

A NUMERICAL APPROACH TO THE ANALYSIS OF SOLITARY VIREO SONGS

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ABSTRACT.—Cluster and principal components analyses were used to represent the variation in Solitary Vireo digitized notes and song compositions. These vireos utter highly stereotyped notes which they sequence as a quasi-periodic Markov chain. Birds from the same locality sing similar compositions of note types, but vary among individuals in the morphology of their notes. Learning is probably important in the development of Solitary Vireo songs and individuals incorporate small changes in their notes.

Songs of the Solitary Vireo (*Vireo solitarius*) consist of long sequences of separate notes, sung at the rate of 20 to 30 notes per minute, with no obvious superstructure. Many of the species in *Vireo* have songs of similar gross organization, but in others, several notes are coupled together forming discrete songs. Even for Solitary Vireos, notes from eastern and western populations are conspicuously different (Borror 1972). Vireos could be an extremely interesting group for studies of the evolution of vocal behaviors, but their songs are difficult to analyze by standard sound spectrographic techniques (for example, Lemon [1971] was able to detail the repertoires of only two individual Red-eyed Vireos, *V. olivaceus*). Vireo songs are well suited for analysis with computerized pattern recognition schemes. I have been studying some of the statistical tools useful for this new approach to bird vocalizations. In the interests of repeatability and rigor, I have employed methods by which large samples of songs from many different individuals and species can be numerically compared.

In this paper, I apply cluster and principal components analyses to digitized sound frequencies, comparing Solitary Vireo notes within and among individuals from several localities in eastern North America. I compare song compositions on the basis of probability vectors of note occurrence, and show that sequencing of the notes can be represented as a Markov process. I then discuss several issues of methodology and speculate on the divergence of Solitary Vireo songs.

METHODS

All field work was performed from 3 May to 10 June 1976. With a Nagra IV-S recorder and Sennheiser MD211 U microphone mounted in a 40-cm metal parabola, I recorded Solitary Vireos in six localities in the Appalachian Mountains, ranging from Tennessee to

Maine. Some localities were represented by two or three study areas, as summarized in Table 1. Birds were recorded from south to north as spring progressed in order to minimize the possible effects of seasonal variation (see King 1972). All birds in a single area were within 1.5 km of each other. Each bird recorded was a territory holder in the early stages of nesting (stages 1 and 2 of Rice 1978; see also James 1978).

Throughout this report, "note" refers to a continuous trace of sound through time. A long sequence of notes (standardized for analysis at 100 notes) is a "song." Solitary Vireo notes are typically less than half a second in duration (mean = 0.34 s, SD = 0.07, n = 105 notes), and sung at a mean rate of 25.9 notes/min (SD = 6.9, n = 2,900 notes). Compound notes contain subunits separated by a very short break (less than 0.15 s). If the subunits occurred alone, I considered them to be separate notes, but if they occurred only when coupled, I defined the compound as a unique type.

Frequency spectrum analysis of about 3,500 Solitary Vireo notes was performed at the State University of New York at Stony Brook. I analyzed the tapes at one-quarter or one-half speed with a Spectral Dynamics SD301C Real Time Analyzer coupled to a storage oscilloscope. All the notes were stopped on the oscilloscope screen while I studied or measured them. I photographed each perceptibly different frequency trace, and used the 200 resulting photographs to establish classes for the notes in my sample of songs. Without knowledge of the individual or geographic origin of the notes, I grouped the photos into categories which I could visually recognize on the oscilloscope screen. I used a classification of 35 types (Fig. 1) to categorize all the notes in my sample. As discussed below, I found variation within each category, and I sometimes encountered intermediates. My note assignments were consistent and repeatable, however, as a reanalysis of several songs has shown.

I numerically characterized songs as probabilities of occurrence (i.e., the proportion) of each possible note type in a long sequence. For this, samples of 100 notes from each bird were used, since sampling effort curves (Fig. 2) indicated that such a sequence would adequately encompass the repertoires of these vireos. Where large samples were available, I analyzed two nonoverlapping sequences from the same individual. Twenty-nine songs from 22 individuals were thus represented as probability vectors with 35 dimensions. For each song, character *i* was the probability that a randomly chosen note would be in the *i*th category of Figure 1. I used cluster and principal components analyses to compare songs on the basis of these characters.

Hopkins et al. (1974) outlined the operating princi-

TABLE 1. Study locations and dates. The first two letters of each bird's label are an abbreviation for the state where the song was recorded.

Bird identity	Date recorded	Latitude and longitude
Smoky Mountain National Park, Tennessee		
TN1	3 May	35°41'N, 83°27'W
TN2	3 May	
TN3	3 May	
TN4	3 May	
Shenandoah National Park, Virginia		
VA1	10 May	38°30'N, 78°24'W
VA2	11 May	38°34'N, 78°22'W
VA3a	11 May	
VA3b	13 May	
VA4	12 May	
Catskill Mountains, New York		
NY1	22 May	42°12'N, 74°04'W
NY2	27 May	
NY3	24 May	
NY4	27 May	
Woodford State Park, Vermont		
VT1	30 May	42°53'N, 73°02'W
VT2	30 May	
Jamaica State Park, Vermont		
VT3	30 May	43°07'N, 72°45'W
Hubbard Brook, New Hampshire		
NH1	2 June	43°56'N, 71°42'W
Woodstock, New Hampshire		
NH2	4 June	44°04'N, 71°51'W
Jefferson Gap, New Hampshire		
NH3	5 June	44°18'N, 71°22'W
NH4	5 June	
Baxter State Park, Maine		
ME1	7 June	45°54'N, 68°51'W
ME2	8 June	
ME3	10 June	45°57'N, 69°05'W
ME4	10 June	
ME5	10 June	

ples of the Analyzer. The device can provide a continuous output of digitized fundamental frequencies measured at equal intervals in time. Since I did not have the equipment needed to connect the sound analyzer with a computer capable of handling the output, I used several alternative methods to digitize notes for numerically comparing them. I made sonograms with the wide band setting on a Model 6061B Sonagraph (Kay Elemetrics Co.). On each sonogram, I took 22 consecutive measurements of the median of the fundamental frequency trace (at 15-ms intervals). For these digitized notes, character j was the fundamental frequency at time t , where t is equal to j multiplied by 15 ms. Cluster and principal components analyses were again used to show first the structure of an individual's repertoire and then the differences among birds in the sound morphology of a single note type. For the individual repertoire, I arbitrarily selected 18 copulatory notes and 45 territorial notes from bird VA3, for which I had a large sample of recordings. I digitized 33 replicates

of the ubiquitous note 18 from 20 different Solitary Vireos for the comparison among birds.

I ran all three sets of cluster and principal components analyses using standardized characters with NTSYS (Rohlf et al. 1974) on a Univac 1100 computer. Missing characters were omitted from the analysis of digitized notes so that differences in duration would not heavily influence the correlations used to measure similarity. Zero probabilities were included in the comparisons of song composition, however, because I considered the absence of particular notes from a repertoire to be as important as the presence of others. I used Euclidean distances to measure differences among song compositions. For each cluster analysis, phenograms were constructed using weighted, unweighted, single, and complete linkage algorithms (see Sneath and Sokal [1973] for a review of these methods). In each case, I present only the phenogram which had the highest cophenetic correlation coefficient (Sneath and Sokal 1973: 278, 304) as being most representative of the data matrix. Principal components in all cases were calculated from the correlations among characters.

RESULTS

VARIATION WITHIN A REPERTOIRE

Figure 3 shows the results of unweighted clustering of correlations among the 63 frequency-digitized notes from bird VA3. The average correlation among any two groups in such a diagram is indicated by the level at which a vertical line connects those particular groups. The diagram represents the similarities in frequency patterning among all the notes, portraying the physical structure of the repertoire. For example, notes 3 and 5 are quite similar (average correlation of 0.84), but are very different from notes 23 and 25 (-0.40). When comparing short notes to long ones, this analysis considers only the first t time units, t being the duration of the shorter note. Hence, note 1 is similar to the first part of note 18, note 13 is similar to the first part of note 25, etc. Repetitions of the same note are extremely similar in all cases. Notes that occur in both copulatory and territorial song are virtually identical in both, except for note 12. Although not indicated by this analysis, the difference in note 12 appears to be that the first part of the copulatory version was sung at higher frequencies. In nearly all cases, different note types are distinctly separated by much lower average correlations than repetitions of the same type, indicating that notes are organized into discrete, stereotyped signals.

Projections on the first three principal components axes, which together explain 76% of the total variance, are shown in Figure 4. The weights assigned to the frequencies at each time (Table 2) indicate that the notes are composed of three covarying sec-

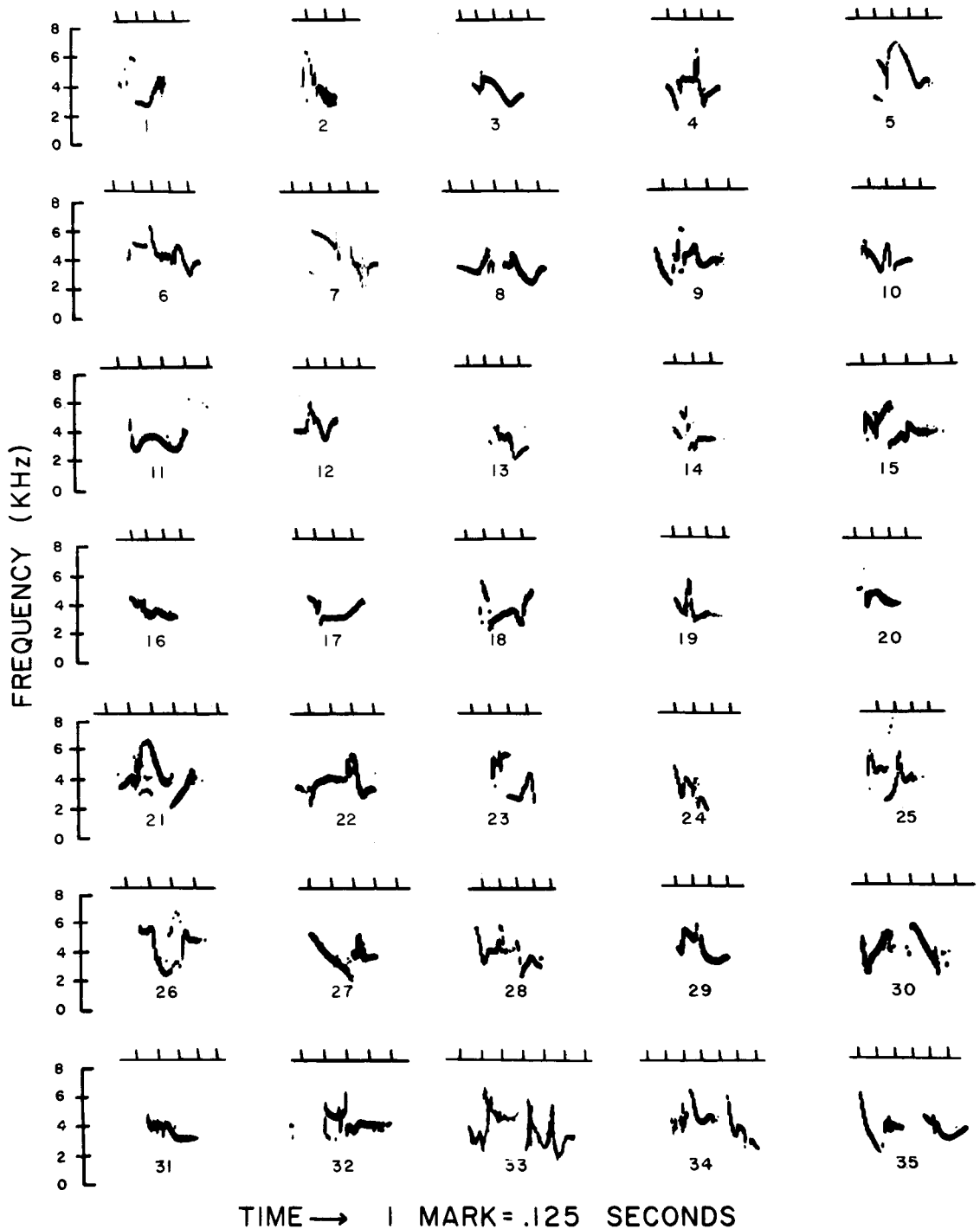


FIGURE 1. Real-time sound spectrograms representing the Solitary Vireo note categories.

tions in time. On the first axis, the last third of the time units (0.25 to 0.33 s) are most heavily weighted, separating out those notes which end on high frequencies (on the left in Fig. 4) from those which end on low frequencies (on the right). On the second dimension high values correspond to

low frequencies in the middle third of the notes (0.11 to 0.24 s), and on the third dimension high values correspond to high frequencies at the beginning (0 to 0.10 s) of the notes. Most repetitions of the same type are close together in this three-dimensional space. The copulatory note 12 is separated

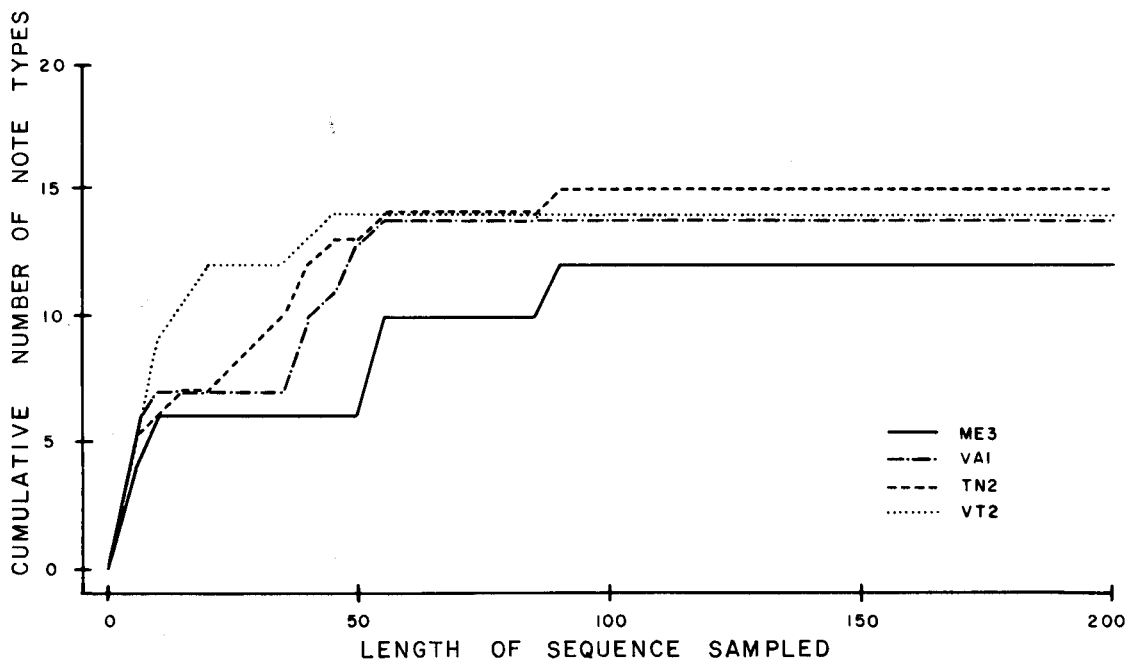


FIGURE 2. Number of different note types found in long sequences from four Solitary Vireos.

from the territorial version on the third axis as expected, since the first part of the copulatory version was sung at a higher frequency. Both cluster and principal components analyses of digitized notes within a repertoire gave results consistent with the subjectively identifiable differences among notes.

GEOGRAPHIC VARIATION IN NOTE MORPHOLOGY

Figure 5 depicts one note of type 18 from each of 20 Solitary Vireos, and Figure 6 shows the phenogram resulting from unweighted clustering of correlations among frequency-digitizations for replicates from these birds. Subtypes *a*, *b*, and *c* form distinct clusters, correlations within subtypes being 0.75 or greater. The methods employed are extremely sensitive to the small differences among birds, since the correlations among these and the other two subtypes are as low as -0.40 . I labelled subtypes *d* and *e* on the basis of the principal components analysis (Fig. 7). Differences at the very beginning of the notes, and in the interval from 0.15 s to 0.25 s account for most of the variance, since these frequencies are weighted most heavily on the first axis (Table 2). Thus, subtype *a* is projected onto the left end of component 1 (Fig. 7) because it has a low-frequency introductory slur and midsection. Similarly, the second axis shows differences near the end of the

notes, and the third axis shows differences near the beginning. The first two axes together indicate substantial separation between *a*, *d*, and *e*, while the third shows *b* to be aberrant. The differences indicated among *d* and *e* are surprising, because these subtypes are visually indistinguishable (see Fig. 5). The variance arises from small differences in duration (*d* is longer than *e*), even though duration per se was not a character and variables with missing values were deleted. The slight temporal differences caused the upward sweep at the end of the shorter notes to be compared with the downward sweep near the end of the longer notes, and hence greatly affected the results.

GEOGRAPHIC VARIATION IN SONG COMPOSITION

Table 3 shows the geographic occurrence by locality of all the note types. Tennessee and Virginia populations have several unique types, but this was not the case for any of the New England populations. Figure 8 shows the phenogram resulting from weighted clustering of the distances among song compositions (probabilities of note occurrence). In general, Solitary Vireo songs from one locality are more similar to each other than to songs from other localities. The effect is most pronounced for the southern birds. Tennessee and Virginia birds are very different from each other, and from all

the other birds as well. The New England songs also tend to form clusters corresponding to localities, but with overlap among these geographically closer areas. The phenogram indicates that where replicate songs from the same individual are included, they are extremely similar in composition, except for bird VA3. The second of these sequences (VA3b) is the bird's copulatory song. Even though the composition differs from VA3's territorial song, it still resembles those of other Virginia vireos more than those from other localities.

Regional differences in song composition are also clearly indicated in the results of the principal components analysis (Table 4, Fig. 9). Three dimensions, however, account for only 56% of the total variance. In fact, the first 10 axes explain just 90% of the variance among birds. An important biological implication is that among different birds, notes are used independently and not as large sets of covarying types.

Since much of the variation among the 22 vireos reflects regional differences (Tennessee, Virginia, and New England), relationships within each region are not well represented in Figure 9. Therefore, I repeated the analysis using only New England songs (Table 4, Fig. 10). The first three axes still explain only 57% of the variance among songs. Even within New England, occurrences of different notes are not highly correlated. A tendency toward geographic clumping in song compositions is obscured by inclusion of the Vermont birds, which span the entire range of compositions in New England.

SEQUENTIAL ORDERING OF THE NOTES

Hoel's (1954) statistical test for sequential independence showed Solitary Vireo note sequencing to be a first order process (e.g., for a sequence of 200 notes from bird VA3: first order $\chi^2 = 639$, d.f. = 225, $P < .001$, but second order $\chi^2 = 110$, d.f. = 3,600, n.s.). At any given time, then, the probability that a particular note will be sung depends on which note the bird sang last, but not on notes previous to that one. Sequences satisfying this property are known as (first order) Markov chains.

Transition probabilities were calculated for all the songs studied above. Table 5 shows these probabilities for a sequence of 200 notes from bird VA3's copulatory song (the most diverse I recorded), and Table 6 shows a sequence of 100 notes from the territorial song of bird VT3 (the least diverse). James (1973) referred to the latter type of

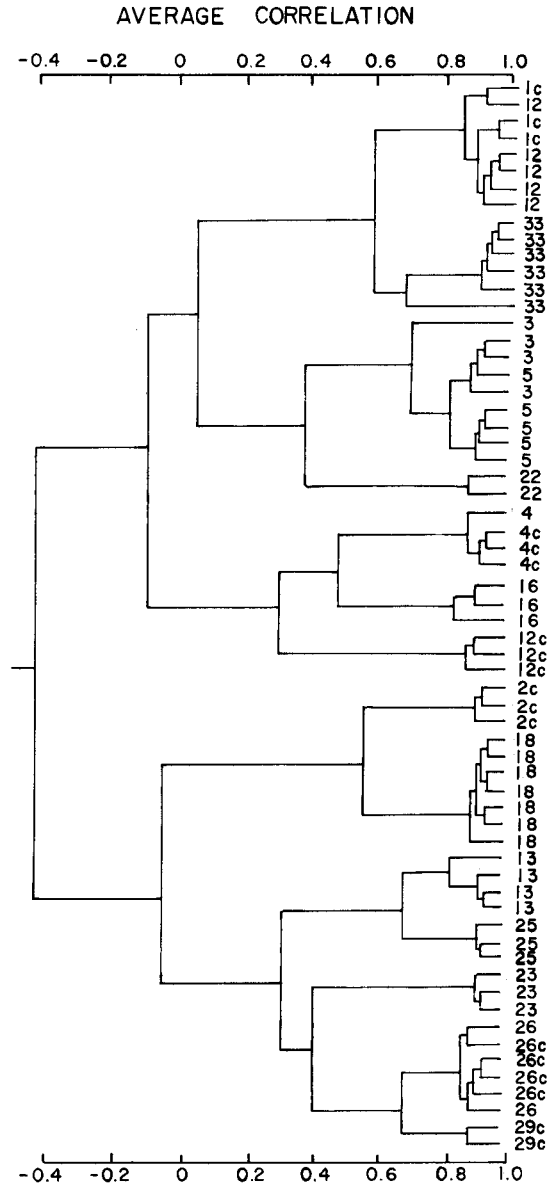


FIGURE 3. Phenogram from unweighted clustering of frequency-digitized notes encompassing the repertoire of bird VA3. Labels correspond to the categories of Figure 1. Notes from the copulatory song are indicated by a "c" suffix. The cophenetic correlation coefficient is 0.79.

song as "monotonous" because of its repetitive nature. In all cases, very few of the possible transitions occur. For instance, since bird VA3 sang 15 different types of notes, there were 225 possible two-note transitions, but only 8 of these occurred with high probability ($0.9 \leq P \leq 1.0$). Of the other possible transitions, 203 occurred very infrequently or not at all ($0 \leq P \leq 0.1$). For bird VT3, 7 of the 81 possible transitions were highly probable, but 69 were most improbable. All Solitary Vireos stud-

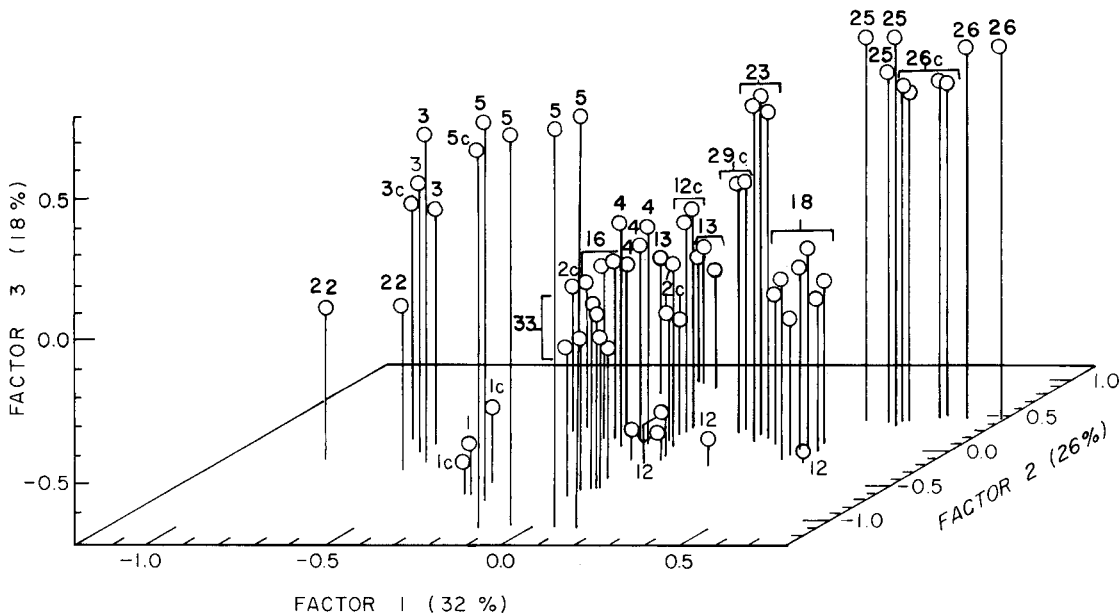


FIGURE 4. Projections of frequency-digitized notes from bird VA3 on the first three principal component axes.

ied showed the same patterns of organization.

DISCUSSION

METHODOLOGY

Descriptive categories of behaviors are necessary for testing hypotheses about their

causes or functions. To construct categories, most students of animal vocalizations have simply lumped together sonograms which look "similar," although it is clear that subjective judgements of similarity have many inherent problems. When one compares bird songs, it is difficult not to weight small differences among notes which happen to catch one's eye (or ear), and to lump notes which resemble forms common in one's experience. This process distorts the actual

TABLE 2. Loadings for the digitized sound frequencies on the principal component axes. One time unit is 15 ms. Projections of the notes are shown in Figures 4 and 7.

Time unit	Repertoire of bird VA3 Component			Note 18 from 20 birds Component		
	1	2	3	1	2	3
1	.21	-.02	.47	.87	-.30	.30
2	.47	.05	.57	.66	-.05	.69
3	.45	.18	.74	.64	.27	.60
4	.50	.17	.76	-.48	.67	-.28
5	.38	.14	.73	-.51	.76	-.05
6	.04	-.08	.85	-.19	.79	.06
7	-.08	-.31	.57	.71	.50	-.08
8	-.11	-.81	.08	.79	.50	-.16
9	-.08	-.90	.07	.83	.48	-.12
10	-.10	-.91	.03	.83	.35	-.04
11	-.39	-.88	-.04	.88	.25	.18
12	-.29	-.92	.05	.94	.00	.21
13	-.05	-.77	.13	.87	-.19	.02
14	.43	-.64	.04	.82	-.36	-.19
15	.70	-.37	.13	.68	-.42	-.59
16	.82	-.30	-.01	.76	-.34	-.55
17	.99	-.15	-.12	.62	.41	-.42
18	.87	.27	-.08	.25	.79	-.18
19	.92	.16	-.42	-.02	.90	.07
20	.85	-.05	-.44	-.16	.80	.15
21	.80	-.29	-.21	.00	.66	-.04
22	.78	-.32	-.15	.08	.46	-.13

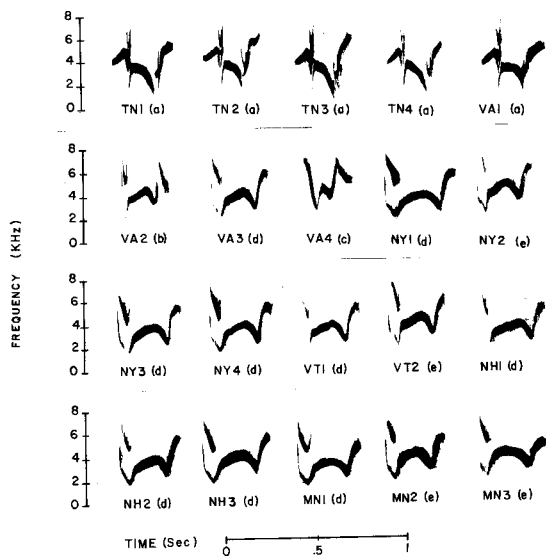


FIGURE 5. Sonograms of replicates of note 18 from 20 different birds. Labels a through e correspond to subtypes.

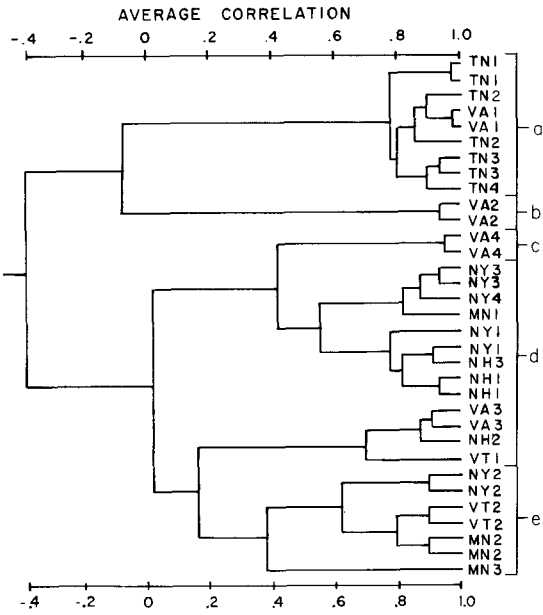


FIGURE 6. Phenograms from unweighted clustering of frequency-digitized replicates of note 18. Some Solitary Vireos are represented by two such notes. Lower case letters indicate subtypes, as in Figure 5. The cophenetic correlation coefficient is 0.87.

relationships among sounds in unpredictable ways. Also, some people split songgrams into many narrowly defined types, while others lump them into broader

groups. Thus, results from different workers have not been strictly comparable. The degree to which vocalizations should be lumped or split depends in part on the goals of the particular project, so we can never expect uniform standards for deciding category boundaries. It is desirable, however, to develop methods for reporting the similarity levels represented by the categories, and to base the signal classification process on precise and repeatable criteria.

Sparling and Williams (1978, but see also Martindale 1980) have suggested various multivariate techniques for comparing songs. Morgan et al. (1976) argued that clustering is generally to be preferred over principal components analysis, but the optimality criteria for constructing clusters need to be more fully explored, and there is no adequate significance test for the cophenetic correlation coefficient, a measure of distortion. Clustering also forces songs into discrete groups, even when the variation among them is continuous, so the results must be interpreted cautiously. Nonetheless, I have found both techniques helpful for representing the numerical differences among digitized notes and song compositions of Solitary Vireos.

Decisions on how to quantify songs are quite important because any ensuing analysis can strictly pertain only to the mea-

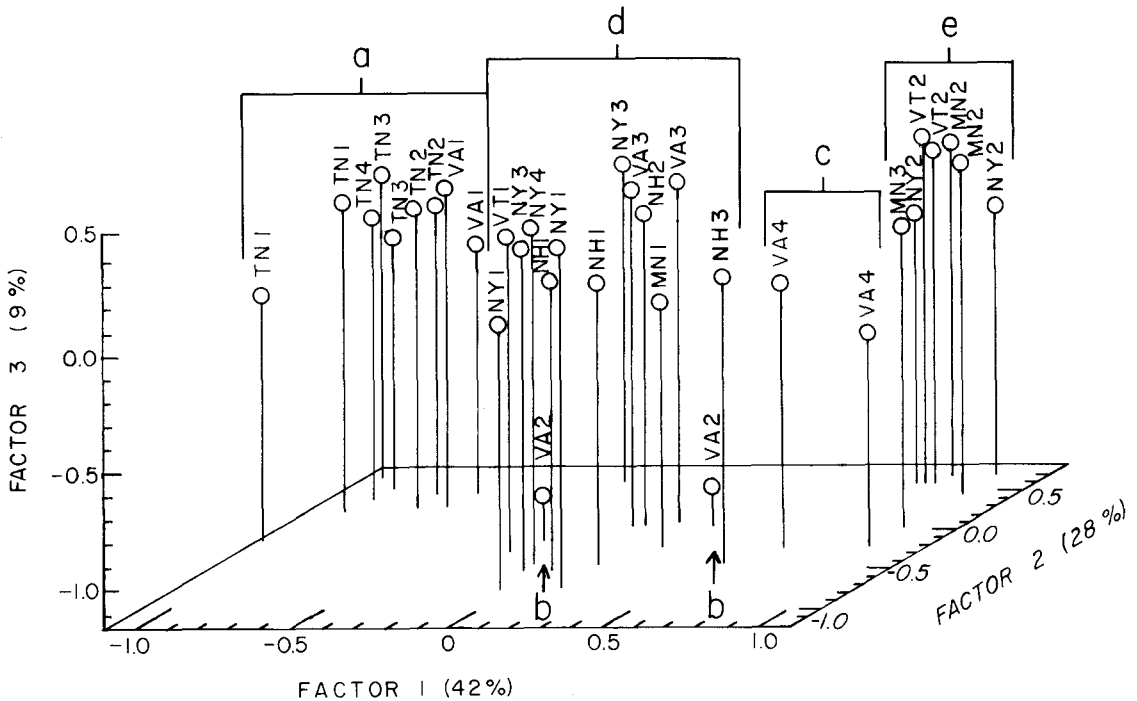


FIGURE 7. Projections of frequency-digitized replicates of note 18 on the first three principal component axes. Labels as in Figure 6.

TABLE 3. Geographic occurrences of the notes. Locality names given in Table 1. Presence of a note in a locality is indicated by an "X."

Note type	Location					
	TN	VA	NY	VT	NH	ME
1		X			X	
2		X			X	X
3		X	X	X	X	X
4		X				
5	X	X	X	X	X	
6			X	X	X	X
7			X	X	X	X
8	X					
9					X	X
10		X	X	X	X	X
11	X					
12		X	X	X	X	
13		X	X	X	X	X
14	X					
15	X					
16	X	X				
17				X	X	X
18	X	X	X	X	X	X
19		X				
20	X			X		X
21	X					
22	X	X				
23		X	X	X	X	X
24			X	X	X	X
25		X				
26	X	X	X	X	X	X
27		X	X	X	X	X
28		X				
29	X	X	X	X	X	X
30	X					
31				X	X	
32	X					
33		X				
34			X	X		
35			X	X		
No. unique	7	4	0	0	0	0

sured variables. Sonograms have generally been quantified by summary descriptive measurements (see Goldstein 1978 for a multivariate example). The method is convenient and works well for long, complex songs like those of various sparrows (unpubl. data). Also, an analysis of Solitary Vireo notes based on 10 descriptive measurements gave results quite close to those reported herein for the frequency-digitization methods. Digitizations, however, have several potential advantages over summary measurements, especially for comparing short, simple songs. If the period between measurements is sufficiently brief, digitizations contain the information of the summary measurements, so the latter can always be computed from the former, if desired, but not vice versa. Also, digitizations require no subjective assignments of character homology or relevance. A consid-

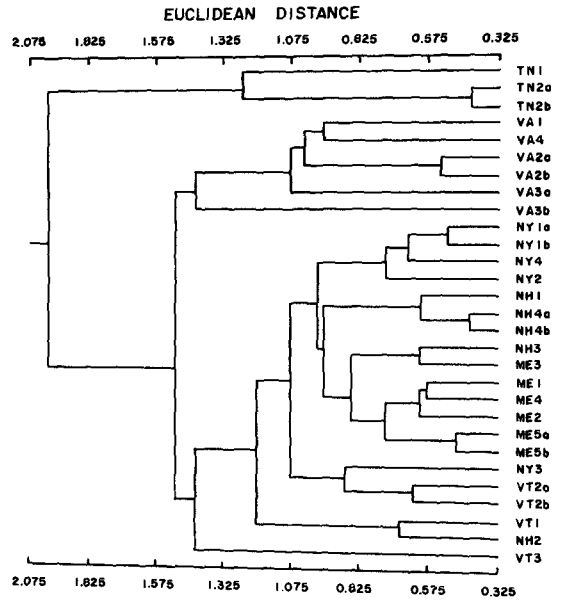


FIGURE 8. Phenogram from weighted clustering of the distances among songs based on usage of the 35 different note types. The cophenetic correlation coefficient is 0.95.

eration likely to be important in future studies is that the digitizations can be performed and categorized automatically from the field tape recordings if the computer apparatus is available (a real-time sound spectrum analyzer and a compatible minicomputer are required). Completely automated analysis of the tapes would allow one to process much larger samples of songs than considered by any study to date. Sequential frequency-digitizations also mimic the raw information available to the birds for neural processing, so results from behavioral and ecological studies may in the future be more closely tied to the neurophysiological components of signal production and reception.

Some aspects of the digitizations, however, require further consideration. Since a bird cannot change sound frequencies infinitely quickly, the sequential measurements are not independent. That is, the frequency at any time t will necessarily be correlated with the frequency at times close to t . The magnitude of this autocorrelation depends on the time interval between measurements as well as on the form of the songs. I have simply used principal components analysis to combine correlated frequencies, but time series analysis (e.g., Box and Jenkins 1976) provides more appropriate statistical tools for studying the temporal dependencies in detail. Also, I used cross-correlations of zero time lag to compare Sol-

itary Vireo notes. In the comparisons of note 18 from different birds, slight differences in duration caused the upsweep of some notes to be compared with the downsweep of others, resulting in negative correlations among notes of very similar form. In the future, nonzero time lags can be introduced so as to give the highest possible cross-correlations among pairs of notes before proceeding with the similarity analyses. This process would minimize the effects of small introductory flourishes and time shifts. Various smoothing and forecasting techniques are applicable, and transfer functions may provide a way of studying developmental or evolutionary changes in the notes.

SEQUENCING AS A MARKOV CHAIN

Solitary Vireos often sing sequences of 1,000 notes or more without stopping. The note types are not always repeated in the same order, so sequencing is appropriately treated as a random (stochastic) process. This is the case for many (probably most) birds' songs, and other behaviors as well. There exists a rich and well developed theory concerning such processes (e.g., Bailey 1964). Here, I briefly discuss the approach as applied to Solitary Vireo songs.

The probability, P_i , that a randomly chosen note is type i equals the proportion of type i notes in the whole song. "Sequentially independent" means that the probability of a given sequence occurring equals the product of the individual probabilities for each note type (i.e., the probability of i - j - k occurring is $P_i \cdot P_j \cdot P_k$). Sequential independence seldom holds for bird songs, however, since some combinations of notes occur more often, and others less often, than predicted on the basis of the individual probabilities. A Markov chain is a sequence in which the probabilities of occurrence depend solely on what type occurred last. In this case, a transition matrix (e.g., Table 5) is required to show the "conditional" probabilities—the probabilities that the notes will occur, given that type i occurred last. Conditional probabilities are usually symbolized as $P_{j|i}$, and read "the probability of j given i ." The probability of any sequence i - j - k occurring is now $P_i \cdot P_{j|i} \cdot P_{k|ij}$. This multiplicative process can be continued to find the probability (proportion) of occurrence for any chain of any length. For example, to find the probability that a randomly chosen four-note sequence in bird VA3's song (Table 5) is of the form 12-1-2-5, one multiplies: $0.20 \cdot 0.61 \cdot 0.93 \cdot 0.58 = 0.07$. One therefore expects about 7 out of every 100 four-note

TABLE 4. Loadings of the note type occurrence probabilities on the principal component axes. Projections of the songs are shown in Figures 9 and 10.

Note type	Songs from all localities Component			Songs from New England Component		
	1	2	3	1	2	3
1	.09	-.22	.10	.23	.77	.22
2	.13	-.08	.45	-.32	.26	.31
3	.56	.04	-.28	.39	-.69	-.44
4	-.21	-.90	-.06	.00	.00	.00
5	-.43	-.23	-.12	.28	.58	-.46
6	.45	.25	-.18	.30	.09	-.61
7	.53	.39	-.39	.41	-.78	-.22
8	-.86	.39	-.09	.00	.00	.00
9	-.16	.48	-.36	.30	-.44	.41
10	.74	-.01	-.23	.51	-.21	.13
11	-.87	.39	-.09	.00	.00	.00
12	-.43	-.69	-.12	.19	.27	-.55
13	.17	-.61	-.29	.46	.45	-.12
14	-.88	.39	-.09	.00	.00	.00
15	-.85	.15	-.13	.00	.00	.00
16	-.71	-.56	-.15	.00	.00	.00
17	.39	.28	-.10	.25	.44	.61
18	.52	-.31	-.17	.23	.06	.08
19	-.23	-.89	.06	.00	.00	.00
20	.17	.14	.26	-.40	-.57	.41
21	-.90	.37	-.13	.00	.00	.00
22	-.94	.24	-.12	.00	.00	.00
23	.67	.24	-.13	.41	-.18	.67
24	.69	.48	-.13	.49	.30	.23
25	-.20	-.91	.01	.00	.00	.00
26	-.38	.27	.53	-.66	-.14	.56
27	.03	.29	.34	-.38	.37	-.37
28	-.17	-.64	-.01	.00	.00	.00
29	.06	.10	-.57	.47	-.31	-.13
30	-.74	.27	-.12	.00	.00	.00
31	.23	.10	-.20	.38	.77	.33
32	-.77	.37	-.06	.00	.00	.00
33	-.19	-.69	.13	.00	.00	.00
34	.18	.18	.73	-.79	.13	-.52
35	.09	.17	.90	-.93	.15	.06

sequences to be of the form 12-1-2-5, and that was the case for bird VA3. (Notice that this number is different from the proportion of 12-1-2-5 strings expected if the notes were sequentially independent: $0.20 \cdot 0.14 \cdot 0.13 \cdot 0.12 = 0.00$.) If one knows, in addition, that note 12 just occurred, then there is a 0.33 chance that notes 1-2-5 will be next (as opposed to a 0.00 chance if the notes were sequentially independent). Dependencies on the last two or more types are also possible, but I believe these will seldom be found in songs, partly because very large sample sizes are required to demonstrate them. Hoel (1954) presented an appropriate test for all orders of dependence, and Cane (1978) discussed ways in which categories can be lumped so as to reduce the order of the process, when higher orders of dependence are found.

Markov chains have several important properties. If the transition probabilities are constant in time (stationary), they deter-

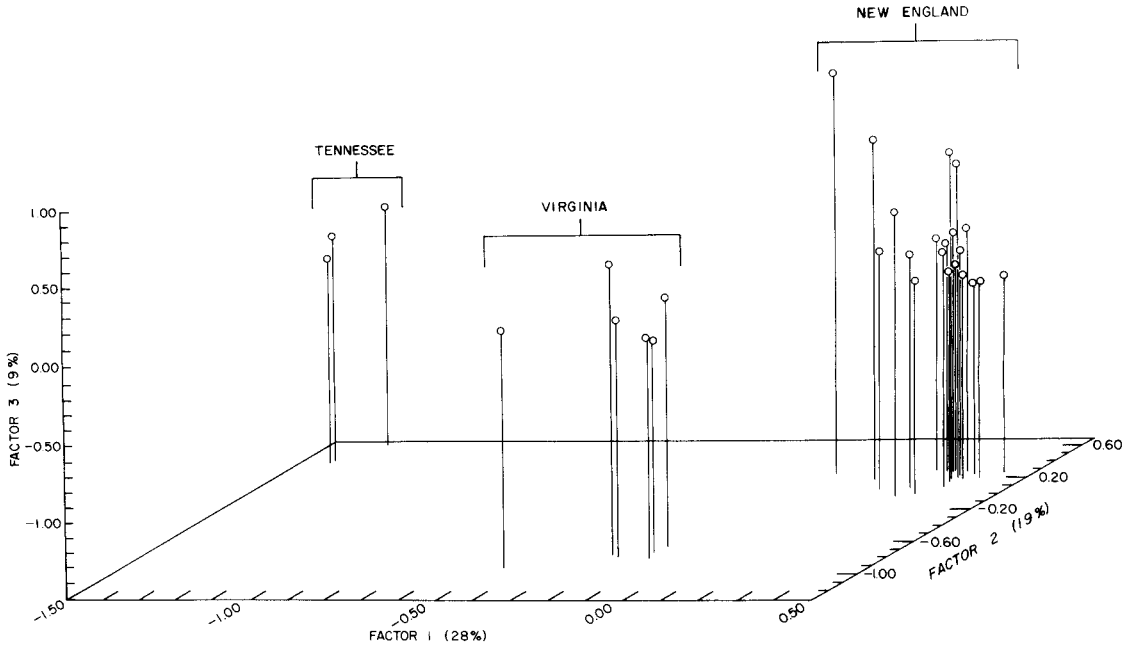


FIGURE 9. Projections of all the songs on the first three principal component axes based on the 35 note types.

mine the proportions of note types in the song, and the expected recurrence time for each note. For all of my Solitary Vireos, except one, transition probabilities were close to being stationary. The notable exception was an individual recovering after having avoided a hawk, probably a Cooper's Hawk (*Accipiter cooperii*). It is possible that transition probabilities reflect the strength of

neural connections between centers in the brain corresponding to each note type. Hormonal changes may affect song compositions by altering the relative strength of the different neural pathways. If all transition probabilities were zero or one, the sequences resulting would be strictly periodic (notes would be sung in the same order every time). My results show Solitary Vireo

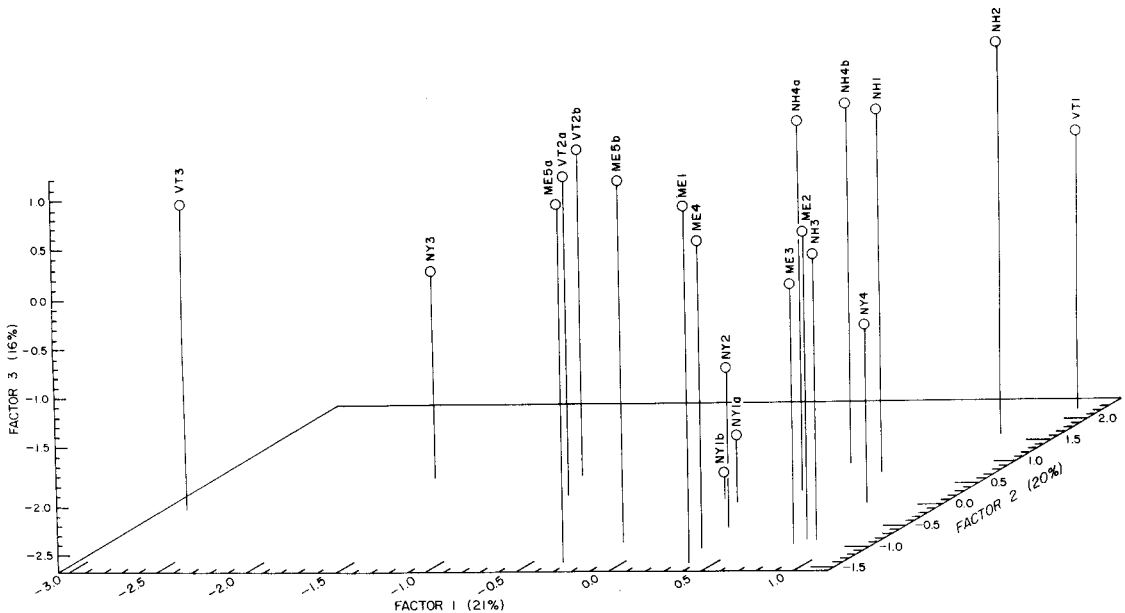


FIGURE 10. Projections of the New England songs on the first three principal component axes based on the 35 note types.

TABLE 5. Transition probabilities for bird VA3's copulatory song. P_i is the proportion of note i in the song. The other entries are the probabilities that note j will occur, given that note i occurred last in the song. Missing entries are zero probabilities.

i	P_i	Note j															
		1	2	3	4	5	10	12	13	16	18	23	25	26	29	33	
1	.14		.93	.04		.04											
2	.13					.58		.08									.35
3	.04																1.00
4	.01																
5	.12																
10	.01	1.00				.04	.04	.43		.04					.04		.40
12	.20	.61	.06					.06	.28								
13	.03														.80		.20
16	.03								1.00								
18	.02																
23	.02				.50												.50
25	.03			1.00													
26	.07								.77	.23							
29	.02																
33	.15	.48							.39								.10

transition matrices to be close to this requirement for periodicity. These birds tend to repeat the same string of notes several times, but randomly switch to other highly probable strings as they cycle through their repertoires in a quasi-periodic fashion.

I have so far discussed sequencing of notes in a song as a "discrete time" process. Each time unit has corresponded to the occurrence of a note in the song. If the actual durations of the notes and the pauses between them are also considered, the process is said to be modelled in "continuous time." In the simplest case (see Bailey 1964), the durations are assumed to be random and independent for each note and for the pauses. Also, the times between notes are assumed to be independent of the identity of the notes. On these assumptions, one expects an exponential distribution of durations for each different note type, and also for the pauses between notes. If the probability of a note type occurring depends on the duration of the pause before it, however, the situation is more complex, and has been

called a "semi-Markov" chain (see, e.g., Cane 1959).

There are several biological reasons for predicting that most bird songs will be structured as semi-Markov chains. For instance, it may simply take a bird's brain and musculature longer to prepare for singing a long note than a short note, so longer notes will be preceded by longer pauses. If a long pause has occurred, then, the transition probabilities are different from those after a short pause. If individual birds change their transition matrix depending on how fast they are singing at the moment, then the probabilities would be stationary only as long as the singing rate remained constant. I do not have enough data for individual birds to test this possibility. The transition matrix would be time-dependent, also, if the sound patterns in the song were selected for their joint (sequential) ability to keep the listener from habituating to the song, or becoming confused by new sounds. Moles (1968) related this idea to various problems of esthetic perception,

TABLE 6. Transition probabilities for bird VT3's territorial song. Explanation as in Table 5.

i	P_i	Note j								
		5	10	18	23	24	26	27	34	35
5	.09									1.00
10	.05		.33					.33	.33	
18	.03				1.00					
23	.04					1.00				
24	.04		1.00							
26	.25	.37		.04						.59
27	.02			1.00						
34	.24							.96		.04
35	.24					.04				.96

and Kroodsma (1978) recently summarized the evidence for bird songs. A prediction based on this assumption is that birds singing at faster rates should have a higher diversity of note types. I did find a significant positive correlation between singing rate and the Shannon-Wiener diversity index for different Solitary Vireos (Spearman rank $r_s = 0.52$, $n = 29$ songs, $P < .01$). (Krebs [1976] argued that habituation by intruders is maladaptive, and proposed that the function of song diversity is to increase the apparent population density so intruders will move on rather than invade. But if this were the function of song diversity, habituation by intruders would be adaptive, as then intruders would not be fooled by the ploy of the residents.)

THE DIVERGENCE OF SOLITARY VIREO SONGS

I have shown that Solitary Vireos from the same locality have similar song compositions, except for the aberrant Vermont birds. I noticed that two of the latter were peculiar when I recorded them. Bird VT1 was apparently countersinging to a Red-eyed Vireo, and bird VT3 was singing a low diversity song like those noted by James (1973) as "monotonous." I do not know if the monotonous song has a different function than the other songs.

James (1976) presented evidence that learning is important in vireo song development. My results show that there is continuous variation among notes from different individuals (see also Martindale 1977), and it is likely that these birds include small behavioral changes in the learning process. Once learned, notes are stereotyped, as shown above for adult repertoires. This stereotypy could be a simple result of the frequent and continuous reinforcement of neuromuscular pathways involved in note production. If, for instance, a Solitary Vireo sings 10 equiprobable notes at the rate of 30 notes per minute, eight hours a day, then in one week he will have repeated every note type over 10,000 times. For the transmission of songs across generations, the birds need only to learn about 15 Solitary Vireo note types, and a small number of ways of pairwise ordering them (rather than long sequences). Sequencing might be learned by a process similar to operant conditioning as studied in various laboratory animals.

Individuals apparently make small changes in the sequential frequencies of a note type, including prefixes, suffixes, and timing shifts. Accumulated changes in the notes, and perhaps occasional drastic

changes like the mimicry studied by James (1976) and Adkisson and Conner (1978) for other vireos, eventually result in the formation of different notes. As the process continues, notes diverge in morphology. Solitary Vireos of the southern Appalachians use several notes not found in New England, and these populations have been geographically separated for a relatively long time. Lemon (1975) studied song drift in detail, and summarized much evidence for emberizids, showing that dialects are created by young birds carrying developmental alterations to new populations. Lemon treated the behavioral drift of notes as being neutral, in that small changes in the songs were assumed not to alter the individual's success in communicating. Following the approach of Dawkins (1976), I consider various note morphs to be in competition with each other for use by the birds. Solitary Vireos may learn which notes and sequences of notes are particularly useful in meeting their communications requirements. Songs must be easily produced by an individual's neuromusculature, they must have appropriate transmission properties through the environment (see Wiley and Richards 1978), and they must elicit suitable responses from other birds in the area. For a note to be successful (i.e., used often by many birds), it must meet these requirements when in conjunction with the other notes of individual repertoires. Notes which are particularly well suited with each other should be coupled by high transition probabilities.

Smith et al. (1978) indicated that Yellow-throated Vireo (*V. flavifrons*) song compositions are correlated with other behavioral activities, and my data for Solitary Vireo VA3 show copulatory song to differ from territorial song. More work is needed to assess the importance of microgeographic and momentary changes in song composition. Also, I collected all my data during the same part of the season (early spring), and it is possible that seasonal changes in the songs occur (see Rice 1978). Numerical analyses of notes and song compositions similar to those I have used may in the future help sort out the various components of variation in these and other songs as well.

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