

SONGS OF THE FOX SPARROW. II. INTRA- AND INTERPOPULATION VARIATION

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Melospiza and *Passerella* have been considered congeneric by taxonomists under the name *Passerella* (Linsdale 1928a, b, Grinnell and Miller 1944, Paynter 1964, Mayr and Short 1970). Paynter (1964) and Mayr and Short (1970) suggested further that this enlarged genus may be most appropriately considered congeneric with *Zonotrichia*. Many aspects of the vocal behavior of species presently assigned to *Melospiza* and *Zonotrichia* (A.O.U. 1957) have been thoroughly studied (for a literature review see Baptista 1975, Martin 1976, 1977). Knowledge gained from studies of species in these genera has been important to our understanding of concepts dealing with geographic variation in behavior, dialects, local gene pool adaptation, and function of avian song (e.g., Mulligan 1966, Harris and Lemon 1974; Handford and Nottebohm 1976; Marler and Tamura 1964, Nottebohm 1969, 1972, 1975; Baker 1975; Hinde 1969, respectively). Given the close phylogenetic relationship of *Zonotrichia* and *Melospiza* to the monotypic *Passerella*, study of Fox Sparrow (*Passerella iliaca*) vocal behavior should yield valuable insights into our understanding of bird song and this taxonomic group.

With such interrelationships and Linsdale's (1928a) suggestion that there might be a correlation between the geographic morphological variation in Fox Sparrows and variation in their vocal behavior, I have studied: (1) how songs of individual Fox Sparrows are structured; (2) how the structure of song compares with that of species in *Melospiza* and *Zonotrichia*; (3) how singing behavior is organized; (4) the significance of song in Fox Sparrows; and (5) the extent, if any, of variation in song structure within and among populations.

Earlier, I (1976, 1977) demonstrated that the structure of the syllable-types which compose songs of individual Fox Sparrows in Utah and Idaho is most similar to the components found in song in the Song Sparrow (*Melospiza melodia*). Sequencing of syllable-types within song-types and the uniformity of these song patterns among individuals, however, is most like that in *Zonotrichia* sparrows. But, the ordering of songs within singing bouts is unlike that in either *Melospiza* or *Zono-*

trichia. During singing, each song of a Fox Sparrow is presented once until the entire repertoire is exhausted and then the sequence begins anew. The order in which an individual presents its repertoire and the syllable-type structure of its songs does not change through time (Martin 1976). This report will concentrate on variation in song structure within and among geographically isolated, yet near, populations of Fox Sparrows in Utah and Idaho; although the song structuring and organization of singing in the eastern race (*P. i. iliaca*) is apparently unlike that of the western races, I will proceed with a comparison of the structure and apparent function of song among the *Melospiza-Passerella-Zonotrichia* complex.

METHODS

Fox Sparrows were studied on their breeding grounds in the Blacksmith Fork, Logan, and Cub River canyons of the Bear River Mountains which border Cache Valley of northern Utah and southern Idaho (Fig. 1). Only these three canyons emptying into Cache Valley support rivers large enough to provide the extensive habitat needed for Fox Sparrow populations. The entrance of Blacksmith Fork Canyon is 13.6 km south of Logan Canyon and 56.8 km south of Cub River Canyon. Although a few pairs of Fox Sparrows may breed along the floor of the Cache Valley proper, no continuous band of breeding birds connects the three populations. Thus, the canyon populations are distinct geographically. I recorded 71 male Fox Sparrows in 1973 and 62 in 1974. Of these birds recorded in 1973, 22 resided in Blacksmith Fork Canyon, 39 in Logan Canyon, and 10 in Cub River Canyon. During 1974, 25 birds were recorded in Blacksmith Fork Canyon, 28 in Logan Canyon, and 9 in Cub River Canyon. Twelve birds in Logan Canyon were color-banded in 1973, permitting confirmation of the stability of an individual's songs through time.

Tape recording methodology, observations, and production of sonagrams were similar to those described in Martin (1977). Analysis of variance tests (Sokal and Rohlf 1969) were used to evaluate statistical significance ($P < 0.05$). Mathematical derivations and computer programs for cluster analysis followed Sneath and Sokal (1973). For these analyses, each of the 71 individual Fox Sparrows recorded in 1973 was considered an operational taxonomic unit (OTU). Two separate, yet related, groups of unit characters (i.e., song-types and syllable-types) represented these OTUs for each analysis. Each character was weighted equally (i.e., song-type A was no more important than song-types B, C, D, and E).

Three clustering methods were applied to the resemblance matrices: single linkage, complete linkage, and unweighted pair-group method using arithmetic

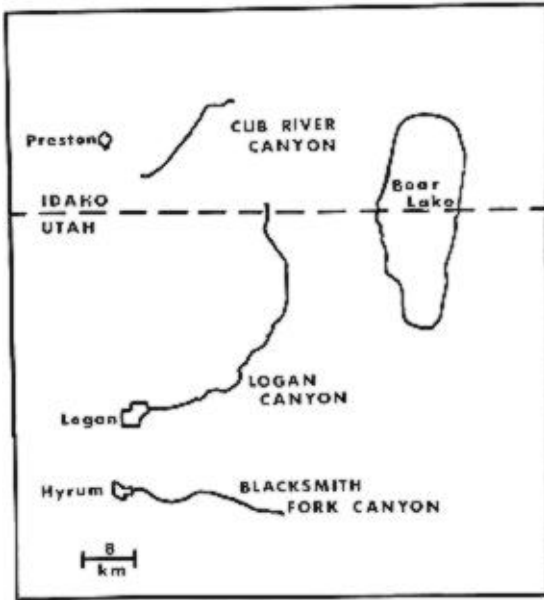


FIGURE 1. Geography of Cub River, Logan, and Blacksmith Fork canyons.

averages (UPGMA). For each dendrogram, a cophenetic correlation was computed to determine the amount of distortion imposed on the data by the technique. Single linkage led to "chaining," with large clusters that were poorly defined. Complete linkage resulted in vague clusters that were joined by other OTUs or clusters only at very low levels of similarity. Cophenetic correlations indicated that the UPGMA clustering techniques best represented the data. I judged it important to acknowledge the 0-0 matches between unit characters of OTUs in the original data matrices and, therefore, used the simple matching association coefficient.

Each bird usually possesses a repertoire of three songs. A song consists of sequences of single- or multi-noted sounds (called syllable-types), which may or may not be repeated within a song. Forty-nine syllable-types were recognized. Typically, the syllable-types and sequence in the first half of particular songs vary among individuals, whereas the terminal portion of particular songs tends to be uniform among birds. This uniformity allows virtually all songs to be grouped

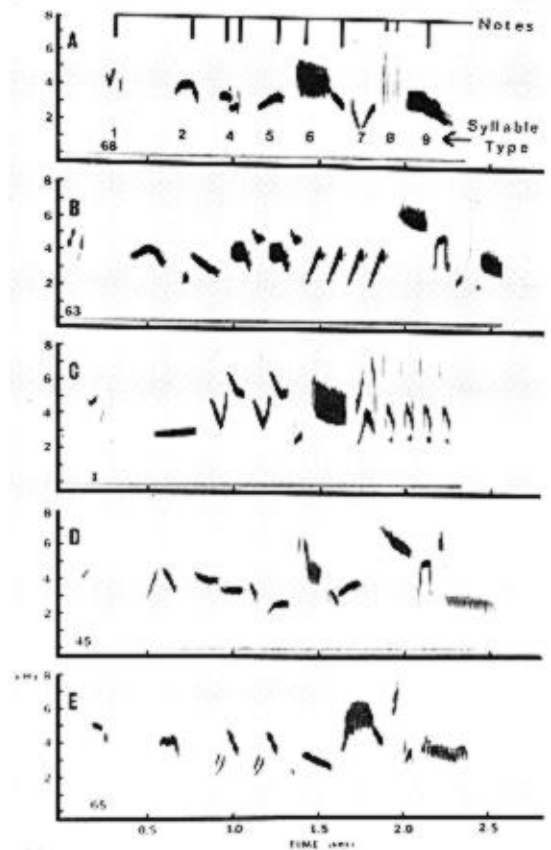


FIGURE 2. Typical renditions of song-types A, B, C, D, and E.

into one of five major song-types: A, B, C, D and E (Fig. 2). All major song-types were each represented by a large number of versions (i.e., 13 for A, 67 for B, 31 for C, 22 for D, and 13 for E). Also, 38% of all birds recorded possessed more than one version of some major song-type, usually B or C. But, although birds may possess more than one version of a song-type, these versions are used as functionally independent units while singing (Martin 1976). For further details, including a complete listing of the syllable-types comprising each song-type that was recorded, see Martin (1977).

TABLE 1. Mean number of song-types and syllable-types recorded from individual Fox Sparrows in Cub River, Logan, and Blacksmith Fork canyons during 1973 and 1974.

Location	Year	Song-types			Syllable-types			N
		\bar{x}	SD	Range	\bar{x}	SD	Range	
Cub River	1973	3.9	1.9	2-4	22.1	2.9	18-27	10
	1974	3.1	0.6	2-4	21.4	2.4	18-26	9
Logan	1973	3.2	0.7	2-5	20.1	3.4	13-28	39
	1974	2.9	0.7	2-4	19.1	4.8	13-27	28
Blacksmith Fork	1973	3.6	1.1	2-7	21.2	4.7	15-33	22
	1974	3.3	1.0	2-5	20.4	5.3	12-33	25
All locations	1973	3.2	0.8		20.8	3.8		71
	1974	3.1	0.8		20.2	4.2		62
	Total	3.2	0.8		20.6	4.0		133

TABLE 2. Mean number of syllable-types composing particular song-types for the birds inhabiting Cub River, Logan, and Blacksmith Fork canyons during 1973 and 1974. N = number of songs of that type analyzed.

Song-type	Year	Cub River				Logan				Blacksmith Fork				All locations		
		\bar{x}	SD	Range	N	\bar{x}	SD	Range	N	\bar{x}	SD	Range	N	\bar{x}	SD	N
A	1973	7.0	0.0	7-8	8	7.5	0.6	6-9	27	7.9	0.9	7-10	10	7.5	0.7	45
	1974	7.6	1.5	7-11	7	7.8	0.8	6-10	18	7.9	0.6	7-9	10	7.7	0.9	35
B	1973	7.7	1.4	5-9	7	8.5	1.0	6-10	38	8.7	1.0	6-10	21	8.5	1.1	66
	1974	9.0	-	-	4	9.2	0.8	7-10	31	8.2	0.9	7-10	24	9.1	1.2	59
C	1973	7.7	1.4	5-9	7	7.3	0.7	5-9	43	8.5	1.2	7-10	31	7.8	1.1	81
	1974	7.4	1.6	5-11	9	7.2	0.6	6-8	24	8.2	1.2	6-11	34	7.8	1.2	67
D	1973	10.0	1.5	7-11	7	9.5	1.1	9-11	6	8.6	1.1	7-10	5	9.4	1.3	18
	1974	10.8	0.1	10-11	7	9.3	1.0	8-10	4	8.1	1.0	7-9	7	9.4	1.4	18
E	1973	-	-	-	-	9.0	0.0	-	2	9.0	0.0	-	5	9.0	0.0	7
	1974	-	-	-	-	7.4	0.6	7-8	5	7.6	0.8	6-8	7	7.5	0.7	12

RESULTS

NUMBERS OF SONG-TYPES AND SYLLABLE-TYPES

Table 1 shows little variation in the mean number of song-types or syllable-types within any population between years or between populations within 1973 and 1974. The most obvious variability in the mean number of syllable-types possessed by any group of Fox Sparrows was related to the number of songs comprising individual repertoires. Numbers of syllable-types recorded from birds varied directly with the number of songs an individual exhibited. Birds with two songs possessed a mean of 15.8 syllable-types (1973, \bar{x} = 15.9, SD = 2.8, N = 10; 1974, \bar{x} = 15.6, SD = 2.4, N = 14); those with three songs possessed 19.8 (1973, \bar{x} = 19.8, SD = 2.4, N = 32; 1974, \bar{x} = 20.0, SD = 2.0, N = 27); and birds with four songs had 23.6 (1973, \bar{x} = 23.7, SD = 2.6, N = 26; 1974, \bar{x} = 24.3, SD = 2.4, N = 16).

NUMBERS OF SYLLABLE-TYPES PER PARTICULAR SONG-TYPE

There was little variation in the mean number of syllable-types composing particular

song-types (Table 2). Song-type D had the greatest number of syllable-types at Cub River and Logan canyons but not at Blacksmith Fork. There was no significant difference in the number of syllable-types composing song-type A or C within populations between years, and between populations within the same year for both 1973 and 1974. Song-type B differed significantly in the number of syllable-types between 1973 and 1974 in the Logan and Cub River populations, but the variation in song-type B within and among Blacksmith Fork birds was not significant. Variation of song-type D between the two years also was not significant within populations, but it was significant between Cub River-Blacksmith Fork and Cub River-Logan canyons in 1974. Although little variation was evident in song-type E in 1973 and 1974 (no individuals in Cub River possessed song-type E), the numbers of syllable-types composing song-type E within the populations of Logan and Blacksmith Fork canyons did vary significantly between years.

Some variation was present in the number of syllable-types composing particular song-types, both within and among populations.

TABLE 3. Percent of Fox Sparrows, by canyon and as a whole, that exhibited song-types in 1973 and 1974*.

Song-type	Cub River		Logan		Blacksmith Fork		All locations		
	1973 (10)	1974 (9)	1973 (39)	1974 (28)	1973 (22)	1974 (25)	1973 (71)	1974 (62)	Total (133)
A	80	67	69	64	45	36	63	53	59
B	90	67	92	96	82	84	89	87	88
C	100	89	97	89	100	96	99	92	95
D	70	78	15	14	23	28	25	29	27
E	0	0	5	18	23	28	10	19	14

* Sample size (i.e., number of birds) given in parentheses.

However, this appeared to be an exception rather than the rule. When data for the three populations were pooled, no significant difference emerged between 1973 and 1974 in the number of syllable-types forming song-types ($\bar{x} = 8.1$, $SD = 1.2$, $N = 217$; $\bar{x} = 8.2$, $SD = 1.2$, $N = 199$, respectively). And, as expected, when all song-types were pooled, there was no significant difference in the mean number of syllable-types used by the Fox Sparrows of the Cub River, Logan, and Blacksmith Fork canyons in the formation of song-types (Table 2).

SPATIAL AND TEMPORAL DISTRIBUTION OF SONG-TYPES

Fox Sparrows of all three populations were essentially uniform in exhibiting approximately three songs per individual (Table 1). However, the three songs of a bird's repertoire were not necessarily one each of a major song-type; 38% of the sparrows possessed two versions of one of the major song-types (Martin 1977). Song-types A, B, and C were by far the most common in all three populations (Table 3). Although no song-type was unique to a particular population, there were significant differences between canyons in the frequency of occurrence of certain song-types. Types B and C were the most common and evenly distributed among the three populations (Table 3), whereas the distributions of song-types A, D, and E differed significantly among populations. Song-type D was more common in the Cub River population than it was in the Logan or Blacksmith Fork populations, while song-type E was most prevalent in the Blacksmith Fork population (Table 3).

When the individuals of all three canyons were pooled, this larger grouping had a uniform-sized song repertoire of three songs (which were customarily A, B, and C) and yet also had significant variation in the incidence of song-types D and E. This apparent inconsistency may have resulted from instances in which the number of songs per repertoire was increased to four (see Cub River data for 1973 in Table 2); this occurred infrequently and did not affect the overall mean number of songs per individual. Also, there was a decrease in the incidence of song-type A with an increase in usage of song-types D and E (Table 3).

Neither the incidence of versions of song-types nor the overall percentage of birds singing particular song-types (Table 3) varied significantly from 1973 to 1974. The

variation that was meaningful appeared to be due to a decrease in the frequency of song-type A in all the populations during 1974 and to an increase in the frequency of song-type E in the Logan Canyon population in 1974 (Table 3).

The incidence of song-types A, B, and C was high in all populations (Table 3). Song-type D was most common in the Cub River population, the northernmost canyon. Song-type E was most common in the southerly population (Blacksmith Fork Canyon), was totally absent from the Cub River population, and was more prevalent in the centrally-located Logan Canyon population. Overall, individuals of Blacksmith Fork Canyon possessed both high numbers of song-versions and the most diversified repertoires of song-types (Table 3).

SPATIAL AND TEMPORAL DISTRIBUTION OF SYLLABLE-TYPES

Since major song-types were formed from a limited array of syllable-types (Martin 1977), the same general distributional patterns observed in song-types were evident in syllable-types. The large numbers of combinations of syllable-types, especially in the first halves of song-types, permitted a more even distribution of syllable-types than of song-types (see Appendix). However, an exception to this rule (illustrated by syllable-types 4, 21, 23, 26, 33, 36, 40, 43, 44, 45, 46, and 48 in Appendix) was that the frequency of occurrence of certain syllable-types in the Cub River population was either much higher or lower than in the other populations. Most of this variability in the Cub River population could be attributed to three factors: the absence of song-type E, the high incidence of song-type D, and the fact that few individuals possessed multiple versions of any given song-type.

POPULATIONS GENERATED BY CLUSTER ANALYSIS

Cluster analyses of individual Fox Sparrows, based on syllable-type and song-type data, were performed to determine whether more precisely-defined aggregations of individuals than those groupings just described could be elucidated. The clusters resulting from an analysis of syllable-types support the conclusions reached previously (Fig. 3). Few populations emerged below the level at which 20–30% of the clusters were formed. Those birds which possessed the syllable-types commonly associated with song-types A, B, and

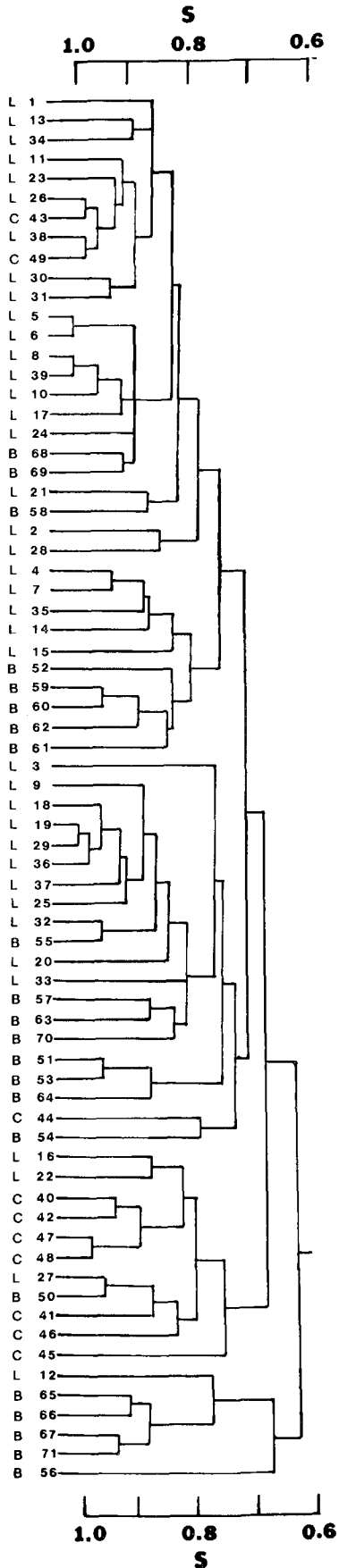
APPENDIX. Percent of Fox Sparrows that possessed a particular syllable-type.

Syllable-type	Cub River		Logan		Blacksmith Fork		All locations		Total
	1973	1974	1973	1974	1973	1974	1973	1974	
1	100	100	90	100	100	100	95	100	98
2	30	22	26	42	32	36	34	37	36
3	80	67	69	36	82	60	75	50	63
4	10	11	46	64	72	64	49	56	53
5	80	67	62	64	82	36	70	55	73
6	80	67	69	64	41	32	62	53	58
7	80	67	69	64	32	32	59	52	56
8	80	67	69	64	45	32	63	52	58
9	80	67	69	64	45	32	63	52	58
10	90	89	69	57	27	36	59	53	56
11	100	89	95	93	95	96	96	94	95
12	60	56	69	61	27	64	55	61	58
13	70	56	5	11	18	24	18	23	21
14	10	11	20	36	64	44	32	35	34
15	0	0	3	0	0	4	1	2	2
16	0	0	23	11	0	24	13	15	14
17	80	89	87	50	32	64	69	61	65
18	0	0	3	4	0	0	1	2	2
19	0	0	3	4	0	4	1	3	2
20	10	11	20	36	86	60	39	42	41
21	60	56	8	11	14	20	17	21	19
22	80	67	82	79	64	72	76	74	75
23	0	0	13	11	23	16	14	11	13
24	50	100	10	79	9	40	15	66	41
25	100	100	97	93	86	92	94	94	94
26	20	23	85	86	95	92	79	79	79
27	80	33	92	96	86	92	89	85	87
28	70	33	67	57	86	84	73	65	69
29	90	78	100	75	95	84	97	79	88
30	0	0	13	18	27	4	15	10	13
31	0	11	8	11	68	36	25	21	23
32	0	11	5	18	23	16	10	16	13
33	30	57	0	7	0	0	4	11	8
34	90	78	46	39	32	48	48	48	48
35	50	67	36	43	36	48	38	48	43
36	0	11	72	57	73	76	62	58	60
37	100	89	100	82	95	92	99	87	93
38	100	89	97	82	91	92	98	87	93
39	10	11	15	14	59	56	28	31	30
40	60	67	5	7	5	0	13	13	13
41	10	23	10	4	5	0	8	4	6
42	20	33	8	0	5	0	8	4	6
43	50	78	8	4	5	0	13	13	13
44	0	0	5	11	27	36	11	19	14
45	0	0	3	14	18	24	7	16	12
46	0	0	3	18	23	24	8	18	13
47	0	0	8	0	0	4	4	2	3
48	10	11	0	7	0	0	1	4	3
49	100	89	79	32	73	56	80	50	65

C (see Martin 1977) tended to aggregate first. The integrity of the Cub River sample was maintained due to the preponderance of the syllable-types composing song-type D. This cluster was not particularly close to that for the majority of other individuals. The sample from Blacksmith Fork Canyon formed three small clusters that were quite discrete. The Blacksmith Fork population was the most variable with respect to the types of syllables it exhibited. This cluster analysis supports the contention that about 20% of

the individuals in the Blacksmith Fork Canyon, although not geographically isolated, were more dissimilar than any other group of Fox Sparrows.

Both the clusters of populations and the interpopulation relationships based upon song-types were much more distinct than those founded upon syllable-types (compare Figs. 3 and 4). Much of the "cleaner" appearance of Figure 4 was a result of using many fewer characters in the analysis, but this was not the only factor. I conclude that



possession of particular syllable-types varied independently of the types of songs an individual possessed. Such a phenomenon, however, is not unexpected in the Fox Sparrow's system of complex song structuring. In this system, the general framework of song is based on similarity (among birds) in the form and sequence of the terminal portion of songs; in contrast, the introductory portion varies considerably among individuals.

As in the dendrograms of syllable-type analysis, those Fox Sparrows which exhibited song-types A, B, and C (birds 1 through 69 in Fig. 4), clustered first. Of these individuals, 59% were from Logan Canyon. This group was fairly distinctive from those individuals who possessed only song-types B and C (birds 3 through 70 of Fig. 4). These two clusters accounted for over 75% and 50% of the individuals in Logan and Blacksmith Fork canyons, respectively. The Cub River population maintained its integrity, due to its maintenance of song-types A, B, C, and D; 50% of the most dissimilar individuals (located at the lower third of Fig. 4) were residents of Blacksmith Fork Canyon. This recurring dissimilarity of the songs of a significant portion of the Blacksmith Fork population appeared to be related to both the prevalence of song-type E and to the scant representation of song-type A.

I inspected data for those birds who had identical song-type repertoires (i.e., clustered at 1.0 S, Fig. 4) to determine whether these individuals were within hearing distance of each other. I estimated the territory boundaries of each bird and then added to these the distance at which I could hear the bird sing. A "buffer" distance was also added to compensate for any differences in hearing abilities, depending upon the location of a bird's territory with respect to the surrounding vegetation, geological features, and proximity of the river. After plotting the listening radii for each bird, only one pair in Cub River, five in Logan, and three in Blacksmith Fork canyons that possessed identical repertoires were thought to be within hearing range of each other. These birds represented only a small fraction of the possible combinations of birds which either: potentially heard each other sing, but did not exhibit identical song-

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FIGURE 3. Dendrogram showing results of UPGMA cluster analysis based on syllable-types. Similarities (S) were computed using the simple matching coefficient. The cophenetic correlation coefficient was 0.713.

type repertoires; or possessed identical song-type repertoires, but could not hear each other sing.

DISCUSSION

SONG STRUCTURING IN FOX SPARROW POPULATIONS

Fox Sparrows of the Cub River, Logan, and Blacksmith Fork canyons exhibited extraordinary homogeneity in major parameters of their song. The mean numbers of song-types, songs, and syllable-types did not differ within populations in consecutive years or between populations within a given year. The number of syllable-types possessed by individuals with variously-sized song repertoires was different, but it was not related to the location of the birds.

Although number of syllable-types composing specific song-types varied among populations, it was not related to any particular geographic location or year. Further, this variation was not strongly correlated with the general level of variability in the sequences of syllable-types forming the song-versions in particular song-types. The most variable song-type (B) and the two least common song-types (D and E) were responsible for most of the significant between-canyon variation in the numbers of syllable-types composing particular song-types (Table 2).

Because of the uniformity in the terminal portions of major song-types sung by individuals, the syllable-types possessed by the individuals correlated closely with their song-type repertoires. This relationship appeared to affect syllable-type heterogeneity both within and among populations. This heterogeneity also was due, in part, to the high number of song-versions and the distinctiveness of the Cub River Canyon population. The latter phenomenon was partly due to the high incidence (over 70%) of song-type D in the Cub River population. The lack of any definitive terminal structure in song-type D, coupled with the few unique syllable-types included in the first half of the song, resulted in the statistical uniqueness of the Cub River birds. Another more general factor which affected the relationship of the Cub River birds to the populations of the other canyons was the "conservative habits" of the Cub

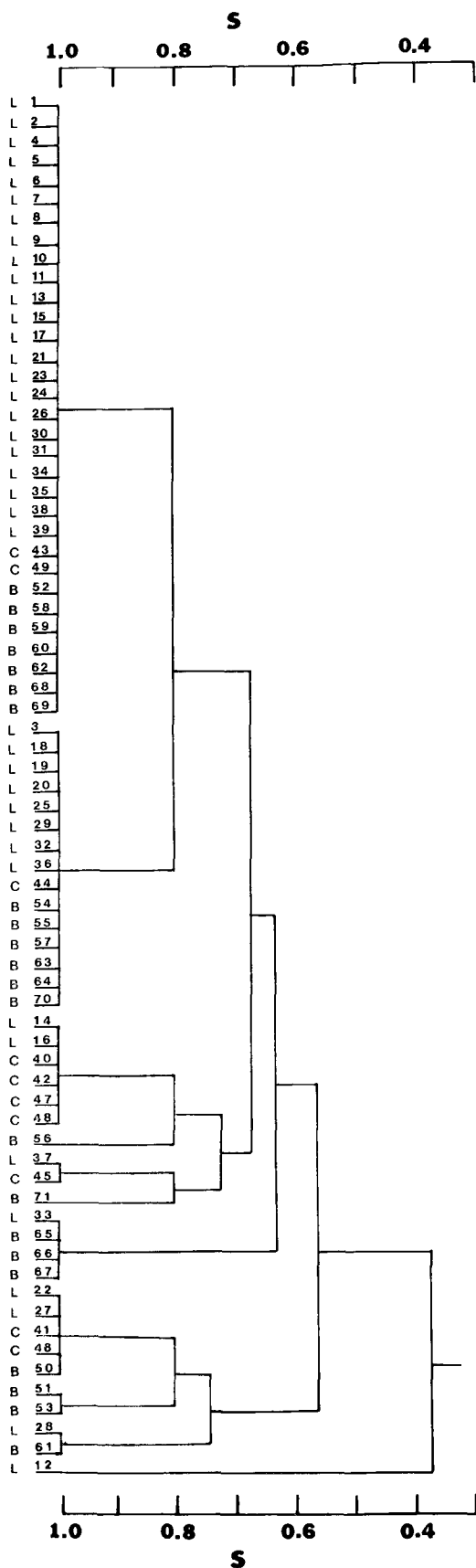


FIGURE 4. Dendrogram showing results of UPGMA cluster analysis based on song-types. Similarities (S) were calculated using the simple matching coefficient. The cophenetic correlation coefficient was 0.734.

River individuals. Birds of both the Logan and Blacksmith Fork populations possessed many song-versions of song-types B and C, and a proportion of individuals sang song-type E (Table 2). The conservatism of the Cub River birds was reflected in their paucity of song-versions and the absence of song-type E.

Cluster analysis is a valuable tool for summarizing and synthesizing large amounts of data. My primary conclusions reached after examining the results of cluster analyses were: (1) nothing appeared from the data that had not been surmised from the initial analyses and (2) the preliminary conclusions concerning the song structuring in the populations appeared correct. This finding, in and of itself, was important because of the uncertainty as to whether such potentially subjective data had been initially processed in a thorough and unbiased manner.

COMPARISONS WITH OTHER SPECIES

Intra- and interpopulation variation in bird song has been described in species both closely and distantly related to Fox Sparrows. At one extreme are populations with rather inflexible song systems (e.g., White-crowned Sparrows, *Zonotrichia leucophrys*) where a bird possesses one song-type that may be virtually identical with that of its neighbor (Marler and Tamura 1964). At the other end are populations in which individuals exhibit little similarity in the structure of their songs (e.g., Song Sparrow), although geographic variation in song structure may be evident (Borror 1965). Intermediate species, such as the Fox Sparrow, demonstrate varying degrees of similarity in the structure of song among the members of a population. Both ends of this continuum are represented by species phylogenetically close to Fox Sparrows.

White-crowned Sparrows (Marler and Tamura 1962, 1964, Baptista 1975) and Rufous-collared Sparrows (*Z. capensis*) (Nottebohm 1969, King 1972), both closely related to Fox Sparrows (Mayr and Short 1970), sing only one song-type per individual, consisting of a limited number and diversity of syllable-types. In both, the terminal portions of the songs are rigidly structured within populations, but differ between contiguous populations. Such precise but differing song systems have been termed "dialects." One song-type per individual also is characteristic of White-throated Sparrows (*Z. albicollis*); while exhibiting geographic or clinal variation in song, this species does not have dialects

(Borror and Gunn 1965, Lemon and Harris 1974). Juncos, also closely related to the Fox Sparrow (Short and Simon 1965), have more than one song-type per individual. However, each song-type consists of only one (as in the Dark-eyed Junco, *Junco hyemalis oreganus*, Konishi 1964) or a few (as in the Yellow-eyed Junco, *J. phaeonotus*, Marler et al. 1962) syllable-types. Although little work has been done on the structure of song at the population level, none of the studies of *Junco* thus far has hinted at well-defined dialects or geographic variation (Williams and MacRoberts 1978).

Of those species closely related to Fox Sparrows, the Song Sparrow best approximates the form of song structuring in Fox Sparrow populations. Some populations of Song Sparrows in California have little between-individual sharing in their syllable-types or song-types (Mulligan 1966). However, populations in Maine (Borror 1965), Quebec (Harris and Lemon 1972), and Glendale, California (Eberhardt and Baptista 1977) share syllable-types and, to a limited extent, song-types. Borror (1965) and Harris and Lemon (1972) have termed the similarity of shared song structure "dialects." I consider that the fairly great distances between the populations involved in these studies, especially when compared with *Z. leucophrys* and *Z. capensis*, do not rule out the possibility that the differences simply reflect geographic variation.

The system of song structure in Fox Sparrows does not appear to be equivalent to that of its nearest relatives. Populations of juncos and White-throated Sparrows do not possess complex song-type or syllable-type repertoires as does the Fox Sparrow. Individuals within populations of White-crowned and Rufous-collared sparrows share similarly structured song-types and share a large percentage of their syllable-types, as do Fox Sparrows, but neither of the former species maintains extensive repertoires of syllable-type or song-type. Populations of Song Sparrows, although possessing song-type and syllable-type repertoires more diverse than those of Fox Sparrows (Mulligan 1966, Harris and Lemon 1974), usually do not exhibit such well-defined and unvarying songs or the degree of sharing of song-types and syllable-types on either the individual or population level. However, the amount of sharing in Song Sparrows varies geographically—those in Glendale, California, extensively share notes, syllables and songs (Eberhardt and Baptista 1977).

Investigations of the ontogeny of song in estrildid finches (Immelmann 1969) and fringillids (the Chaffinch, *Fringilla coelebs*, Thorpe 1958a, b; *Z. leucophrys*, Marler and Tamura 1964, Konishi 1965; *J. h. oreganus* and *J. phaeonotus*, Marler and Isaac 1961, Marler et al. 1962, Konishi 1964; *M. melodia*, Mulligan 1966; the Indigo Bunting, *Passerina cyanea*, Rice and Thompson 1968; and the Cardinal, *Cardinalis cardinalis*, Lemon and Scott 1966, Dittus and Lemon 1969) indicate that the species of this finch-sparrow group have an inborn tendency to produce sounds approximating those of their species' songs. Young of those species (e.g., *M. melodia* and *Z. leucophrys*) with complex songs and/or dialects probably learn their appropriate song patterns from their male parent or neighboring males which usually possess similar repertoires. Song is transferred with only slight modification from one generation to the next (Marler and Mundinger 1971, Nottebohm 1972). Most of the learning of specific song characteristics occurs early in the life of young birds and is fixed before the first breeding effort (but see Dittus and Lemon 1969, Nottebohm 1972).

The method of song learning in Fox Sparrows is unknown. However, given the method of song learning that characterizes relatives of this species, it is not surprising that neighboring Fox Sparrows do not sing identical song-types or syllable-types. By the time of first breeding, the song repertoire of a young Fox Sparrow, although possibly slightly different than that of its male parent, probably is "fixed"; furthermore, individuals have little influence over Fox Sparrows that chose to reside next to them. Possibly a Fox Sparrow could modify its song structure after beginning its first breeding effort, but I have recorded no within- or between-year modification of any individual's song-types or syllable-types (Martin 1977). It is almost certain that some of the birds I recorded were one year old (i.e., engaged in their first year of breeding).

FUNCTIONS OF SONG

Recently, investigators have implied that vocal variation in individuals and populations may be not only taxonomically useful, but also important in promoting and maintaining geographic variation in other characters (Nottebohm 1969). But, as noted by Nottebohm (1969:299), "Any intelligent statement about the role of dialects . . . or individual and geographic variation in song presupposes a

knowledge of the functions of song." I propose that the variability in songs may convey information concerning the singer's sex, location, species and individual identity, motivation, and mating status (Marler 1956), and that it may act to stimulate reproductive development in the female (Kroodsma 1976a). Variability in song structure among avian populations, when the songs of all members of single populations have unique traits in common (i.e., dialects), may also function to attract those females and repulse those males which also share the population-specific songs. Hence, by enabling individuals to identify each other as to their population affiliation, song may facilitate formation of "closed" breeding units with restricted gene pools (Nottebohm 1969:313, Nottebohm and Selander 1972, Baker 1975, Nottebohm 1975; but see Handford and Nottebohm 1976).

The evolutionary implications of such functions of song, if associated with the ability of the individuals within populations to transmit these functions through successive generations, are many. Most importantly, with respect to interpopulation variation in song, is that it affects reproductive isolation which in turn may have a profound effect in the adaptation of populations to specific habitats (Nottebohm 1969:313).

Paramount to an understanding of the importance of song variation in populations is the determination of: (1) whether or not the local variants are stable through time and passed from one generation to the next; and (2) whether they correlate with other characters, which, if maintained or varied in frequency, would affect the fitness of the individuals in the population.

Most investigations have failed to produce an answer to at least one of the above questions. My study has been no exception. I ascertained that the song structure of Fox Sparrow populations does differ slightly between geographically-separate populations, and that these variations remain fairly stable through two years. These findings imply that the population variants in songs are accurately passed from one generation of sparrows to the next, but presently I have no evidence that variation in certain parameters of song among populations and individuals (or lack of variation in other parameters) confers added fitness to particular individuals.

Below I develop several ideas concerning the possible functions served by the structure of Fox Sparrow songs by comparing their songs to those of other species. Communica-

tion of species identity of the singer is thought to be one of the foremost functions of song. Milligan (1966) has shown that male White-crowned Sparrows make stronger agonistic territorial responses to the songs of conspecific sparrows than to those of other species. White-crowned Sparrows also form song dialects in which all members of dialect-populations, which may be contiguous with other dialect-populations, share, with few exceptions, a similar composition of syllable-types in the terminal portion of their songs (Marler and Tamura 1962). The dialects of this species are transmitted from generation to generation by learning (Marler and Tamura 1964). Also, the aggressive responses of White-crowned Sparrows are stronger to intradialect songs than to interdialect songs (Milligan and Verner 1971). Such differences in the responses to intra- and interdialect songs have also been described in Song Sparrows (Harris and Lemon 1974).

In some species in which dialects have not been found, including White-throated Sparrows (Falls 1969, Brooks and Falls 1975, Falls and Brooks 1975), Indigo Buntings (Emlen 1971), Ovenbirds (*Seiurus aurocapillus*; Weeden and Falls 1959), and Song Sparrows (Kroodsma 1976b, Harris and Lemon 1976), the song structure, although conforming to a species-specific pattern, has peculiarities which distinguish one individual's song from another's. The agonistic territorial responses elicited by the songs of non-neighboring conspecifics are greater than those of neighbors' songs. Thus, information denoting an individual's identity and geographic affiliation is also conveyed in song.

Females of some species which are known to return and breed at their region of birth also learn the species-specific (Bertram 1970) and population-specific (Milligan and Verner 1971) song patterns. The ability of these returning females to discriminate between the songs of males with different dialects has been shown to occur in the White-crowned Sparrow (Milligan and Verner 1971). Generalizations about the response of females to conspecific male song are, however, not applicable to all passerines; Emlen et al. (1975) have shown that the songs of Indigo Buntings and Lazuli Buntings (*Passerina amoena*) function only in male territoriality, whereas, male plumage characteristics are used by females for selecting the appropriate mate.

Hypothetically, many of the functions of song just described are served by the song

of the Fox Sparrow. This view is bolstered in light of the close phylogenetic relationship of *Passerella*, *Zonotrichia*, and *Melospiza*. Songs of Fox Sparrows consist of many syllable-types which are specifically distinct and yet are shared among individuals (Martin 1977). Limited analyses of small samples of song from other races (both eastern and western) show that, although the songs sound different to a human listener, considerable structural similarity exists in the syllable-types used by the various races. Thus, this structural similarity among individual Fox Sparrows should afford easy species identification. In support of this belief, my initial playback experiments—broadcasting conspecific songs from the local population and eastern *P. i. iliaca*—resulted in agonistic response to both treatments. Similar tests by R. Blacquirere (pers. comm.) on Fox Sparrows in Newfoundland, which usually possess one song-type per individual, indicate that these birds also respond strongly to songs from my study populations as well as those of local birds.

Sufficient variation and individual uniqueness exists in the syllable-type composition in the first halves of the songs of Fox Sparrows to permit individual recognition, as in White-throated Sparrows, Indigo Buntings, and Ovenbirds. Even the practiced human listener can distinguish neighboring birds which have similar song-type repertoires. Further, the uniformity in the terminal syllable-type flourish composing song-types in Fox Sparrows, along with the slight geographic shift in the frequency of occurrence of song-types, may enable individuals to ascertain one another's population or geographic affiliation, as in White-crowned Sparrows and Song Sparrows. Also, female Fox Sparrows occasionally sing (Martin 1977) and, therefore, presumably know the song-types common to the area where they are breeding; they may selectively respond more strongly to songs with which they are familiar, as do female White-crowned Sparrows. I suspect, though, that the ability of Fox Sparrows to identify each other's population affiliation may be limited or may operate only upon a broad geographic scale. In Utah and Idaho, I have not detected discrete dialects comparable with those of White-crowned Sparrows or Rufous-collared Sparrows (Nottebohm 1969, 1977, King 1972). Individual Song Sparrows can ascertain one another's population affiliation even though individuals within dialect-populations share fewer syllable-types than do Fox Sparrows.

If Fox Sparrows cannot identify each other at the population level, it is probably because the individuals from different populations share too many components of their songs.

SUMMARY

Little intra- or interpopulation variation in songs of Fox Sparrows was found in Utah and Idaho. Variations in the geographic distribution of syllable-types and song-types were mutually dependent due to uniformity in the syllable-types used to form song-types. One population tended to form a unique grouping due to the high incidence of song-type D and the absence of song-type E. Individuals of another population displayed the greatest diversity of song-types. Cluster analyses based on syllable-types and song-types emphasized and supported the contention that the incidence of syllable-types and song-types was very uniform within and among all populations.

The song structure in populations of Fox Sparrows appears intermediate between those species that exhibit no intrapopulation structuring of song and those that maintain well-structured dialects. I suspect that Fox Sparrows learn their song repertoires early in life, and do not change the structure of their repertoires after the first autumn. Song in this species appears well adapted for encoding messages of sexual, individual, population (or geographic), and species identity.

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