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THE SONGS AND SINGING BEHAVIOR OF THE RED-EYED VIREO

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ABSTRACT.—An audiospectrographic study of some 12,500 songs of Red-eyed Vireos (*Vireo olivaceus*), from over 46 birds from nine states, provided data on song structure, vocal repertoires, and the birds' use of their repertoires.

These songs have one or more syllables, each syllable consisting of one or more abrupt musical slurs. Each bird has a sizeable repertoire of syllable types, each of which may be used alone and/or with one or more other syllables to produce a number of different song types. The song type repertoires of individual birds ranged from 12 to 117 (average, 39.4). There is relatively little sharing of songs and syllable types among individuals and that which occurs is not always in proportion to the proximity of the birds concerned.

A bird sings its different song types in a varied sequence, and rarely sings the same song type twice in succession; some types in the repertoire are sung frequently, while others are sung only rarely. No correlation was found between the song types sung, or their sequence, and the observable circumstances under which the songs were sung.

Some geographic variation was found in the birds studied, but the significance of this variation is open to question.

A Red-eyed Vireo in an early stage of song development has a very large repertoire of syllable types and uses them in many different combinations; as primary song is developed, some syllables and syllable combinations are perfected and others are discarded. It is probably largely a matter of chance what particular syllable and song types remain in the primary repertoire, but birds may tend *not* to duplicate the song and syllable types of their neighbors.

The Red-eyed Vireo (*Vireo olivaceus*) is one of a number of passerines in which each individual has a repertoire of several to many different songs (song types, song patterns, themes, etc.), which it sings in a varied sequence, rarely, if ever, singing the same one twice in succession. Such singing was described as "immediate variety" by Hartshorne (1956, 1958, 1973), and may be represented ABCDEFG .... This sort of singing occurs, for example, in some other vireos (Borror 1972), the Wood Thrush (*Hylocichla mustelina*; Borror and Reese 1956, Borror 1964), and the Long-billed Marsh Wren (*Cistothorus palustris*; Verner 1975).

My purpose here is to examine the songs and singing behavior of Red-eyed Vireos, and to determine the general features of the songs and the way they are sung. Lemon (1971) made a somewhat similar study, but he was concerned chiefly with the character of the songs and syllables, based on about 500 songs from only two birds; my study is based on considerably more material and it covers some aspects of Red-eyed Vireo singing not treated by Lemon.

METHODS

I studied 53 recordings (containing 12,509 songs), all made by me and in the tape collection of the Borror Laboratory of Bioacoustics, Department of Zoology, Ohio State University. I tape-recorded the songs at 15 inches per second, using a 24-inch parabola; most were made with a Nagra III recorder, but those made before 1960 (birds 30–49) were made with a Magnemite recorder. Forty-seven of the recordings (11,403 songs) represent 45 birds; it is uncertain how many birds are represented by the other five recordings. I numbered the birds individually and designated the five recordings representing an uncertain number of birds as "bird" 115. The birds studied included 2 from Maine, 5 from New Hampshire, 29 (+2 or more) from Ohio, 4 from North Dakota, and 1 each from Montana, Minnesota, Oklahoma, Texas, and Florida. Individuals are referred to in this paper by number; data on each bird are given in Table 1.

Nearly all (about 94%) of the songs studied were graphed (with a Kay Sona-Graph, Model 7029A), as the songs were seldom positively identifiable by ear, even when the recording was played at a reduced tape speed. Song duration was measured to the nearest 0.01 s, and the maximum and minimum pitch was measured to the nearest 0.1 kHz; the time scale was based on the time of the Sona-Graph drum revolution and its circumference, and frequencies were based on a frequency scale put on the graph (by the Sona-Graph) with the songs. Measurements of songs not graphed were recorded as the average of those of other songs of the

TABLE 1. The Red-eyed Vireos studied and their vocal repertoires.

Bird no.	Recording number	Date	State	Locality	No. of songs	No. of song types	No. of syllable types
44	4296	9-VII-59	Maine	Medomak, Lincoln Co.	67	39	56
49	4702	5-VI-60		Webber Pond, Lincoln Co.	64	48	69
114	14123	8-VII-76	New	Durham, Strafford Co.	96	36	46
129	14633	7-VII-77	Hampshire	Durham	857	33	47
130	14634	7-VII-77		Durham	130	31	51
131	14644	9-VII-77		Durham	378	43	60
132	14646	9-VII-77		Durham	243	29	42
30	2539	3-V-57	Ohio	Blendon Woods, Franklin Co.	80	28	39
35	2653	16-V-57		Columbus, Franklin Co.	170	21	26
48	4679	24-V-60		Blacklick Woods, Fairfield Co.	67	24	35
57	6445	8-VI-63		Blendon Woods, Franklin Co.	57	23	38
65	8565	18-VI-66		Lucas Co.	74	26	38
75	9987	6-V-69		Darby Creek Park, Franklin Co.	68	24	34
77	10502	6-V-70		Blendon Woods, Franklin Co.	113	28	42
80	10564	10-V-70		Blendon Woods, Franklin Co.	85	12	19
87	11291	30-V-71		Darby Creek Park, Franklin Co.	107	25	32
104	12889	9-V-74		Shawnee State Forest, Scioto Co.	51	22	32
106	13107	19-VI-74		Mohican State Park, Richland Co.	102	29	46
107	13119	2-VII-74		Darby Creek Park, Franklin Co.	127	26	40
111	13829	2-V-76		Blendon Woods, Franklin Co.	49	30	39
	14289	5-V-77					
	14456	22-V-77					
115[a]	14457	22-V-77		Blendon Woods, Franklin Co.	1,106	194	158
	14473	29-V-77					
	14502	4-VI-77					
116	14289	7-V-77		Shawnee State Forest, Scioto Co.	66	16	29
120[b]	14407	20-V-77		Darby Creek Park, Franklin Co.	101	55	75
121[b]	14408	20-V-77		Darby Creek Park, Franklin Co.	293	94	58
122[b]	14410	20-V-77		Darby Creek Park, Franklin Co.	139	86	104
123	14463	25-V-77		Darby Creek Park, Franklin Co.	326	22	30
136	14798	21-V-78		Darby Creek Park, Franklin Co.	188	23	31
139	14860	20-VI-78		Shawnee State Forest, Scioto Co.	704	38	43
	14865	21-VI-78					
141[b]	15074	8-V-79		Burr Oak State Park, Morgan Co.	474	82	80
142	15079	9-V-79		Burr Oak State Park, Morgan Co.	162	47	60
145[b]	15129	20-V-79		Darby Creek Park, Franklin Co.	314	84	68
147	15134	30-V-79		Darby Creek Park, Franklin Co.	428	73	76
	15141	5-VI-79					
148	15148	3-VII-79		Blendon Woods, Franklin Co.	1,897	25	30
149	15149	8-VII-79		Blendon Woods, Franklin Co.	174	23	32
150[b]	15151	18-VII-79		Blendon Woods, Franklin Co.	1,071	117	82
	15152	20-VII-79					
151	15135	3-VI-79		Clear Creek Valley, Hocking Co.	296	49	55
154[b]	15539	25-V-80		Darby Creek Park, Franklin Co.	220	58	48
89	11374	14-VI-71	North	Kenmare, Renville Co.	100	24	36
126	14577	14-VI-77	Dakota	Kenmare	475	48	60
127	14624	19-VI-77		Medora, Billings Co.	133	41	56
128	14625	19-VI-77		Medora	433	35	39
53	5629	24-IV-62	Texas	Austin, Travis Co.	53	16	25
68	9091	19-VI-67	Montana	Polson, Flathead Co.	72	47	56
81	10892	7-VII-70	Minnesota	L. Itasca State Park, Clearwater Co.	80	26	44
94	11879	19-VI-72	Oklahoma	Hinton, Caddo Co.	100	35	39
134	14712	23-IV-78	Florida	Wakulla Springs, Wakulla Co.	119	30	47
Total					12,509	1,965[c]	2,292[c]

[a] More than one bird is involved here.
[b] Subsong.
[c] Excluding pattern sharing by two or more birds.

same type by that bird. Some averages in this paper are given plus or minus the standard error.

Playbacks (of unmodified song, from a cassette recorder) were occasionally used in the field in order to see what effect they might have on a bird's singing. I did not make a detailed study of the effects of playbacks, and used them only on a few birds from which a large number of songs were recorded; the singing, which was taped, following a playback was the only effect of the playback that was recorded.

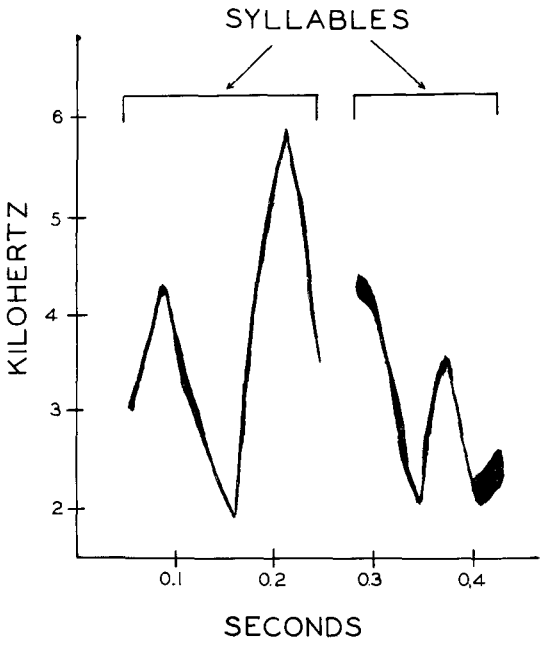


FIGURE 1. Sonogram of a two-syllable song of a Red-eyed Vireo (type B of bird 139). Each syllable here contains four slurs.

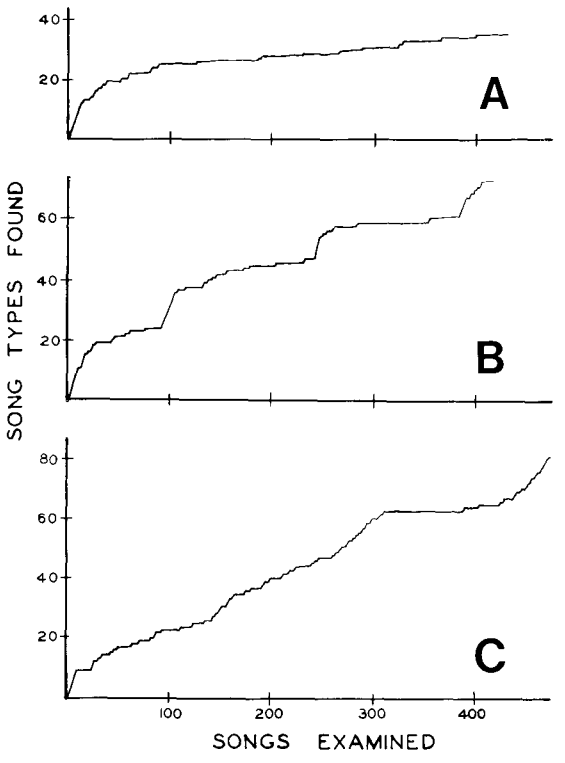


FIGURE 2. Graphs for three birds showing the number of song types found after varying numbers of songs had been examined. (A) Bird 128. (B) Bird 147. (C) Bird 141.

THE NATURE OF RED-EYED VIREO SONGS

The songs of a Red-eyed Vireo (Figs. 1 and 3–71) consist of one or more short syllables (termed "elements" by Lemon 1971), each syllable containing one or more slurs. The slurs in a syllable are usually connected; slurs separated by more than 0.01 s were considered to be in separate syllables. The syllables of a song are usually only a few hundredths of a second apart; syllables more than 0.3 s apart were considered separate songs.

Most slurs are relatively abrupt; rarely a portion of a syllable (up to about 0.03 s in length) may be steady in pitch. Rarely also a short portion of a syllable may show frequency modulation, but never enough to give the syllable a burry quality; the songs have a musical quality.

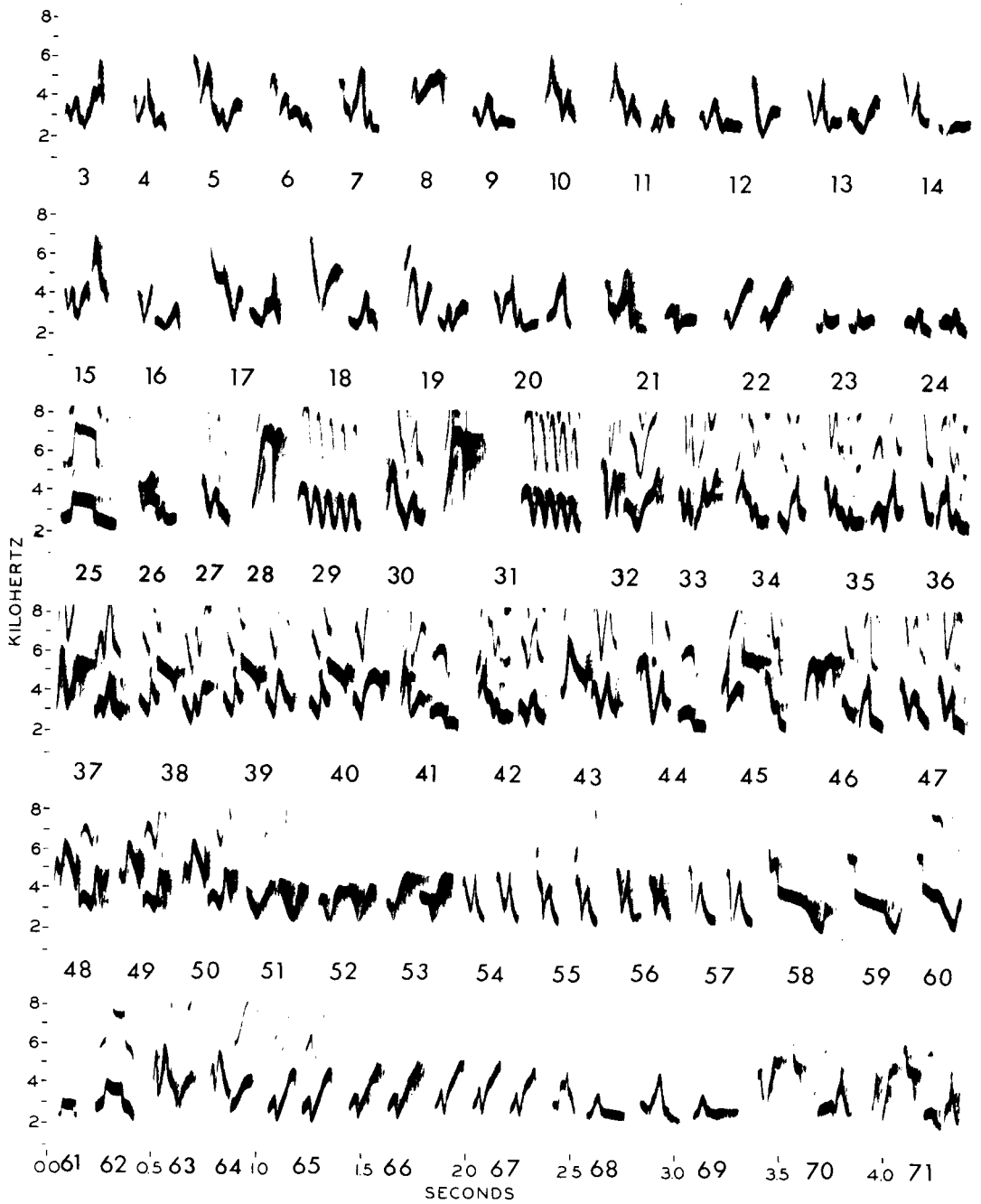
Each bird has a sizeable repertoire of syllables, which are used alone and/or in combination with one or more other syllables to form a number of different song types; a song type is thus a particular syllable, or combination of syllables. Some syllables are used in only one song type, while others are used in two or more. A syllable used in two or more song types is not always in the same part of the song: it may be the first syllable in one song type, and the second syllable in another. In songs with two or more syllables the syllables are usually different; occasionally one or two of the syllables may be repeated in a given song type.

Some characters of the songs studied are summarized in Table 2. I found a great deal of variation in these songs: sometimes the songs of different birds in the same area differed significantly in some features of their songs. For example, two North Dakota birds (birds 127 and 128), recorded about 150 yards apart on the same day, had average song lengths of 0.33 ± 0.01 and 0.44 ± 0.01 s. About 60% of the songs had their highest pitch near the beginning of the song; this percentage was higher (up to about 80%) in songs of three or more syllables.

The songs studied contained from one to five syllables, but songs of four and five syllables were relatively rare. Of the 12,509 songs studied, 2,249 contained one syllable, 7,980 contained two, 2,003 contained three, 245 contained four, and 32 contained five syllables; only 2.2% of the songs contained four or five syllables.

VOCAL REPERTOIRES

A Red-eyed Vireo has many different song types in its repertoire, but it is impossible to determine by ear how many types are



FIGURES 3–71. Sonograms of Red-eyed Vireo songs. *3–24*, the song types of bird 123; *25–47*, the song types of bird 136; *48–50*, three renditions of a song type by a bird in primary song (type B of bird 132); *51–53*, three renditions of a song type by a bird in subsong (type U of bird 150); *54–57*, a two-syllable song, the syllables alike, shared by four Ohio birds (birds 111, 77, 57, and 48) (the song of Fig. 47 is of this same type); *58–60*, a one-syllable song shared by a bird in New Hampshire (bird 114), one in central Ohio (bird 107), and one in Montana (bird 68); *61–62*, a one-syllable song shared by a bird in Ohio (bird 106) and one in North Dakota (bird 89) (the song of Fig. 25 is of this same type); *63–64*, a one-syllable song shared by a bird in Maine (bird 44) and one in North Dakota (bird 89); *65–66*, a two-syllable song, the syllables alike, shared by a bird in North Dakota (bird 89) and one in Ohio (bird 106) (the song of Fig. 22 is of this same type); *67*, a three-syllable song by an Ohio bird (bird 48), the syllables of the same type as those in Figs. 22 and 65–66); *68–69*, two two-syllable songs that are similar, by an Ohio bird (bird 111) and an Oklahoma bird (bird 94); *70–71*, two three-syllable songs that are similar, by two Ohio birds about 60 mi apart (birds 57 and 106).

TABLE 2. Characteristics of Red-eyed Vireo songs.

Character			Primary song	Subsong	All song
Number of birds[a]			38	7	45
Number of songs[b]			9,897	2,616	12,509
Song types per bird[a]		Range	12–73	55–117	12–117
		Aver. ± SE	31.4 ± 1.9	82.3 ± 8.0	39.4 ± 3.4
Syllable types per bird[a]		Range	19–76	48–104	19–104
		Aver. ± SE	42.6 ± 2.1	73.6 ± 6.9	47.4 ± 2.6
Song duration (s)		Range	0.07–0.83	0.07–1.06	0.07–1.06
		Aver. ± SE	0.32 ± .002	0.34 ± .002	0.32 ± .002
Minimum kHz		Range	1.5–3.6	1.8–4.5	1.5–4.5
		Aver. ± SE	2.3 ± .003	2.3 ± .01	2.3 ± .003
Maximum kHz		Range	2.9–8.5	3.2–8.4	2.9–8.5
		Aver. ± SE	5.5 ± .01	5.8 ± .02	5.6 ± .01
Syllables per song		Range	1–5	1–5	1–5
		Aver. ± SE	2.0 ± .01	2.1 ± .01	2.0 ± .01
Slurs per syllable		Range	1–17	1–9	1–17
		Aver. ± SE	3.7 ± .04	3.5 ± .06	3.7 ± .03
Song types in which a syllable occurs[a]		Range	1–8	1–15	1–15
		Aver. ± SE	1.4 ± .04	2.4 ± .2	1.6 ± .1
Percent of the syllables occurring in only one song type[a]		Range	42.9–94.7	37.5–72.0	37.5–94.7
		Aver. ± SE	73.4 ± 2.0	51.7 ± 4.9	70.0 ± 2.2
Percent of the songs with syllable repetition	2-syll.	Range	0–26.9	0–13.8	0–26.9
		Aver.	9.6	7.1	9.0
	3-syll.	Range	0–100	0–75.0	0–100
		Aver.	24.7	24.6	24.7
	4-syll.	Range	0–100	0–88.9	0–100
		Aver.	60.8	71.6	64.1
	5-syll.	Range	100	0–100	0–100
		Aver.	100.0	61.5	84.4
Songs per minute		Range	28.7–71.3	27.9–47.4	27.9–71.3
		Aver.	42.7	33.2	40.3
Percent of the bout consisting of song		Range	15.2–38.3	14.2–28.8	14.2–38.3
		Aver.	22.6	19.0	21.7

[a] Excluding "bird" 115.
[b] Including "bird" 115 (with 1,106 songs).

sung in a given bout. Very few of the songs are recognizable in the field; most of them must be rendered into audiospectrograms before one can determine the bird's repertoire. The several renditions of a particular song type (in primary song) are practically identical (Figs. 48–50), and it is generally easy to determine from the diagrams how many different types are sung, even though two or more types are sometimes very similar.

I made graphs for each bird (like those in Fig. 2) showing the number of song types found after varying numbers of songs had been examined. Most (all but 12) of these graphs (e.g., Fig. 2A) rose sharply at first, then leveled off, thus resembling graphs by some other workers (e.g., Kroodsma 1975 and Verner 1975). Some, however, were a little different, and of two general types: (a) like those just described but with a second abrupt rise followed by a leveling off, and sometimes with a third such rise (Fig. 2B), or (b) rising continuously, with little or no indication of a leveling off (Fig. 2C). The figures for five of the birds studied (birds 77, 114, 127, 142, and 148) were like those in Figure 2B; in one of these (bird 148: Fig. 2B) the second and third rises came after playbacks, but in the others I noted nothing that might have produced the second rise. The graphs for seven birds (birds 120, 121, 122, 141, 145, 150, and 151) were like that shown in Figure 2C; I believe that these birds were uttering subsong.

Data on the number of song and syllable types found in each bird are given in Table 1. I found considerable variation in the size of the vocal repertoires of these birds—from 12 to 117 (average, excluding "bird" 115, 39.4) song types and 19 to 104 (average, excluding "bird" 115, 47.4) syllable types. For birds in primary song, the repertoires ranged from 12 to 73 (average, 31.4) song

types and 19 to 76 (average, 42.6) syllable types.

A Red-eyed Vireo with 43 syllable types (about the average of birds in primary song) could, if it used every possible combination of 1, 2, and 3 syllables (and with the percentages of types with syllable repetition indicated in Table 2), make up over 100,000 different song types. Since these birds average only about 31 song types, it is obvious that only a very small percentage of the possible song types are actually sung.

Most of a bird's syllable types were used in only one song type; the rest were used in from 1 to 15 song types (Table 2). Syllable use varied somewhat among individuals but primary song and subsong differed significantly in this respect. The numbers of song and syllable types were significantly correlated in primary song ($r = .9292$, $n = 38$, $t = 15.0910$, $P < .001$) but not in subsong ($r = .3448$, $n = 7$, $t = .8215$, $P = .5 - .4$), and the syllables of birds in subsong were used in significantly more song types than those of birds in primary song (Table 2). In primary song, new song types were more likely to be made of new syllable types, while in subsong new song types were more likely to be types with different syllable combinations.

The different song types in a vireo's repertoire were not sung with equal frequency, some being sung very often, and others only rarely. In the largest sample studied (bird 148, with 25 song types in 1,897 songs) the incidence of the different types ranged from 2 to 200; five of the song types were sung only 2–4 times, two others were sung 13 and 14 times, and the rest were sung 23 or more times. In the second largest sample of primary song (bird 129, with 857 songs), 10 of the 33 song types were sung only once or twice, and the rest from 19 to 56 times. In the birds from which the largest samples were studied, and probably in most birds, 95% of the songs represented about two-thirds of the song types, with a third of the song types making up only 5% of the songs.

The incidence of the different syllables of a bird's repertoire was much like that of its song types; some were used in many songs, and others were used in only a few. In bird 148, for example, the least common syllable occurred in only 13 songs; in bird 128 (433 songs, of 35 types, with 40 syllable types) the least common syllable occurred in only one song.

The "rare" song types in a bird's repertoire were sometimes those consisting of a single syllable that was usually found in a song type with one or more other syllables, and hence might be considered incomplete songs (the five rarest song types of bird 148 were such one-syllable songs); other "rare" song types contained syllables not found in other song types. It is possible that these "rare" song types may be sung more often under certain circumstances, or at other times in the life of the vireo. The repertoires of many birds contained one or a few song types that might be considered somewhat atypical of the species (e.g., Fig. 29); such songs were not necessarily the most or the least common used by the bird.

The graphs (e.g., Fig. 2B) indicate that under certain circumstances (such as the presence of another bird), or for no apparent reason, a bird may suddenly introduce a number of song types it had not used previously, and sing rarely or not at all some types previously sung. On the other hand, some birds do *not* introduce new song types in the presence of another bird; playbacks were used in obtaining the recording of bird 148, but this bird did not introduce new song types after the playbacks.

Samples of a few hundred, or even thousand, songs may not yield a Red-eyed Vireo's complete repertoire, or tell fully how that repertoire is used. It would be instructive to have many thousands of songs from an individual, sung under different circumstances and throughout the bird's life.

TABLE 3. Vocal pattern sharing in five New Hampshire birds.[a]

Birds sharing	Distance apart	No. of syllable types shared	No. of song types shared
129 and 130	100 yd.	8	4
114 and 129	2 mi	5	0
114 and 130	2 mi	4	0
114 and 132	2½ mi	2	0
129 and 132	4 mi	6	2
130 and 132	4 mi	4	1
114 and 131	5 mi	13	0
131 and 132	6 mi	9	3
129 and 131	7 mi	9	1
130 and 131	7 mi	13	3

[a] The vocal repertoires of these birds are given in Table 1. Some song and syllable types are involved in two or more lines of this table.

SHARING OF SONG AND SYLLABLE TYPES

The determination of vocal pattern sharing is complicated by the large number of vocalizations to compare; excluding sharing, I found 1,965 song types and 2,292 syllable types in the recordings studied (Table 1). Comparing all of these would require nearly 4 million comparisons of song types and

TABLE 4. Song and syllable type sharing by four North Dakota birds.[a]

Birds sharing	Number of syllable types shared	Number of song types shared
Two Kenmare birds only	3	0
Two Medora birds only	8	1[b]
One Kenmare bird and one Medora bird	10	2[c]
Both Medora birds and one Kenmare bird	8	0
Both Kenmare birds and one Medora bird	1	0
All four birds	1	0

[a] Data on recording localities and dates, and the vocal repertoires of each bird, are given in Table 1.
[b] A two-syllable song, the syllables alike.
[c] One-syllable songs.

TABLE 5. Song and syllable type sharing in three central Ohio birds.[a]

Birds sharing	Number of syllable types shared	Number of song types shared
148 and 149 only	1	0
148 and 150 only	8	1[b]
149 and 150 only	3	2[c]
All three birds	2	0

[a] Data on the recording localities and dates, and the vocal repertoires of each bird, are given in Table 1.
[b] A one-syllable song.
[c] One a one-syllable song, the other of two different syllables.

about 5¼ million comparisons of syllable types. I have not attempted to compare all the song and syllable types found, but have compared some from different areas and all from a few areas. I considered the vocalizations of different birds to be the same type if they differed no more than those of a given individual; this excludes the many cases of vocalization types that were very similar and would sound alike to the human ear (e.g., Figs. 68–69 and 70–71).

An interesting finding was the *difference* in the songs and syllables of different birds. I found no two birds with identical vocal repertoires, and sometimes birds fairly close together (e.g., birds 87 and 107, recorded one-fourth mile apart) did not share *any* song or syllable types.

NEW HAMPSHIRE BIRDS

Five recordings were made in or near Durham, New Hampshire: birds 114, 129, 130, 131, and 132 (Table 1). The sharing of song and syllable types by these vireos is summarized in Table 3.

Ten song types were shared by two or more of these birds: eight by two birds, and two by three birds; the number of song types shared and the distance between the birds were not strongly related. Forty-three syllable types were shared by these birds: 31 by two birds, 10 by three birds, and 2 by four birds; birds farther apart shared more than those close together.

NORTH DAKOTA BIRDS

Four recordings were made in North Dakota, two (birds 127 and 128) near Medora and two (birds 89 and 126) near Kenmare. The two Medora birds were recorded the same day, about 150 yards apart; the two Kenmare birds were recorded about four miles (and six years) apart. Kenmare and Medora are about 150 miles apart. Data on the repertoire sizes of these birds are given in Table 1, and data on song and syllable type sharing are given in Table 4.

The Medora birds shared more than the Kenmare birds, possibly owing to their greater proximity in time and space. These vireos shared more syllable types than song types. In Medora there was as much (bird 127) or more (bird 128) sharing with a local bird than with a bird 150 miles away, but in Kenmare the situation was reversed; there was more syllable sharing with a bird 150 miles away than with the other bird in that area.

OHIO BIRDS

Two Ohio birds (123 and 136), recorded about one-fourth mile (and one year) apart and with similar-sized vocal repertoires (see Table 1 and Figs. 3–47), shared only three syllable types, one of which was used alone as a song by each bird (Figs. 10 and 30). The other two shared syllables were used in two-syllable songs: the second syllable in Figure 11 and the second one in Figure 37, and the second syllable in Figure 17 and the second one in Figure 34. Three of the Ohio birds (148, 149, and 150) were recorded in a period of three weeks in the same woods, with the most widely separated birds being about 150 yards apart (Table 5).

The vocal pattern sharing in these Ohio birds involved more syllable types than song types; at most only three song types, and 10–37% of their syllable types, were shared with nearby birds.

BIRDS FROM VARIOUS AREAS

I examined seventeen birds from various areas for vocal pattern sharing: 10 from Ohio (birds 35, 48, 57, 77, 80, 87, 104, 106, 107, and 111), 2 from Maine (birds 44 and 49), and 1 each from New Hampshire (bird 114), Texas (bird 53), Oklahoma (bird 94), North

TABLE 6. Syllable sharing in 17 Red-eyed Vireos.

Distance apart	Instances of syllable sharing
30 mi or less	53
100–200 mi	25
350–900 mi	61
1,000–1,500 mi	29
1,540–2,000 mi	41

Dakota (bird 89), and Montana (bird 68). Not counting sharing, these comparisons involved 485 song types and 677 syllable types. Birds 125 and 130 (song types shown in Figs. 3–47) were not included in these 17 birds, but they shared some song types with one or more of the 17 birds (cf. Figs. 22 and 65–66, 25 and 61–62, and 47 and 54–57).

Seven song types (involving 3.1% of the types in the 17 birds) were shared by two or more birds:

1 (of two similar syllables) by four birds in central Ohio (Figs. 54–57)
1 (of one syllable) by three birds: in Montana, central Ohio, and New Hampshire (Figs. 58–60)
3 (of one syllable) by two birds each: North Dakota and Ohio (Figs. 61–62); Texas and Oklahoma; and Maine and North Dakota (Figs. 63–64)
1 (of two similar syllables) by a bird in North Dakota and one in Ohio (Figs. 65–66); another Ohio bird had a song type consisting of three of these same syllables (Fig. 67)
1 (of two different syllables) by the two Maine birds (about two miles apart).

There were five instances in these 17 birds of two individuals with very similar (but not quite identical) song types—four consisting of two different syllables: Ohio and Oklahoma (Figs. 68–69), Ohio and New Hampshire, Ohio and Maine, and Maine and North Dakota; and one consisting of three different syllables: two Ohio birds about 60 miles apart (Figs. 70–71).

Eighty syllable types (involving 37.9% of the types in these birds) were shared by two or more birds: 34 by two birds, 23 by three birds, 10 by four birds, 7 by five birds, 3 by six birds, and 3 by seven birds. The instances of syllable sharing by birds different distances apart are summarized in Table 6.

The songs of the foregoing birds represent only a very small sample of the songs of the Red-eyed Vireo, but the conclusions regarding vocal pattern sharing in these birds may be valid for the species. There is more sharing of syllable type than song type and the amount of sharing is not proportional to the distance between the birds. Vireos some distance apart may share more than those closer together. There is very little sharing of song type, even by birds in the same area, and most of the song types shared are either one-syllable songs or two-syllable songs with the syllables alike.

THE USE OF THE VOCAL REPERTOIRE

In a species capable of singing songs of more than one type, it is conceivable that the different types may be used in different circumstances. In a species such as the Red-eyed Vireo, where each individual has a fair-sized repertoire of song types that are sung in a varied sequence, it may be that the sequence as well as the song types involved reflect the circumstances.

Many species of passerines, in several families, have more than one song type, but in most cases the significance of the different types is not well understood. Some wood warblers have two different song types, one of which is used primarily in sexual situations and the other in aggressive situations (Morse 1966, 1967). Verner (1975), working with the Long-billed Marsh Wren, did not associate song types with circumstances, but suggested that even one song in a sequence might indicate particular circumstances.

The songs of a Red-eyed Vireo are sung in a varied sequence. For example, the first 25 songs recorded from bird 148 were as follows: A-B-C-D-E-F-B-G-H-D-E-I-J-A-D-H-E-K-B-L-M-E-N-A-D; similar sequences were sung throughout all the recordings. This method of singing appears to be a species-specific feature; a Red-eyed Vireo never sings the same song over and over (as do many other passerines), and only very rarely sings the same song twice in succession. A tape recording that I made of a single song type (considered typical), putting the songs at the rate of 40 per minute, did not sound like a Red-eyed Vireo (to me, or to other people who listened to it); and playbacks of this tape to Red-eyed Vireos in the field elicited no apparent reaction from the birds who heard it.

The numbers of songs between successive utterances of each song type were counted in the recordings studied. The figures obtained were determined only for those song types uttered two or more times in a continuous series of songs, and they may not represent the maximum number by

TABLE 7. Song transition data for six Red-eyed Vireos.

	Bird number						All six birds
	123	126	128	129	139	148	
Number of songs studied	326	475	433	857	704	1,897	4,642
Number of song types (n)	22	48	35	33	38	25	201
Number of possible different transitions (n^2)	484	2,304	1,225	1,089	1,444	625	7,171
Number of transitions present (T)	324	467	432	846	699	1,883	4,651
T/n^2	.67	.20	.35	.78	.48	3.0	.65
Number of different transitions found	188	327	245	305	373	310	1,748
Percent of the possible transitions that were found	38.8	14.2	20.0	28.0	25.8	49.6	24.4

the bird. The longest continuous series in my recordings contained 433 songs (bird 128); the most separated utterances of any song type in this series had 260 songs of other types between them, but the last song type found was in song 400 (and was not repeated in the rest of the recording), which means that there could have been at least 399 songs between successive utterances of this type.

The numbers of intervening songs (called "recurrence numbers" by Kroodsma 1975, and others) in the recordings studied ranged from 0 to 260. They did not vary consistently through a series of songs, as Kroodsma (1975) found for the Rock Wren (*Salpinctes obsoletus*), nor was any special sequencing present such as Verner (1975) found for the Long-billed Marsh Wren. These numbers varied considerably in the Red-eyed Vireo, not only for songs of different types but also for songs of a given type. For example, for the six most common song types of bird 148 the ranges of these numbers were 1–43, 0–27, 2–32, 2–37, 0–60, and 2–38, and for the four least common song types for which at least three numbers were available the ranges were 2–96, 4–149, 7–42, and 3–137. The averages were generally lower for the more commonly sung song types, but sometimes common song types were sung far apart and rarer types were sung close together.

I found only 13 instances of a given song type being sung twice in succession, five in primary song and eight in subsong. In some of the cases in primary song the silent interval preceding the second song was longer than usual, and in some of the cases in subsong the two songs were a little different but enough alike to be considered the same type. Successive songs by a Red-eyed Vireo are almost always of different types.

The sequences of song types sung by a Red-eyed Vireo, where successive songs are nearly always different and a given type is repeated after varying numbers of intervening songs, is sometimes referred to as stochastic variation; certain statistical procedures have been developed for studying such sequences (e.g., Isaac and Marler 1963, Altmann 1965, Chatfield and Lemon 1970, Slater and Ollason 1972, Maurus and Prusche 1973, Morgan et al. 1976, Dobson and Lemon 1977, Cane 1978, and Smith et al. 1978).

The two-song transitions by the six birds in primary song from which the most songs were recorded were tabulated in cluster analysis tables, and some data from these tabulations are summarized in Table 7. For only one of these birds were there more transitions present than there were possible different ones (three times as many); for the other five birds there were .20 to .78 times as many (T/n^2 in Table 7). If all the possible transitions in these birds occurred with equal probability we would expect to find about two-thirds of them; actually, I found less than one-fourth.

If the transitions occur at random, the expected number of instances of a given transition, e.g., A to B (e_{A-B}) may be calculated by the formula:

$$e_{A-B} = \frac{\text{number of transitions from A} \times \text{number of transitions to B}}{\text{total number of transitions}}$$

The numbers of different transitions found in the six birds represented in Table 7 varied from none to considerably more than would be expected if the transitions were random. A sample of these figures—the expected and observed transitions from one song type of bird 148—is given in Table 8. The incidence of 7 of the 25 different transitions in Table 8 was significantly different from the expected, higher in two and lower in the other five; the two occurring

TABLE 8. Number of transitions from song type D by bird 148.

Transition	Expected[a]	Found	P[b]
D-A	21.03	32	near .01
D-B	16.89	11	
D-C	8.71	11	
D-D	21.14	1	<.001
D-E	20.92	71	<.01
D-F	11.05	6	
D-G	6.16	1	<.05
D-H	16.99	19	
D-I	7.22	4	
D-J	17.42	17	
D-K	8.28	1	<.01
D-M	6.48	0	<.01
D-N	8.39	7	
D-O	6.48	1	<.05
D-P	1.27	0	
D-P′	1.59	3	
D-Q	7.54	7	
D-Q′	0.21	0	
D-R	4.46	2	
D-S	0.42	1	
D-T	4.12	2	
D-U	2.44	1	
D-V	0.21	0	
D-W	0.32	0	
D-X	0.21	2	

[a] If all transitions occurred at random.
[b] The probability, if transitions were random, of getting the observed number of transitions (as determined by chi square tests); *P* values not given are above the 0.05 level.

significantly more often (D-A and D-E) made up over half (103 of the 200) of the transitions from this song type. Most transitions appear to be at random, but apparently a few are not.

Smith et al. (1978) found certain song type sequences of the Yellow-throated Vireo (*Vireo flavifrons*) correlated with certain activities of the bird. I have found no such correlation in the Red-eyed Vireo. In my recordings, if the incidence of a particular transition was relatively high, this transition occurred throughout the recording, not significantly more or less often following playbacks, or along with particular observable activities of the bird.

SINGING RATE

The singing rate in passerine birds is subject to both inter- and intraspecific variation. In most passerines it varies from about 3 songs per minute (e.g., in the Ovenbird, *Seiurus auricapillus*) to 60 or more per minute (e.g., in the Red-eyed Vireo), and is sometimes a useful character for distinguishing species in the field by their songs. Within a species the rate may be influenced by the reproductive state of the bird, its state of aggression, and other factors (see Hartshorne 1973 for a summary on this point).

Singing rates in this study were calculated from average cadences in song series, and found to vary from 27.9 to 71.3 (average, 40.3) songs per minute (Table 2). The highest rate was found in an Oklahoma bird (bird 94), and the lowest in an Ohio bird (bird 150) believed to be in subsong. No significant change in singing rate was noted

TABLE 9. Comparison of Red-eyed Vireo songs from different areas.[a]

Character		Ohio	N.H. and Me.	N.D. and Mont.
Number of birds		23[b]	7	5
Number of songs		6,497[b]	1,835	1,213
Song duration (s)	Range	0.07–0.78	0.07–0.64	0.15–0.83
	Aver. ± SE	0.31 ± .002	0.31 ± .002	0.37 ± .004
Song types per bird[c]	Range	12–73	29–48	24–48
	Aver. ± SE	28.8 ± 2.8	37.0 ± 2.6	39.0 ± 4.4
Syllable types per bird[c]	Range	19–76	42–69	36–60
	Aver. ± SE	38.5 ± 2.6	53.0 ± 3.5	49.4 ± 4.9
Syllables per song	Range	1–5	1–4	1–5
	Aver. ± SE	1.95 ± .01	2.13 ± .02	2.18 ± .02
Song types in which a syllable is used[c]	Range	1–8	1–7	1–8
	Aver. ± SE	1.36 ± .05	1.43 ± .09	1.65 ± .12
Total songs of 2–5 syllables		5,177	1,538	956
Songs of 2–5 syllables with syllable repetition		688	239	142
Percent of the 2- to 5-syllable songs with syllable repetition[d]		13.3	15.5	14.9
Average singing rate in songs per minute		39.7	50.9	47.3

[a] Primary song only; most averages are given plus or minus the standard error.
[b] Including "bird" 115 as one bird (with 1,106 songs).
[c] Excluding "bird" 115.
[d] A chi square test of these figures gives a *P* value of a little over .05, hence these differences in percentages cannot be considered significant.

following playbacks. My data do not provide much information on the factors influencing singing rate in this vireo, though my observations indicate that moving about or feeding during singing generally results in a longer silent interval between songs.

The Red-eyed Vireo is usually considered a "continuous singer," which Hartshorne (1973) defined as a bird in which 50% or more of the total time of a singing bout consists of song. In my sample this percentage varied from 14.2 to 38.3 (average, 21.7) (Table 2), a much smaller percentage than 50%, and would in most cases be what Hartshorne described as a "semicontinuous singer"; when the percentage is 20% or less, as it was in 11 of my birds (all from Ohio), he termed the bird a "discontinuous singer."

GEOGRAPHIC VARIATION

Some of the differences found in songs from different parts of the United States are given in Table 9. Red-eyed Vireos in the Northeast (Maine and New Hampshire) and Northwest (North Dakota and Montana) had larger vocal repertoires and more syllables in their songs than those in Ohio. Northwestern birds had longer songs and used their syllables in more song types than birds in Ohio and the Northeast. Singing rates averaged lower in Ohio than in the Northeast or Northwest. The significance of the geographic differences is unclear because of the small numbers of birds involved—whose songs may or may not be representative of the songs in their areas. I have found no evidence of local dialects.

SONG DEVELOPMENT

The singing of the seven birds studied that were believed to be in subsong (see Table 1) has implications regarding song development in this vireo; some differences between primary song and subsong are shown in Table 2. The song and syllable types of the birds in subsong varied more than in the other birds (Figs. 51–53), and it was sometimes difficult to distinguish between one song or syllable type and the next. Graphs for these seven birds showing the number of song types found after varying numbers of songs had been examined (e.g., Fig. 2C) rose continuously, with little or no indication of a leveling off.

All the birds believed to be in subsong were recorded in Ohio, and all but one was recorded May 25 or earlier (about a month after the species arrives in this part of the country), making it appear that song development is a prolonged process. One of the birds in subsong (bird 150) was recorded July 18–20, when two nearby birds (birds 148 and 149) were in primary song; this may have been a bird of the year.

Red-eyed Vireos apparently tend to utter syllables containing one or more slurs, and use these syllables singly or in combination with one or more other syllables to produce individual songs. The syllables vary at first but become more stereotyped as song development continues. A bird in subsong appears to try various syllable combinations, but eventually discards some of them and perfects others. It may be largely a matter of chance which particular syllables and syllable combinations remain in the primary repertoire, but—in view of the small amount of local song and syllable type sharing—there may be a tendency *not* to duplicate the vocalizations of nearby birds, a tendency that may be responsible for the lack of local dialects. The variability in the singing of this vireo is one of its most distinctive features.

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RECENT PUBLICATIONS

The Age of Birds.—Alan Feduccia. 1980. Harvard University Press, Cambridge, Mass. 196 p. $20.00. This is a book about the evolution of birds, intended for readers at the *Scientific American* level and above. Starting with *Archaeopteryx* and its ancestors, it examines the evolution of flight and of flightlessness, and the histories of avian orders. Cognate subjects, such as anatomy, historical geology, and the methods of paleontology, are introduced where necessary. "Some of the ideas expressed . . . are new ones that have not yet withstood the test of time, but [the author's] aim has been to provide the reader with more than the static dogma of the past century." The text is written in a clear and interesting style and it is illustrated with many drawings and photographs. Altogether a model of scientific exposition and a fine overview of present knowledge and theories about the fossil history of birds.

Voices of New World Nightbirds: Owls, nightjars, and their allies.—Compiled, narrated, and produced by John William Hardy. 1980. 33⅓ rpm phonograph record, ARA-6. ARA Records and Bioacoustic Laboratory and Archive, Florida State Museum. Source: ARA Records, 1615 N.W. 14th Ave., Gainesville, FL 32611. Being largely nocturnal, owls, nightjars, and their allies rely on voice as a means of communication more than other birds. For the same reason, their voices are often the only sign of their presence. As an aid to the detection, identification, and study of these birds, Hardy presents this collection of recordings of 75 species from the Americas. That so many of these elusive birds have been recorded is a remarkable accomplishment and a tribute to Ben B. Coffey, Jr. and the other diligent recordists. The cuts are arranged in taxonomic order and are each announced by name only. Locality, date, and recordist for each cut are listed on the album cover.