SONGS OF THE FOX SPARROW. I. STRUCTURE OF SONG AND ITS COMPARISON WITH SONG IN OTHER EMBERIZIDAE

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Analyses of avian vocalizations have been useful in delineating avian taxonomic relationships (Lanyon 1969, Payne 1973), functions of primary song (Falls 1969) and non-song vocal signals (Crook 1969), and the development of vocal displays (Nottebohm 1972). However, for many groups of birds the data needed for comparative vocal analyses are not available. One such case is the complex of North American sparrow genera *Melospiza, Zonotrichia, Junco, and Passerella* considered to be closely related by Mayr and Short (1970) and Paynter (1964, 1970). Vocalizations have been described in selected species presently assigned by the A.O.U. Check-list Committee (1957) to *Melospiza* (Borror 1965, Harris and Lemon 1972, 1974, Mulligan 1966, Nice 1937, 1943, Stefanski and Falls 1972a, b) and *Zonotrichia* (Borror and Gunn 1965, Falls 1969, King 1972, Konishi 1965, Lemon and Harris 1974, Marler and Tamura 1964, Milligan 1966, Milligan and Verner 1971, Nottebohm 1969, Nottebohm and Selander 1972, Stefanski and Falls 1972a, b, Verner and Milligan 1971). Although the Fox Sparrow (*Passerella iliaca*) is the only representative of its genus, and is restricted both in its wintering and breeding ranges to North America, no in-depth study of its behavior has been conducted.

All major investigations of Fox Sparrows have dealt with their external (Swarth 1920) and/or internal (Linsdale 1928a, b) morphology. Linsdale (1928a) compiled some records on natural history and behavior of Fox Sparrows and thought that the geographic variation in the morphology of Fox Sparrows might be correlated with the variation he thought was present in their vocal behavior, especially song.

I investigated the singing of Fox Sparrows in an effort to elucidate the form, extent, and function of their variations in song. My objective is to present data describing the structure of the songs in Fox Sparrows and compare this structure with that of other species in Emberizidae (Storer 1971), most particularly those in *Melospiza, Zonotrichia,* and *Junco.*

METHODS

The Fox Sparrows I studied breed in the thick deciduous growth associated with the water courses in the canyons of the Bear River Mountains along Cache Valley in northern Utah and southern Idaho. Only three canyons emptying into Cache Valley support rivers large enough to provide the extensive habitat needed by Fox Sparrow populations. A few pairs of Fox Sparrows may breed along the floor of Cache Valley proper, but no continuous band of breeding birds connects the three canyons. Although the breeding populations of the canyons appear to be geographically distinct, all three will be considered here as one large population. A comparison of the variation in song among these canyon populations will be presented elsewhere.

During the breeding season, I recorded 71 male Fox Sparrows in 1973 and 62 in 1974. Twelve birds were color banded in 1973, permitting a check on the stability of individual's songs through time.

Tape recordings were made with a Uher 4000 IC tape recorder at 19 cm/sec which was equipped with a Uher M-517 microphone mounted on a 60.9 cm parabolic reflector. Sound spectograms were produced with a Kay Electric Company Sonagraph (6061-B). Although both narrow and wide bandpass filter settings were used to produce sound spectrograms, only those made with the wide bandpass setting are illustrated.

While the songs of Fox Sparrows have been designated as A, B, C, D, and E, this does not imply any a priori hierarchical or probabilistic sequence to the occurrence of particular songs during singing sessions. Analysis of variance tests (Sokal and Rohlf 1969), with a α at 0.05, were used to determine if the various parameters of song and singing measured were statistically significant.

RESULTS

GENERAL SINGING BEHAVIOR

Fox Sparrows produce a number of vocalizations, the most distinctive of which is the male's primary song. Males are extremely vociferous and may be heard singing during the day throughout spring and early summer. Although the females may at times produce song, their rendition is much softer and tends to be incomplete (Saunders 1910, unpublished data). The structure of Fox Sparrow song reportedly varies over broad geographic areas (Linsdale 1928a, Austin 1968), but it is always characterized by its complexity, richness of tone, and great amplitude. The messages that I consider encoded within Fox Sparrow song are similar to those messages Mulligan (1966:2) believed were encoded in the songs of the Song Sparrow (*Melospiza melodia*), i.e., "sex, location, possession of a territory, aggressive and sexual motivation, and individual identity."

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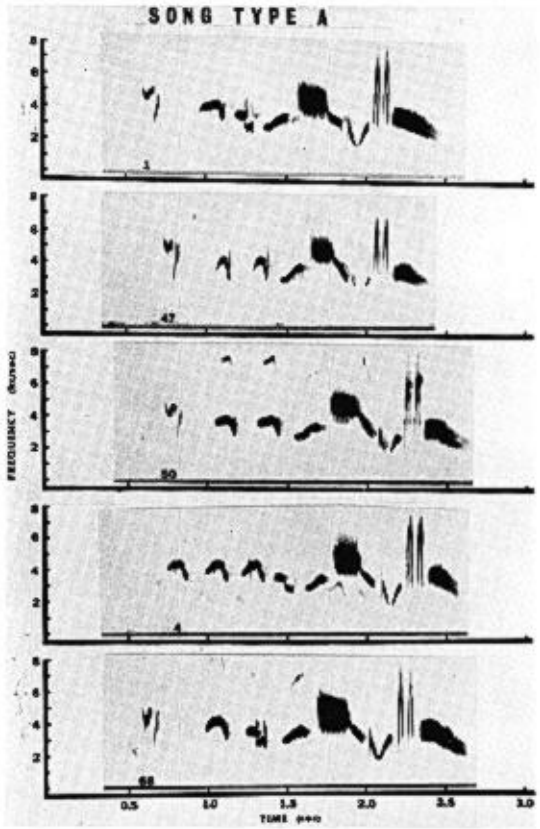

FIGURE 1. Sound spectrograms illustrating five song versions of song-type A. Each version was sung by a different Fox Sparrow.

Fox Sparrows apparently sing along some of their routes northward during spring migration, although most of these efforts produce only subsong (see review in Austin 1968). By the time males arrive at their breeding grounds most of them are singing full song. Only one individual was recorded singing a subsong at the time of arrival (24 March 1974), and it progressed into full song within three days.

Seasonally, the Fox Sparrows I studied began singing within a few days of their arrival on the breeding areas (late March through April) and continued singing vigorously until their young hatched. From the third week of May until the first week of June, which constituted the nestling and early fledgling periods, males sang but little, being preoccupied with the care of their young. During mid-June there was a resurgence of singing that persisted until mid-July; after that time singing ceased for the season. Although a few birds sang during the early fall after their postnuptial molt (also see Saunders 1948), this behavior was neither common nor persistent.

Song appeared to function more as a distant threat rather than a proximal territorial proclamation between rival males. Displays accompanying disputes in which the contestants were within a few meters of each other or an intruder was within a resident's territory tended to be dominated by "chirping" calls and posturing. After repelling an intruder a resident male would assume an exposed perch and sing vigorously; such singing sessions would, at times, continue for five minutes or more. This behavior lent itself well to the field recording of Fox Sparrow singing. Upon playing a recording of conspecific song within a male's territory, the resident would approach and, if marked, could be identified easily. Then, after failing to locate the intruder (simulated by the playback), the resident would perch nearby and sing, enabling me to obtain high-quality recordings.

Unlike Song Sparrows (Harris and Lemon 1972), Cardinals (*Cardinalis cardinalis*) (Lemon and Chatfield 1971), and Chaffinches (*Fringilla coelebs*) (Hinde 1958), Fox Sparrows do not sing a bout of songs consisting of one type or theme and then switch to another type. Rather, Fox Sparrows tend to organize their song-types in an orderly fashion within singing sessions, and consecutive songs almost always are different (Martin 1976 and unpublished data). Thus, all the song-types of the individual Fox Sparrows I studied are sung with almost equal frequency, and a bird's total repertoire may be sampled quickly.

STRUCTURE OF SONG

The terminology used in this report is not completely synonymous with that of similar studies (Borror 1965, Harris and Lemon 1972, 1974, Lemon 1965, Mulligan 1966, Nottebohm 1969, Thompson 1970, 1972). One cannot expect such uniformity because of specific differences in songs and their modes of development. The unifying feature between this and previous studies is that analyses have been made at the level of what appear to be the components that individual birds use to compose their songs.

Initially, I distinguished the various songs of Fox Sparrows in the field by their overall uniformity, both within and among individuals, and by their organization into discrete units during singing sessions. The organization of the elements that form songs is referred to hereafter as the structure of the songs. Five major song-types were distinguishable and designated alphabetically as A, B, C, D, and E (figs. 1 and 2).

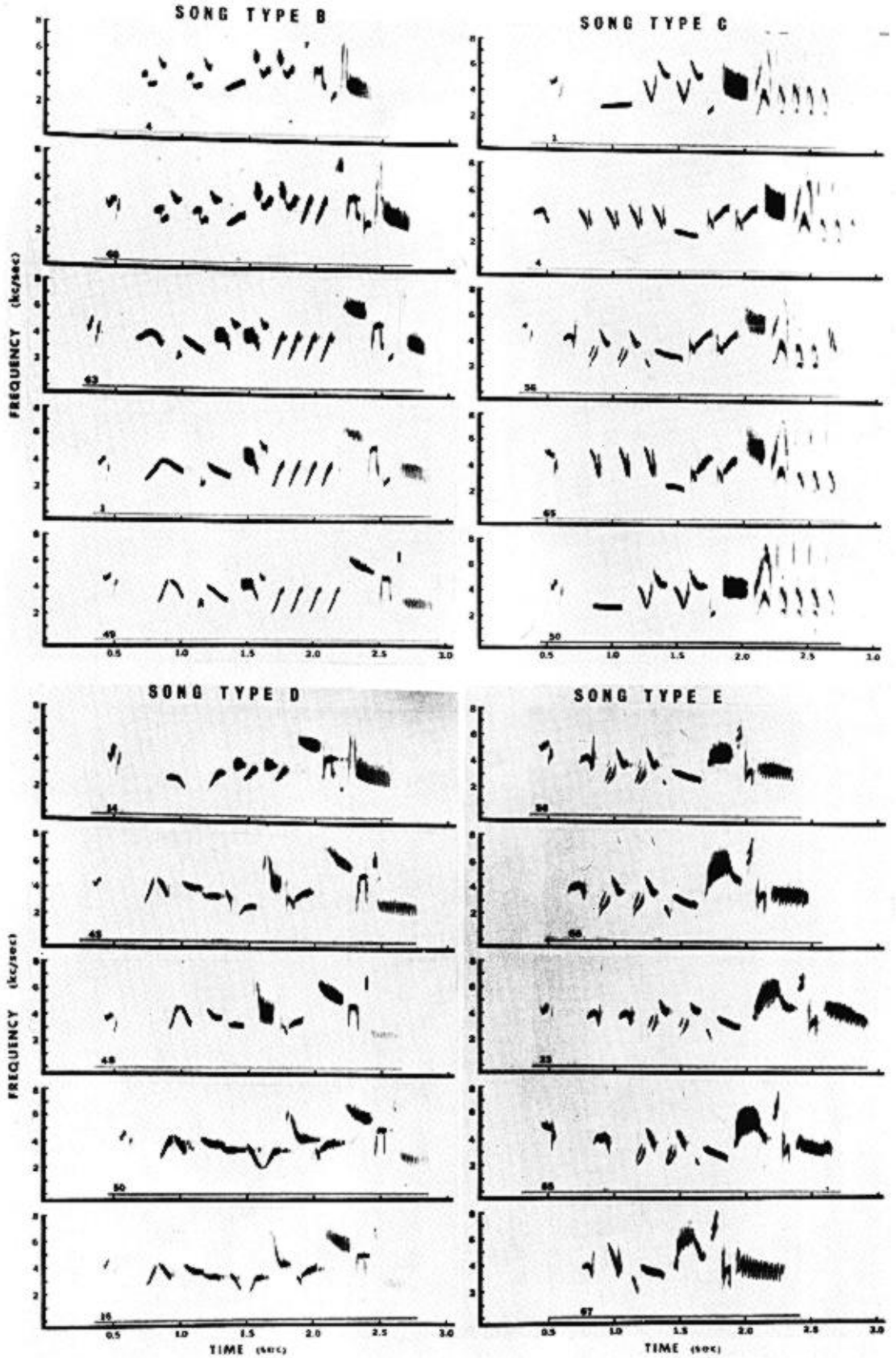

FIGURE 2. Sound spectrograms illustrating the song-versions of song-types B, C, D and E; each version of a particular song-type was sung by a different Fox Sparrow.

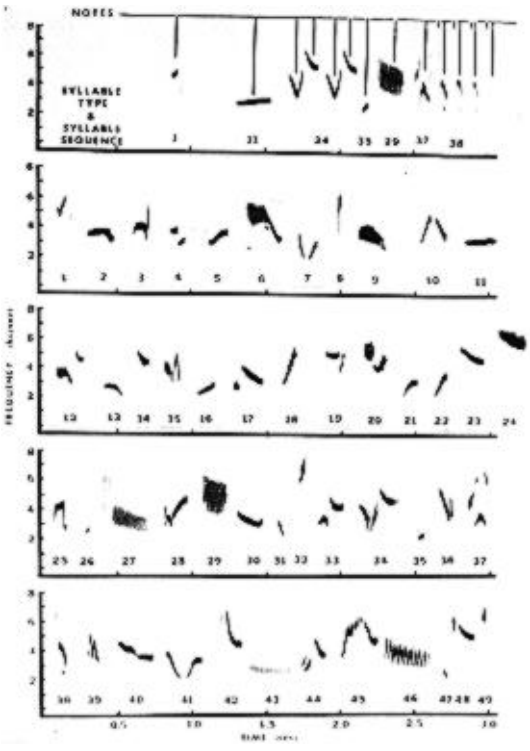

FIGURE 3. Upper line delineates the notes, syllable-types and syllable-type sequence composing a song-version of song-type C. Lower four lines illustrate syllable-types 1 through 49 of the Fox Sparrows of northern Utah and southern Idaho.

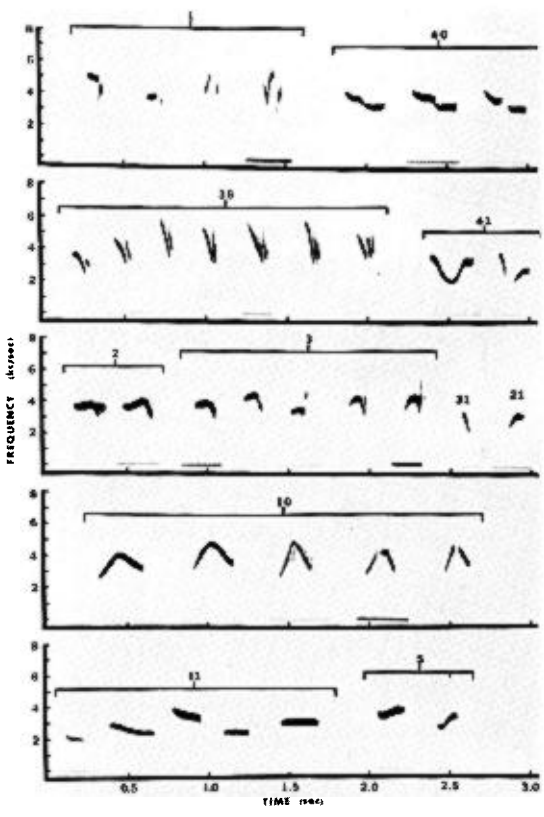

FIGURE 4. Examples of the extent of syllable-type variation among individual Fox Sparrows. Examples are drawn from the most variable of the syllable-types.

Song-types were analyzed further on the basis of their constituent syllable-types. Syllable-types were defined as the single- or multi-noted sounds, which may or may not be repeated, that appear to be the building blocks of a particular song-type (fig. 3). Therefore, a syllable-type may be present or absent, and could be uttered singly or repeated in a particular song-type, but never fragmented so that only a portion of it would be in evidence. This approach although admittedly subjective, permitted me to represent serially repeated syllable-types with a single numerical designation of 1 through 49 when classifying sequences of syllable-types in songs. This convention is illustrated by syllable-types 34 and 38 in figure 3. As defined here, a syllable-type could consist of more than one temporally discrete sound, termed a note (fig. 3). The form of syllable-types which were classified similarly did not vary as much among individuals as the song-versions each individual sang. Most syllable-types were easily identifiable, and only a few (fig. 4) exhibited much variation in form among individuals.

Although songs of individuals may be designated the same type, this does not imply that these songs are structurally identical. All the major song-types were represented by a large variety of song-versions (see Appendix, figs. 1 and 2). As will be shown later, it is the marked similarity of the sequences of syllable-types within certain portions of songs that permitted grouping them into specific classes. Only 15 of the over 390 songs categorized were hard to classify. These "problem" songs are designated with an asterisk in the Appendix.

SONG-TYPE A. Song-type A (fig. 1) was sung by 59% of the Fox Sparrows recorded and was the third most common song-type in the repertoire of the birds (table 1). It consisted of 6 to 11 syllable-types per song, fewer than in any other song-type (table 2). The syllable-types and the sequence of syllable-types composing song-type A were fairly constant (fig. 1, Appendix).

Song-type E appeared to be more uniform than song-type A (especially in 1973; Appendix), but only 19 of 133 birds possessed song-type E.

TABLE 1. Percent of Fox Sparrows during 1973 and 1974 that sang a particular song-type.

Year	N	Song-type A	B	C	D	E
1973	71	63	89	99	25	10
1974	62	53	87	92	29	19
Total	133	59	88	95	27	14

Almost all the variation in song-type A was restricted to the first half of the song, centering in the use of syllable-types 2 and 3 (fig. 1, Appendix). Syllable-types 2 and 3 were very similar in form (figs. 3 and 4), and were distinguished chiefly by the presence of an up-slur tail in syllable-type 3. This terminal feature was not always present and thus not always effective for separating the two syllable-types. Because syllable-types 2 and 3 demonstrated more overlap than any other combination of syllable-types, in reality they may not be distinct. All versions of song-type A terminated with the syllable-type sequence of 6, 7, 8, and 9, which distinguished it from all other song-types (Appendix, fig. 1).

SONG-TYPE B. This type (fig. 2) was sung by 88% of Fox Sparrows recorded and was the second most common song-type in the birds' repertoires (table 1). It consisted of 5 to 10 syllable-types (table 2). This song-type was the most variable of all the song-types both in its syllable-type composition and in its syllable-type sequences. Although two or three generalized sequences of syllable-types predominated, there were many versions in which only one or two syllable-types were added or omitted from the generalized format (Appendix).

As in song-type A, the endings of the various versions of song-type B exhibited great similarity among individuals (Appendix, fig. 2). Even though most songs ended with the syllable-type sequence 25, 26, and 27, this pattern was not as consistent among individuals as the terminal sequence of song-type A.

SONG-TYPE C. Song-type C (fig. 2) was present in the repertoires of 70 of 71 birds in 1973 and 57 of 62 birds in 1974 (table 1); it was the most common of all the song-types. The song consisted of 5 to 11 syllable-types (table 2). The composition of the first half of the song varied considerably but only three of the versions were sung commonly in both 1973 and 1974 (Appendix, fig. 2). Song-type C usually ended with the syllable-type sequence 29, 37, and 38.

TABLE 2. Mean number of syllable-types composing particular song-types of the Fox Sparrows in 1973 and 1974.

Song-type	1973 $\bar{x}$	SD	N	1974 $\bar{x}$	SD	N
A	7.5	0.7	45	7.7	0.9	35
B	8.5	1.1	66	7.6	1.2	67
C	7.8	1.1	81	7.8	1.2	67
D	9.4	1.3	18	9.4	1.4	18
E	9.0	0.0	7	9.0	0.6	12
All types	8.1	1.2	217	8.2	1.2	199

The terminal sequence of syllable-types was, as in song-types A and B, very stereotyped among birds. However, terminal syllable-type 39 was used by some birds and not by others (Appendix), and even individuals who normally terminated their song with syllable-type 39 would infrequently omit it. Syllable-type 39 was the only one which was used in this rather erratic manner, and it occurred only in the terminal position in song-type C.

SONG-TYPE D. Song-type D (fig. 2) was recorded from only 27% of all Fox Sparrows analyzed (table 1). This song-type consisted of 6 to 11 syllable-types whose sequences were the most variable of all the song-types considered (fig. 3, Appendix, and table 2). However, consistency was evident in that 53% of the birds sampled in 1973 sang one or the other of only two versions of song-type D.

Whereas the terminal sequences of syllable-types of song-types A, B, C, and, to a lesser extent, E, were structured, those of song-type D were quite variable. The parameters used to distinguish song-type D from other song-types were the rolling, musical sounds produced by the syllable-types of the first half of the song. These usually resulted from the presence of syllable-types 40, 41, 13, or 21 (figs. 2 and 3, Appendix). Despite the fact that song-type D usually ended with a syllable-type sequence similar to that of song-type B, song-type D was distinct to me.

SONG-TYPE E. This song-type was an uncommon component of the birds' repertoires and occurred in only 14% of the birds recorded (table 1), although it did exhibit considerable uniformity in its syllable-type sequence (fig. 2, Appendix). Of the various patterns resulting from the 6 to 11 syllable-types forming song-type E, only one was common in 1973 and a different one in 1974. Song-type E usually ended in the syllable-type sequence of 45, 32, 25, and 46.

TABLE 3. Percent of Fox Sparrows that possessed a particular syllable-type.

Syllable-type	Percent of birds		
	1973	1974	Total
1	95	100	98
2	34	37	36
3	75	50	63
4	49	56	53
5	70	55	73
6	62	53	58
7	59	52	56
8	63	52	58
9	63	52	58
10	59	53	56
11	96	94	95
12	55	61	58
13	18	23	21
14	32	35	34
15	1	2	2
16	13	15	14
17	69	61	65
18	1	2	2
19	1	3	2
20	39	42	41
21	17	21	19
22	76	74	75
23	14	11	13
24	15	66	41
25	94	94	94
26	79	79	79
27	89	85	87
28	73	65	69
29	97	79	88
30	15	10	13
31	25	21	23
32	10	16	13
33	4	11	8
34	48	48	48
35	38	48	43
36	62	58	60
37	99	87	93
38	98	87	93
39	28	31	30
40	13	13	13
41	8	4	6
42	8	4	6
43	13	13	13
44	11	19	14
45	7	16	12
46	8	18	13
47	4	2	3
48	1	4	3
49	80	50	65

SIZE OF SONG-TYPE AND SYLLABLE-TYPE REPERTOIRES

The distinction between Fox Sparrows' major song-types and songs is important. Individual birds could possess a repertoire containing more than one version of one of the major song-types listed in the Appendix. Although an individual's repertoire may have consisted of more than one version of a song-type, the different versions were used as independent units during singing sessions (Martin 1976). Only one bird recorded in 1973 and one in 1974 exhibited more than five songs. These two individuals had seven and six songs, respectively, and were the only birds which possessed all five major song-types.

Of those birds who sang more than one version of a major song-type ($N = 48$), only two uttered three versions of the same song-type (in both cases song-type C). The song-types most commonly represented by song-versions were B (11 in 1973, 8 in 1974) and C (14 in 1973, 13 in 1974). Only two individuals simultaneously possessed versions of two different song-types, and both sang versions of song-types B and C. Although numerous options are possible, the sizes of song repertoires among members of the population were uniform between years ($\bar{x} = 3.2 \pm 0.8$ SD in 1973, 3.1 ± 0.8 in 1974; $P > 0.05$).

I identified 49 syllable-types from the songs of all males analyzed during 1973 (fig. 3); no new syllable-types appeared in those birds recorded in 1974. Although the size of individuals' syllable-type repertoires ranged from 10 to 33, an analysis of variance indicated that there were no significant differences in size of repertoires between the populations in 1973 and 1974 ($\bar{x} = 20.8 \pm 2.8$ SD and $\bar{x} = 20.2 \pm 4.2$ SD, respectively).

The relative consistency in the number of syllable-types which composed each of the five major song-types is illustrated in table 2. An analysis of variance indicated that there were no significant differences in the number of syllable-types of which major song-types were composed, either within or between years. Likewise, the number of syllable-types composing individuals' songs showed no significant difference (table 2, bottom line).

The sharing of syllable-types among individuals was common; 22 of the 49 syllable-types were shared by 50% or more of the birds, whereas, 18 were shared by 20% or less (computed from data in table 3). Comparing those syllable-types in the terminal portion of songs (Appendix) with the percentage of sharing of syllable-types among birds (table 3), I found that those syllable-types used in the terminal portions of song-types A, B, and C accounted for much of the observed overlap.

Although the number of syllable-types possessed did not differ significantly among birds, it did differ significantly between those groups of individuals having song repertoires of 2, 3, and 4 songs ($\bar{x} = 15.8 \pm 2.6$ SD, $N = 24$; $\bar{x} = 19.8 \pm 2.4$ SD, $N = 59$; $\bar{x} = 23.6 \pm 2.5$ SD, $N = 42$, respectively).

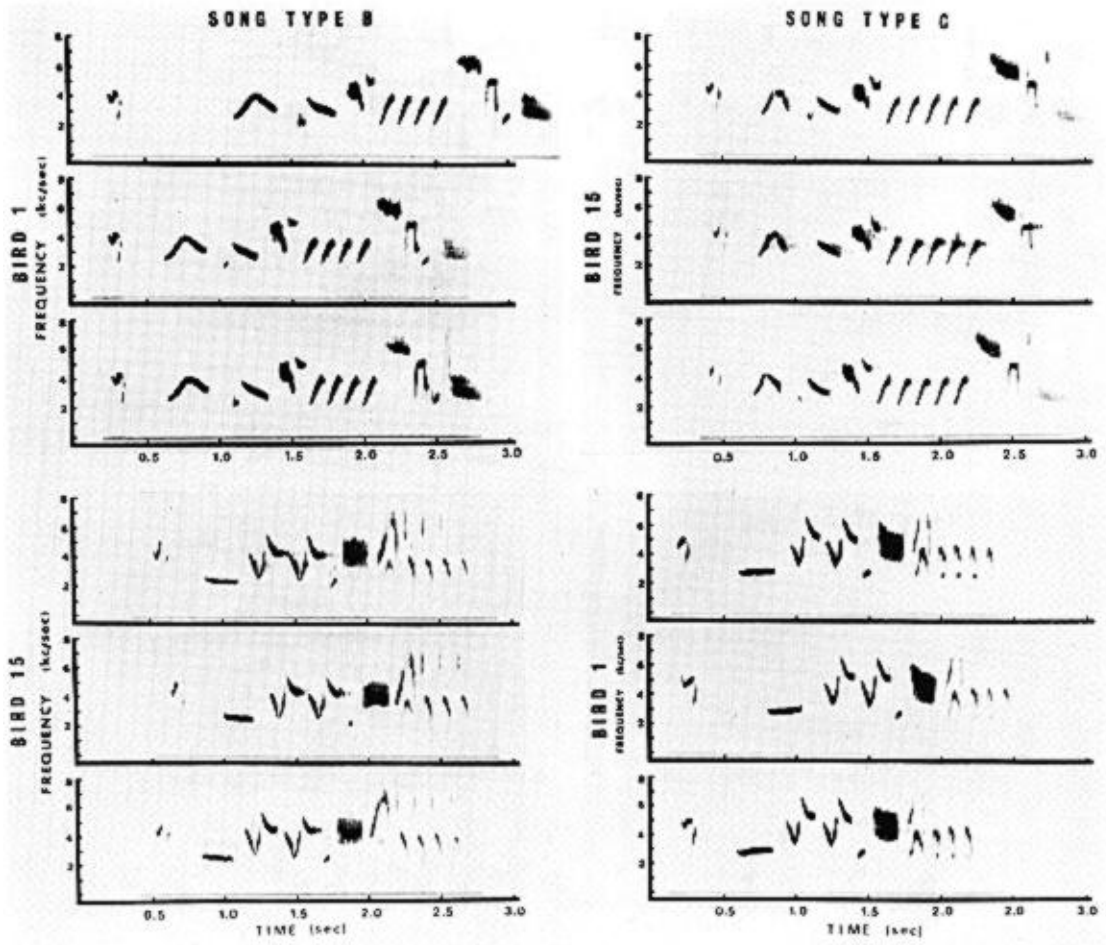

FIGURE 5. Sound spectrograms of three separate renditions of song-types B and C from Fox Sparrows B1-73 and B15-73. Examples illustrate the ability of individuals to duplicate their song-versions and emphasize that two individuals may possess song-types which are nearly identical.

TEMPORAL ASPECTS OF SINGING

Little variation occurred in the temporal aspects of singing. As illustrated by figures 2 and 3, the duration of songs among individuals appeared uniform. Most of the variation could be accounted for either by the number of repetitions of notes composing particular syllable-types (i.e., 22, 28, 34, 39; especially for song-types B and C) or by the variability in the interval between the first and second syllable-types of the songs of particular individuals (see fig. 5, song-type B of bird 1).

The durations of the silent intervals separating songs during singing sessions were not significantly different. The length of the silent interval separating the songs of individuals with repertoires of 2, 3, and 4 songs also was not significant.

CONSTANCY OF SONG THROUGH TIME

The singing behavior of individual Fox Sparrows was constant from one year to the next. Six males marked in 1973 and relocated in 1974 had reestablished themselves on the same general territory site. These birds sang the same song-types, consisting of the same syllable-types and sequences, and they sang them in the identical order within singing sessions as they had in the previous season. General characteristics also persisted from year to year. Those individuals who had varied from the population norm in some aspect of their vocal behavior, such as singing at a faster or slower rate, persisted in their unique manner in 1974.

There was also little variation between 1973 and 1974 in most of the parameters measured. The mean number of song-types and syllable-types possessed by the 1973 population did not differ significantly from those in the 1974 population. The between-year variation in the percentage of birds possessing particular song-types or syllable-types was only 6.4% (computed from table 1) and 7.0% (com-

puted from table 3), respectively. Those song-versions of song-types A, B, and C that were sung most commonly exhibited little variation between years, whereas, the commonly sung versions of song-types D and E were notably different (Appendix). Although there was considerable carry over between years in the frequency of occurrence of major song-types and syllable-types (tables 1 and 3, respectively), the total number of specific song patterns shared between the 1973 and 1974 (23 of the 147 song patterns recorded during both years) was not as pronounced. This suggests a larger yearly-turnover in the breeding individuals than was indicated by the percentage of banded birds which returned.

The mean numbers of syllable-types used by individual Fox Sparrows to form song during 1973 and 1974 were not significantly different. Song-types A, B, C, and D did not differ significantly in the mean number of constituent syllable-types between years, but song-type E was significantly different. Of those birds whose song repertoires contained more than one version of any particular song-type, 53% were from 1973 and 57% from 1974.

DISCUSSION

The affinities of *Passerella iliaca* to other emberizids (see Storer 1971) are still speculative. Linsdale (1928a, b), Grinnell and Miller (1944), Paynter (1964, 1970), and Mayr and Short (1970) considered *Melospiza* and *Passerella* congeneric, and united both under *Passerella*. Paynter (1964, 1970) suggested further that *Passerella* (including *Melospiza*) should be merged with *Zonotrichia*; apparently, Mayr and Short (1970) concurred with such action. However, this lumping trend became carried to a questionable extent (see Paynter 1970) with the suggestion by Short and Simon (1965) that the enlarged genus *Zonotrichia* should be combined with *Junco*. Taxonomic similarities of this entire complex of New World sparrows with the *Emberiza* of the Old World have also been noted by Mayr (Mayr and Short 1970:85).

The species of the above-mentioned genera constitute a natural group and a comparative study of their vocalizations should be of interest. Studies have demonstrated responsiveness between *Melospiza melodia*, *M. georgiana*, and *Zonotrichia albicollis* to certain calls of members of other species of the group (Stefanski and Falls 1972b) and of *M. melodia* and *Z. leucophrys* to each other's primary song (Milligan and Verner 1971). However, in neither study were the intergeneric aggressive responses as strong as the intraspecific or intrageneric responses.

In comparison with songs of other emberizid sparrows, the most salient aspect of the Fox Sparrow's song is its structural uniformity among individuals despite the large number of the constituent syllable-types. My brief analysis of recordings of Fox Sparrow songs from the California-Nevada border (courtesy of K. L. Dixon), San Gabriel Mountains of southern California (Cody 1974 and pers. comm.), and eastern Canada (Library of Natural Sounds, Cornell Univ.) indicates that such uniformity is a constant feature of the individuals of the species.

The songs of White-throated Sparrows (*Z. albicollis*; Borror and Gunn 1965, Lemon and Harris 1974) and Rufous-collared Sparrows (*Z. capensis*; Nottebohm 1969, King 1972) also exhibit pronounced uniformity within species. However, the repertoires of individuals of these species tend to be limited to only one song-type (rarely two or three), each song-type generally consisting of only 2–4 syllable-types. Individual Oregon Juncos (*Junco hyemalis oreganus*) have more than one song-type, but usually each song consists of only one serially-repeated syllable-type (Konishi 1964a, b, Marler et al. 1962).

The opposite extreme in song structure is shown by Song Sparrows. Song Sparrows in Maine possess a mean of 37.6 phrases, 8 to 9 major song-types, and up to 60 variations of each major song-type per individual (Borror 1965). The "phrases" of Song Sparrows appear to equate well to my definition of syllable-types. Thus, each Maine Song Sparrow exhibits about 200 song variations. Song Sparrows in California appear to be even more flexible, possessing approximately 16 song-types per individual (Mulligan 1966). Having such repertoires, one might expect considerable sharing of song-types between individual Song Sparrows, but such is not the case (Borror 1965, Mulligan 1966, Harris and Lemon 1972).

Song structure in Fox Sparrows appears to be intermediate between that of White-throated and Rufous-collared sparrows and that of Song Sparrows. Most Song Sparrows possess twice as many major song-types as do Fox Sparrows; the latter in turn manifest about twice as many major song-types as the *Zonotrichia* sparrows. Oregon Juncos and Fox Sparrows both maintain repertoires of song-types, but the former do not have the syllable-type complexity of Fox Sparrows.

Song structure complexity is least in Oregon Juncos, intermediate and comparable between Fox Sparrows and some of the *Zonotrichia* species considered above, and most pronounced in Song Sparrows.

Zonotrichia sparrows have a fairly simple form of song in certain populations and are known to form dialects (i.e., differences in song occurring in neighboring populations; Marler and Tamura 1964, Nottebohm 1969, Nottebohm and Selander 1972, King 1972, Orejuela and Morton 1975). Dialects of White-crowned and Rufous-collared sparrows are formed by the matching of the syllable-type structure in the terminal portions of songs by all the members of spatially and temporally neighboring populations. This phenomenon appears to correlate with the observed song structure of Fox Sparrows, in which similarity among individuals is most apparent in the terminal portions of song-types (with the possible exception of song-type D). Although the first half of each song-type appeared greatly variable, this impression tends to be exaggerated by the apparent contrast between the first half and the remaining portion of the songs. Visual comparison of the sound spectrograms of the introductory portions of major song-types supports the idea that they tend to have their own characteristic order of syllable-types (Appendix).

Fox Sparrows in California and eastern Canada do not sing the same song-types as Utah-Idaho birds. Whether or not these variations reflect a system of dialects as defined by Nottebohm (1969), possibly related to their subspecific differentiation, must await further investigation.

Well-defined dialects have not been reported either for Oregon Juncos (Konishi 1964b) or for central California populations of Song Sparrows (Mulligan 1966). Borror (1965:16) stated that the songs of Song Sparrows in Maine "from different... areas differed in various characteristics" and he called these dialects. Likewise, Harris and Lemon (1972) described local dialects in Song Sparrows in Quebec. However, in both these studies of dialects, the populations did not appear to be contiguous; rather they were sufficiently distant that geographic variation cannot be eliminated. In any case, the similarity of song organization among individuals is much less evident in Song Sparrows than in White-crowned, Rufous-collared, or even Fox sparrows. Thus, the similarity in organization of song among the populations of *P. iliaca* I studied appears to be intermediate between that observed in populations of *Zonotrichia* sparrows and that in Song Sparrows.

Most of the variation in syllable-types among individual Fox Sparrows is minor, which is unique among those passerines which possess complex songs. Over 50% of the individuals analyzed shared approximately 50% of all identified syllable-types. Such sharing of syllable-types among individuals is, of course, surpassed by many emberizids, but in these cases, the song and syllable repertoires are restricted in size. Thorpe and Lade (1961) illustrated the fact that *Emberiza citrinella, E. schoeniclus, E. hortulana, E. bruniceps, E. calandra, Calamospiza melanocorys, Passerculus sandwichensis* (see also Smith 1954), *Ammodramus bairdii, Ammospiza leconteii, Ammospiza maritima, Junco h. hyemalis, J. h. oreganus, Spizella arborea, S. passerina, S. pallida, S. pusilla, Zonotrichia querula,* and *Melospiza georgiana* all possess structurally rigid songs consisting of few syllable-types.

In addition to Song Sparrows, Hartshorne (1956) and Thorpe and Lade (1961) have shown that the Lark Sparrow (*Chondestes grammacus*) and Bachman's Sparrow (*Aimophila aestivalis*) possess "extremely variable songs which result from... random use of a considerable number of phrases" (Thorpe and Lade 1961:252). Other emberizids which also appear to fit this category (i.e., *Calcarius mccownii, Melospiza lincolnii, Calcarius lapponicus, C. pictus, C. ornatus,* and *Plectrophenax nivalis*; Thorpe and Lade 1961) have not been examined thoroughly enough to permit their comparison.

Somewhat intermediate in song structure are the following emberizids (as classified by Storer 1971): Vesper Sparrow (*Pooecetes gramineus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Green-tailed Towhee (*Chlorura chlorura*), Cardinal, Pyrrhuloxia (*Pyrrhuloxia sinuata*), Painted Bunting (*Passerina ciris*), Varied Bunting (*P. versicolor*), Orange-breasted Bunting (*P. leclancherii*), Rose-bellied Bunting (*P. rositae*), Lazuli Bunting (*P. amonea*), Indigo Bunting (*P. cyanea*), and Mexican Junco (*Junco phaeonotus*). Varied, Painted, Indigo, Lazuli, and Orange-breasted buntings (Thompson 1968) and Mexican Juncos (Marler and Isaac 1961) all possess extensive song-type and syllable-type repertoires, but usually do not share any song-types and share only a limited number of syllable-types. Cardinals (Lemon 1965, 1966), Pyrrhuloxias (Lemon and Herzog 1969), Green-tailed Towhees (Burr 1974), and Rufous-sided Towhees (Kroodsma 1971) like-

wise possess large song-type and syllable-type repertoires, but most individuals of these species do share a considerable amount of their total repertoires. Kroodsma (1971) reported 63.5% sharing of songs by neighboring Rufous-sided Towhees in Oregon, although in eastern North America the towhees apparently share fewer song components (Borror 1975).

Song structure in emberizids may be considered as a long continuum of structural complexity. Almost any conceivable form of song, from the simple structure of the Oregon Junco (Konishi 1964a, b) and the Chipping Sparrow (*Spizella passerina*; Borror 1959) to the complex arrangement of the Song Sparrow (Borror 1965; Mulligan 1966), is represented by some member of the family.

Zonotrichia sparrows and some juncos possess limited syllable-type and song-type repertoires. *Passerella* and *Melospiza* (particularly *M. melodia*) are similar in exhibiting large song-type repertoires characterized by rather lengthy and complex arrangements of extensively modulated syllable-types that result in sounds that are both musical and "buzzy" to the human ear. Individual Song Sparrows, however, exhibit a much greater number of song-versions than Fox Sparrows. The songs of *P. iliaca* and *Melospiza* spp. are more similar to each other in structure than either is to those of *Zonotrichia* or *Junco*. The structural simplicity of songs in the Old World *Emberiza* (Thorpe and Lade 1961) is more similar to the New World *Zonotrichia-Junco* assemblage than to *Passerella-Melospiza*.

SUMMARY

Fox Sparrows in northern Utah and southern Idaho began singing shortly after their arrival on the breeding grounds and continued singing until mid-July. The birds possessed a variety of song-types which, owing to their uniformity in structure within and among individuals, I categorized into five major song-types. Each song-type was composed of a series of syllable-types which were defined as the single- or multi-noted sounds, that form the components of particular song-types. I categorized 49 discrete syllable-types in this manner. Sequences of syllable-types composing each of an individual's major song types, although similar enough to be classified as a particular song-type, were not identical. These variants, which were characteristic to individuals, were designated song-versions. Of the 133 birds recorded, 48 possessed at least two song-versions of some major song-type.

The syllable-type sequence of the introductory portion of song-type A, B, C and E was less rigid than the sequence forming the terminal portion. Song-type A, the third most common song-type, consisted of a mean of 7.5 (1973) and 7.7 (1974) syllable-types. It ended in the syllable-type sequence 6, 7, 8, and 9. Song-type B, the second most common song-type, was composed of a mean of 8.5 (1973) and 7.6 (1974) syllable-types. It was most variable with respect to its constituent syllable-types, but generally terminated with the sequence 25, 26, and 27. Song-type C, the song-type most common to Fox Sparrows, consisted of a mean of 7.8 syllable-types in both years. Its terminal sequence was almost always 29, 37, and 28. Song-type D was sung by only 27% of the birds recorded; it consisted of a mean of 9.4 syllable-types in both years. The terminal sequence of song-type D was not as stereotyped as the other song-types, yet it did contain characteristic syllable-types (40, 41, 13 and 21). The least common song-type was designated E. It was composed of a mean of 9.0 (1973) and 7.5 (1974) syllable-types. Its terminal sequence was characteristically 45, 32, 25, and 46.

Little variation was evident in mean size of song repertoires in individuals ($\bar{x}$ = 3.2, 1973; 3.1, 1974), the temporal length of particular song-types, and the duration of the interval of silence between songs. The syllable-types, song-types, song-versions, and sequence of syllable-types composing songs of individual Fox Sparrows did not change between successive utterances of the same song-type, between days or years. Differences in the mean number of syllable-types or the mean number of syllable-types forming individual's specific song-types were insignificant. However, birds with larger song repertoires did possess significantly larger syllable-type repertoires.

Structure of song in Fox Sparrows, although not closely similar to that of any other emberizid, does include attributes characteristic of song in other emberizids. Species of *Zonotrichia* and *Junco* have less diverse song-type and/or syllable-type repertoires than Fox Sparrows, whereas in *Melospiza* (especially *M. melodia*) the repertoires are more complex than in Fox Sparrows. Most Old World sparrows appear to have songs which are structurally much less complex than those of *Passerella*.

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APPENDIX. Number of Fox Sparrows possessing the particular syllable-type sequences forming the versions of song-types A, B, C, D and E in 1973 and 1974. Parentheses indicate the syllable-type may be present or absent. An asterisk indicates those song-versions where some doubt exists as to their proper classification.

No. of birds		
1973	1974	Syllable-type sequence
		Song-type A
8	9	1,2,4,5,6,7,8,9
9	5	1,3,4,5,6,7,8,9
21	11	1,3,5,6,7,8,9
1	2	1,4,14,16,4,6,7,8,9
1	1	4,5,6,7,8,9
1	0	1,2,5,6,7,8,9
2	0	1,10,4,5,6,7,8,9
0	1	1,4,14,4,14,16,6,7,8,9
0	1	1,4,14,5,6,7,8,9
0	2	3,4,5,6,7,8,9
0	1	1,10,17,8,33,3,5,6,7,8,9
0	1	36,44,17,6,7,8,9
0	1	1,36,11,28,6,7,8,9
		Song-type B
1	2	1,10,17,12,49,25,27
4	4	1,4,14,16,20,22,49,25,26,27
1	1	1,4,14,5,20,49,4,26,27
1	1	1,2,3,4,20,49,25,26,27
19	0	1,10,17,12,49,25,26,27
2	0	1,10,17,12,49,25*
1	0	1,10,17,12,24,25,26,27

APPENDIX *Continued*

No. of birds		
1973	1974	Syllable-type sequence
1	0	1,10,17,12,22,49,25,27
2	0	1,10,17,12,22,23,25,26,27
1	0	1,10,17,8,33,22,49,25,27
1	0	1,10,15,49,25,26,27
1	0	1,10,4,14,5,20,49,25,26,27
7	0	1,4,14,5,20,22,49,25,26,27
2	0	1,4,14,5,20,22,26,27
2	0	1,4,14,16,20,49,25,26,27
1	0	1,4,14,16,20,22,25,26,27
1	0	1,4,14,5,20,22,23,25,26,27
1	0	1,4,14,5,20,26,27
1	0	1,4,14,5,20,49,25,26,27
1	0	1,4,14,20,22,49,25,26,27
1	0	1,11,20,22,49,25,27
2	0	1,11,12,22,49,25,26,27
1	0	1,11,34,22,49,25,26,27
1	0	1,2,10,49,20,26,27
1	0	1,2,44,17,28,29*
1	0	1,2,17,12,22*
1	1	1,2,17,12,22,49,25,26,27
1	0	2,17,12,22,49,25,27
2	0	1,3,36,30,28,29*
1	0	1,3,17,12,22,23,25,26,27
1	0	1,3,22,23,25,27
1	0	1,13,20,22,49,25,26,27
1	0	1,12,16,20,22,49,25,26,27
1	0	4,19,10,17,12,22,49,25,26,27
0	1	1,11,17,36,32,33,24,25,49,27
0	1	1,11,31,30,32,33,24,25,49,27

APPENDIX *Continued*

No. of birds 1973	No. of birds 1974	Syllable-type sequence
0	1	1,11,31,11,12,22,24,25,49,27
0	1	1,11,12,22,24,25,27
0	1	1,10,11,12,22,24,25,26,27
0	1	1,10,17,12,22,24,25,26,27
0	1	1,10,26,11,12,22,24,25,26,27
0	1	1,10,11,12,20,24,25,26,27
0	1	1,10,11,12,22,24,25,26,27
0	1	1,10,17,22,24,25,49,27
0	3	1,10,17,22,24,25,49,43*
0	2	1,10,17,12,22,24,25*
0	1	1,10,4,14,5,20,49,25,26,27
0	4	1,4,14,11,20,22,24,25,26,27
0	2	1,4,14,20,22,49,25,26,27
0	1	1,4,14,16,20,22,26,27
0	1	1,4,14,5,12,22,49,25,26,27
0	1	1,4,14,5,20,49,25,26,27
0	1	1,2,17,12,22,24,25,26,27
0	1	1,2,4,12,22,24,25,26,27
0	2	1,2,17,12,22,23,25,26,27
0	1	1,3,36,47,11,28,29*
0	1	1,3,17,12,22,24,25,26,27
0	1	1,12,16,11,20,22,49,25,26,27
0	1	1,26,6,12,22,24,25,26,27
0	1	10,11,12,22,24,25,26,27
0	1	10,17,12,22,23,25,26,27
0	1	2,36,11,28,24,25,26,27
0	2	4,14,11,20,22,49,25,26,27
0	2	4,14,16,12,22,49,25,26,27
0	1	4,13,20,24,25,26,27
0	1	4,14,20,22,49,25,26,27
0	1	4,14,16,20,49,25,26,27
		Song-type C
24	20	1,11,34,35,29,37,38,(39)
3	1	1,11,34,29,37,38,(39)
2	1	1,11,34,37,38
12	13	1,36,11,28,29,37,38
2	1	1,36,31,11,28,29,37,38,(39)
15	5	1,3,36,11,28,29,37,38,(39)
7	4	1,3,36,31,11,28,29,37,38,39
2	2	1,3,44,31,11,28,29,37,38,39
1	3	1,10,36,11,28,29,37,38
1	1	1,10,11,34,35,29,37,38,(39)
1	0	1,10,36,11,30,29,37,38
1	0	1,10,36,11,28,29,37
3	0	1,11,34,26,29,37,38
2	0	1,11,2,20,35,29,37,38
1	0	1,3,36,11,28,37,38,(39)
1	0	1,3,44,47,11,28,29,37,38,39
1	0	1,3,36,47,11,28,29,37,38,39
1	0	1,3,11,34,35,29,37,38,39
1	0	1,13,11,41,48,28,29,37,38

APPENDIX *Continued*

No. of birds 1973	No. of birds 1974	Syllable-type sequence
1	0	25,36,11,34,35,29,37,38
0	3	1,36,11,28,37,38,(39)
0	1	1,36,30,28,37,38
0	1	1,2,36,31,11,28,29,37,38,(39)
0	1	1,30,34,35,29,37,38,39
0	1	1,31,11,41,48,17,24,25,29,37,38
0	1	1,11,30,35,29,37,38
0	2	3,36,11,28,29,37,38
0	1	3,4,5,29,34,35,29,37,38
0	1	30,34,35,29,37,38
0	1	19,11,34,35,29,37,38,39
0	1	10,34,35,29,37,38
		Song-type D
2	1	1,10,40,41(13&21),27,28,24,25,49,43
1	1	1,41,(13&21),13,20,24,25,26,27
1	1	1,21,20,23,25,26,27
1	0	1,10,41,42,28,29,25,49,43
1	0	1,10,41,42,28,24,25,49,43
1	0	1,10,40,41(13&21),27,28
1	0	1,10,40,27,28,24,25,49,43
1	0	1,41(13&21),13,20,29,25,26,27
1	0	1,41(13&21),20,29,25,27
1	0	1,2,10,17,8,33,24,25,49,43*
1	0	1,2,21,13,20,49,23,26,27
1	0	1,3,21,13,20,23,25,26,27
1	0	1,31,11,10,41,29,28,24,25,26,27
0	1	1,10,30,41,48,28,29,25,49,43
0	4	1,10,40,13,21,42,33,24,25,49,43
0	1	1,13,21,20,24,25,35,27
0	2	1,13,21,13,20,49,25,26,27
0	2	1,13,20,49,25,26,27
0	1	1,31,11,10,29,28,24,25,26,27
0	1	1,31,40,41,48,28,24,25,49,37,38
0	1	1,2,10,17,32,33,24,25,49,43*
0	1	1,3,21,13,20,23,25,26,27
		Song-type E
1	0	1,3,44,31,30,29,32,25,46
4	0	1,3,44,31,30,45,32,25,46
1	0	1,3,36,41,30,45,32,25,46
1	0	1,3,36,30,28,29,37,38,32,46
0	1	1,2,44,17,45,18,25,46
0	1	1,2,17,12,44,17*
0	4	1,2,44,17,45,32,25,46
0	1	1,10,44,17,45,32,25,46
0	1	1,3,44,17,45,25,46
0	1	2,17,12,45,32,25,46
0	1	3,44,17,45,32,25,46
0	1	40,17,11,21,46,4,27
0	1	40,48,2,45,32,44,32,46