	1	C	0	4	0	34												
													B	38	0	0	0							

* An apostrophe indicates a multiple version of song-type.

TABLE 3
SEQUENCES OF SONGS SUNG BY INDIVIDUAL FOX SPARROWS

Bird	Sequence of songs
B4-73-ACBB' ^a	ACBB'ACBB'ACBB'ACBB'AC//= ^b BB'ACBB'ACBB'A//CBB'ACB// B'BB'AC'BB'ACBB'ACB'B'ACBB'AC//BB'ACBB'ACBB'ACBB'A
B15-74-ACB	BACBACBACBACBACBACBACBACBAA// ACBACBACBACBACB//CB//CBAACBA//ACBACBACB// CBACBACBACBACCA//CBACBA//AACBACB
B32-73-BDC	<u>CDBDCBDCBDCBDCBDCBDCBDCBDCBDCBDCBDCBDCBDCBDCB-</u> DCBDCBDCBDCBDCBDCBDCBDCB//CB// BDCBDCBDCBDCBDCBDCBDCBDCBDC//CBDCBCC// BBDCBDCBDCB//DCBDCB
B62-74-BCB' or A	BCB'ACCACB'ACAACBAAA// CBCB'CBCB'ACBCABAACB'CBACABACB'CB// CBCB'CCB'CB'ACAAACBACBCCB'CB'C
B9-73-BC	BCB//CBCB'CBCB'CBCB'CBCB'CBCB'CBCB'CBCB'CBCB'CBCB- CBCB'CBC
B26-74-ABC	ABCBC//CABCABCABCABCABCABCAB- CABCBCABCBCABCBCABCBC// CABCABCABCABCABCBC// BCABCBCABCBCABCABCABCABCBC

^a An apostrophe indicates a multiple version of a song-type within a repertoire.

^b // Denotes end of one singing bout and the start of another; this separation may span minutes, days, or, as in B4-73, B15-74 and B9-73, years.

^c Underlined passages indicate areas where preferred order was lost and quickly regained.

appropriate order of Markov chain model (if there was one) that could predict the observed data using the sequential test of Anderson and Goodman (1957). These analyses are comparable to those used by Lemon and Chatfield (1971, 1973) to investigate the organization of singing in birds.

Markov chain models are distinguished by the concept of order. If the order is zero, knowledge of past events (song-types) provides no information in predicting the current event. If the order of the Markov chain is one, knowledge of the immediately preceding event provides the information for predicting the current event, but information prior to the preceding event does not provide information for a statistically better prediction.

The procedure to find a Markov chain (of some order) that best describes the observed sequences of events (according to Anderson and Goodman 1957), is test $H: u = r$ versus $H_A: u = r + 1$, where r is the order of the Markov chain. The test procedure is sequential in nature. Testing begins with the comparison of $H: u = 0$ with $H_A: u = 1$ by using the data of

events to compute a test statistic T . If T is less than the specified critical value, t^* ($* = P = 0.05$), then H is accepted; otherwise, H_A is accepted. As long as H_A continues to be accepted, further tests of higher orders are continued by increasing the order of r by one and performing the subsequent comparisons. The sequence of tests is concluded when at some point H is accepted. The level at which H (r of H) is accepted defines that level (order) which is appropriate for accounting for the ordering of the data (i.e., knowledge of the r order preceding event provides a better statistical basis for predicting the current event than a model that denies knowledge of the r order preceding event). Thus, the H that is finally accepted indicates the order of Markov chain model which best accounts for the ordering of the observed data. More detailed examples are presented by Anderson and Goodman (1957), Lemon and Chatfield (1971, 1973) and Cane (1978).

My analyses demonstrated that the sequencing of presentation in 17 birds with two song repertoires followed a first-order Markovian model (Table 4). A first-order Markov chain model was also accepted as predicting the sequencing of songs in 36 of 39 birds with repertoires of three or more songs (Table 4).

On the basis of these analyses both zero- and first-order hypotheses were rejected for three birds that possessed repertoires of three or more songs. Insufficient length of song sequences for these three individuals prohibited testing between second- and third-order models of the birds' sequences of songs which could be better accounted for by a higher-order model. Table 4 lists the T values for all tests performed.

Preference for particular song orders.—Birds banded in 1973 that returned to breed in 1974 ordered their songs in the same sequences (B4-73, B15-74, and B9-73 in Table 3), or when they initially deviated from their preferred song order they rapidly regained their preferred sequence (see B4-73 and B15-74 in Table 3). A few individuals with repertoires of three songs alternated between singing a three song sequence and a five song sequence (see B26-74 and B62-74 in Table 3). There was little correlation between the song-type repertoires of neighboring Fox Sparrows (Martin 1976, 1977).

Twelve of the 30 birds in 1973 and four of the 26 birds in 1974 possessed two versions of a single song-type. Nine birds sang multiple versions of song-type C and seven sang multiple versions of B. Of these 16 birds, seven had repertoires of only three songs. Thus, their multiple versions of either B or C were presented sequentially (see B21-74, Table 2). In those remaining nine birds possessing a repertoire of more than three song-types, the preferred sequence of song presentation of five individuals coupled versions of a song-type together (e.g., B4-73-BACB, Table 2).

TABLE 4
VALUES OF *T*-STATISTIC FOR FIRST- AND SECOND-ORDER MARKOV CHAIN ANALYSES

Bird	<i>T</i> value for		df for	
	1st order	2nd order	1st order	2nd order
B5-74	240.32	12.03	4	12
B6-74	132.00	8.5	9	36
B7-74*	162.46	40.6*	9	36
B9-74	616.24	10.67	9	36
B13-74	17.67	1.14	1	2
B14-74	39.09	1.00	1	2
B15-74	26.87	2.00	1	2
B16-74	18.33	3.81	4	12
B19-74	164.55	4.10	4	12
B21-74	430.48	0.08	4	12
B22-74	571.08	15.87	4	12
B26-74	182.16	0.85	4	12
B28-74	86.92	1.52	1	2
B29-74	281.33	0.0	4	12
B30-74	66.83	0.18	4	12
B31-74	226.02	15.98	4	12
B35-74*	32.89	30.66*	4	12
B36-74	28.80	0.18	1	2
B39-74	94.80	13.31	9	36
B47-74	23.23	1.65	1	2
B51-74	263.36	0.0	9	36
B55-74	17.09	0.20	1	2
B58-74	13.40	0.617	1	2
B59-74	364.46	3.50	4	12
B60-74	54.0	0.0	9	2
B62-74	54.17	13.86	4	12
B1-73	166.42	6.6	4	12
B3-73	32.28	0.98	1	2
B4-73	337.54	40.85	9	36
B5-73	97.85	65.70*	9	36
B6-73	137.39	2.57	4	12
B8-73	83.20	3.82	4	12
B9-73	74.86	0.0	1	2
B14-73	188.45	1.47	9	36
B15-73	264.16	19.80	4	12
B18-73	59.66	0.27	1	2
B21-73	138.76	20.04	4	12
B24-73	40.98	16.5	4	12
B25-73	45.52	20.18	4	12
B29-73	182.99	0.0	1	2
B30-73	116.96	2.1	4	12
B32-73	124.77	0.0	1	2
B34-73	188.45	17.69	9	36

TABLE 4
CONTINUED

Bird	T value for		df for	
	1st order	2nd order	1st order	2nd order
B35-73	114.22	25.36	9	36
B37-73	195.10	13.32	9	36
B38-73	254.66	0.0	4	12
B41-73	76.83	0.0	4	12
B44-73	68.93	0.07	4	12
B53-73	58.54	1.63	1	2
B54-73	68.91	0.62	1	2
B55-73	129.80	14.27	4	12
B57-73	122.67	16.77	4	12
B63-73	227.22	14.24	4	12
B65-73	108.03	23.95	9	36
B66-73	98.02	4.95	4	12

First-order $df = (m - 1)^2$ and second-order $df = (m)(m - 1)^2$. An asterisk indicates those second-order values which are significant at $\alpha = 0.05$.

Cadence of song presentation during singing bouts. — Cadence of singing (length of intersong intervals) in those birds that had repertoires of two ($\bar{x} = 6.3 \pm 2.3$, $N = 9$), three ($\bar{x} = 7.3 \pm 3.1$, $N = 10$) and four ($\bar{x} = 7.5 \pm 3.2$, $N = 10$) songs was not significantly different ($F = 0.412$, $df = 2, 27$, $N = 29$). Most singing bouts ended abruptly and there was little consistent variation in the cadence of song presentation between the first and last halves of singing sessions. At times the silent interval between the terminal two or three songs of a singing session was noticeably longer than normal but this phenomenon was rare and did not occur consistently in any particular individual. Two conditions with which aberrant timing did appear to be associated, however, were: (1) long singing sessions, provoked by repetitive playback, and (2) the termination of breeding activities in mid-July. Either of these conditions could have resulted from frustration or decreased motivation to sing arising from the performer's failure to locate the intruding conspecific (simulated by playback) or from decreased hormonally induced impetus to sing, respectively.

DISCUSSION

These data clearly show Fox Sparrows rigidly order the sequence of their songs during bouts of singing and they sing with immediate variety (Hartshorne 1973), singing each of their songs once until all songs in their repertoire have been presented (Tables 2 and 3). Such a system of ordering

is best described by a first-order Markov model (Table 4). Further, the order of song sequencing of an individual does not appear to change through time (Table 3). This method of ordering song is atypical of virtually all passerines (Hartshorne 1973, Kroodsma 1982), except possibly for the Large-footed Finch (*Pezopetes capitalis*) of Costa Rica (D. E. Kroodsma pers. comm.).

Fox Sparrows with multiple versions of a song-type do not appear predisposed to order their songs so that versions are separated by one or more songs of a different type (Tables 2 and 3). Such ordering of song is also quite unlike that observed in other passerines. In species that possess multi-song repertoires, songs that are more similar in structure tend to be grouped into long bouts of near identical songs or ordered in a fairly random manner whereby similar songs are interspersed among dissimilar types (Verner 1975, Kroodsma and Verner 1987, Kroodsma 1982, Lambrechts and Dhondt 1988). Comparison of syllable-type sequences of songs listed in Martin (1977 and unpubl.) indicate that, based upon shared syllables, song versions of a particular song-type are indeed more similar to each other than they are to songs of a different type. Further, playback experiments by Martin (1980) indicate that male Fox Sparrows treat different songs as equivalents.

The style of singing of Fox Sparrows immediately raises two questions: (1) Why do Fox Sparrows possess a repertoire of songs which appear to be identical in function and, therefore, why are they redundant in their singing? and (2) Why do Fox Sparrows order their song-types so precisely during singing bouts?

Redundancy in singing.—Investigators seeking a functional explanation for the existence of repertoires and redundancy in singing have proposed that such behavior may be selected for by pressures of intersexual and/or intrasexual selection and/or individual recognition (see Dawson 1982, Kroodsma 1982). Studies seeking a causal explanation for redundancy in repertoires have proposed hypotheses focusing on physiological exhaustion of the song-producing mechanism (Lambrechts and Dhondt 1988) or habituation processes affecting (either or both) the singer or listener (see Kroodsma 1982) promoted by non-versatility in singing (Hartshorne 1956, 1973) or some form of neurological facilitatory/inhibitory feedback mechanism (Todt 1975, Whitney 1985).

Redundancy is important functionally for decreasing the probability that receivers will miss or “misinterpret” the signals broadcast (Peek 1972a, b) and when there are relationships among individuals which may vary through time (Wilson 1975:200). Frequently repeated signals allow individuals to reassess their relationships, such as fluctuating territory

boundaries (Stenger and Falls 1959). Presumably, redundancy in Fox Sparrow singing has the same functions.

Redundancy, as measured by the total number of songs sung per unit time, also appears important in mate attraction. Regardless of repertoire size, the number of songs sung per unit time is much greater while a male is actively attempting to attract a mate (e.g., Catchpole 1973, Nolan 1978). Male and/or territory quality appears to be positively correlated with the total amount of time spent in song (Møller 1983) or the length of song (Lambrechts and Dhondt 1986). Pied-flycatcher (*Ficedula hypoleuca*, Gottlander 1987) and Willow Warbler (*Phylloscopus trochilus*, Radesater et al. 1987) females select first (prefer?) males singing with the most rapid song rate. The manner in which Fox Sparrows apportion time singing throughout the breeding season (Martin 1979) matches these intra- and intersexual functional explanations for redundancy in song.

Why individual Fox Sparrows sing more than one major song-type and order these so rigidly within singing sessions cannot be answered as easily. In some species with numerous song-types, counter-singing rivals tend to match each other's songs with similar song themes. Such counter-singing may allow for numerous responses (thus, stronger defense) between territorial males (Krebs et al. 1981). Matching of song themes by neighbors may also facilitate neighbor-neighbor recognition (Kroodsma 1976), whereas switching from one song-type to another during counter-singing may enable rivals to retaliate with more forceful threats (Dixon 1969). Thus, matching serves as a graded signal indicating level of aggressive intent (Krebs et al. 1981, Todt 1981, Shy and Morton 1986). Possession of multiple song-types and matched counter-singing have the potential also to convey information about local population density (Krebs 1977, Yasukawa 1981) and the distance between songsters (Morton 1982). McGregor and Krebs (1984) have indicated that birds may range a particular song-type even if they do not possess such a theme in their repertoire, but are familiar with the song-type from the singing of their neighbor. The structure of Fox Sparrow song appears well-designed for encoding individual and population identity (Martin 1977, 1979) and ranging is conceivable based upon shared song units. In 1973 and 1974, 99% and 92%, respectively, of all birds possessed one version of song-type C and there was great sharing of syllable-types and notes among birds (Martin 1977, 1979). Thus, as birds rapidly cycle through their repertoire during counter-singing, the probability is great that they hear both familiar and shared song units.

Such functions, however, do not appear to be the primary objectives of the organization of singing in Fox Sparrows. Matched counter-singing

among rivals is essentially precluded by the rigid ordering of each individual's songs and non-sharing of similar major song-types or size of song repertoire. Interestingly, recent playback experiments have shown that matched counter-singing and increased aggressive intent is not common to all species in which individuals have repertoires of shared song-types. The Wood Thrush *Hylocichla mustelina* (Whitney and Miller 1983) and, most interestingly, the close relative of the Fox Sparrow, the Song Sparrow (McArthur 1986), appear to demonstrate aggressive responses that are inversely related to the closeness of the match between a playback song and one in the test bird's repertoire.

Preliminary playback experiments broadcasting different size song repertoires to male Fox Sparrows indicate that they probably do not habituate less rapidly to larger repertoires (Martin, unpubl. data). In this respect, Fox Sparrows behave similarly to Sedge Warblers (*Acrocephalus schoenobaenus*) (Catchpole 1989) and Song Sparrows (Lemon et al. 1981). In Song Sparrows, the rate of switching between song-types is positively correlated with the intensity of agonistic stimulation and versatility functions both as a stimulus and a response (Kramer et al. 1985). The individual performing the behavior along with its listeners is thus central to any consideration of habituation or potential for what Kramer and Lemon (1983) hypothesize as motivational communication.

The most parsimonious functional explanation for the ordering of songs in Fox Sparrows, therefore, may well be that the increased variety it produces decreases habituation in the singer, allowing for increased song production, which is more stimulatory to the female (Kroodsma 1976) and is also a most effective agonistic signal to males (Kramer et al. 1985). Male Western Meadowlarks (*Sturnella neglecta*) switch song-types at a greater rate during mate attraction (Horn 1987). Recent comparative review by Catchpole and McGregor (1985) of sexual selection pressures and song complexity in birds in the genus *Emberiza*, in the same subfamily as Fox Sparrows, supports the contention that song versatility in monogamous buntings is strongly positively correlated with intersexual selection for male quality (Catchpole and McGregor 1985). Further, high rates of song-types switching in Song Sparrows appears indicative of greater annual and lifetime reproductive success. Males with larger repertoires and, most importantly, larger half-hour repertoires, had higher fitness values and longer territory tenure (Hiebert et al. 1989). Larger half-hour repertoires are the product of rapid song-type switching, a phenomenon that within the complex of *Zonotrichia-Melospiza-Passerella* is taken to its extreme by Fox Sparrows. Taken together, the correlations between Fox Sparrow singing behavior and that of other species indicates it may

have been influenced more by intersexual selection pressures rather than intrasexual pressures.

Ontogeny of song ordering.—The view that versatility in performance decreases either neurological and/or physiological habituation and/or exhaustion has met with agreement in the writings of Hinde (1958), Kroodsma (1982), Whitney (1981, 1985), and Lambrechts and Dhondt (1988). The question remains, however, as to how Fox Sparrows come to sing the order of songs that they do. If the bird has learned three song-types (e.g., A, B, and C), then two possible methods of singing to avoid habituation/exhaustion would be to alternate perfectly among song-types or alternate randomly between song-types. Depending upon the decay value of the song and/or the time-scale of the perception of the bird, either one of these two methods may be selected. Such behavior, however, would not negate an individual's changing the order of song-types between singing bouts, or even within bouts, once an aberration in ordering had been made (see Falls and Krebs 1975). In Fox Sparrows, the retention of particular sequences of song-types between singing bouts, even those separated by days or years, and the rapid compensation of their deviations in ordering during singing sessions (Table 3), suggests that antihabituation/exhaustion pressures, if present, are not the only factors contributing to the unique organization of their singing.

The fact that the sequencing of songs by Fox Sparrows is constant through time requires that one or more additional factors, coupled with habituation/exhaustion avoidance, must be affecting the behavior. Choices for additional effectors appear to be only three. First, rigid ordering could be achieved by the probability that the effects of the several song-types are graded, such that A is always highest and C least. Such gradation should lead to the phenomenon of many singing bouts of an individual beginning and possibly ending with particular song-types. However, as already discussed, this is not the case (Table 3). Those birds with multiple versions of a song-type did not appear to space the occurrence of song-type versions in any specific manner. Two versions of a song-type were as likely to be presented sequentially as not.

Second, rigid ordering could be attained through a system in which all song-types are of equal valence, and an individual learns a particular sequence of song presentation from conspecifics early in life or from neighbors while settling on territory. Acquisition of specific song structure occurs within the first 90 days of life in laboratory-reared White-crowned Sparrows (*Zonotrichia leucophrys*) (Marler and Tamura 1964) and a sensitive period of song learning is most pronounced between three and 10 weeks of age in Song Sparrows (Mulligan 1966, Marler and Peters 1987)

and Swamp Sparrows (*Melospiza georgiana*) (Kroodsma pers. comm., Marler and Peters 1982). Further sequence of song presentation is learned in at least one passerine, the Long-billed Marsh Wren (*Telmatodytes palustris*) (D. E. Kroodsma pers. comm.). Payne (1981, Payne et al. 1981) has shown learning of song during the first spring occurs in Indigo Buntings. Young Fox Sparrows fledge by early June but remain associated with their parents upon the breeding territory until the fall migration; adult males continue to sing until mid-July. Immature Fox Sparrows, thus, have an extended period in which they may learn syllable-types, song-types, and a sequence of song ordering.

Third, a pattern of song ordering may simply crystallize during subsong in a manner similar to song crystallization from subsong during the first spring. Individuals then would follow a prescribed order, regardless of where within the sequence of songs singing began. If either the second or third hypothesis is functioning then the initial song of a sequence could be randomly determined, as observed in the organization of singing by Fox Sparrows. Although the last two hypotheses are both plausible, the culturally transmitted song-sequence model seems unlikely. Such a model would probably result in neighborhood or populational "song-sequence dialects" similar to the song-structure dialects found in many *Zonotrichia* and *Melospiza* sparrows. Dialects consisting of one or a few preferred song-sequences clearly do not occur in Fox Sparrows. Thus, a model of random song-sequence crystallization seems most applicable.

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