

# SONG VARIATION WITHIN A POPULATION OF WHITE-EYED VIREOS (*VIREO GRISEUS*)

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**ABSTRACT**—Intrapopulational variation in the songs of territorial male White-eyed Vireos (*Vireo griseus griseus*) was studied at Gainesville, Florida during 1977 and 1978. The motifs in the song repertoires of 40 color-banded males were analyzed in detail. Individual male White-eyed Vireos used 1–14 different motifs. A quantitative sequence-comparison measure of song dissimilarity was used to compare song repertoires. No relationship was found between the dissimilarity of individuals' song repertoires and the map distances between their territories. Unexpectedly, pairs of neighboring males had more dissimilar song repertoires than non-neighboring pairs of vireos. Received 21 March 1980, accepted 26 July 1980.

In some species of birds, geographic song variation is discontinuous, forming a mosaic of well-defined dialects. Other species, such as the White-eyed Vireo (*Vireo griseus*), possess a more or less continuous pattern of geographic variation. An extensive survey of song variation in White-eyed Vireos (6,193 songs primarily from Ohio, Florida, and Texas) revealed patterns of geographic variation that apparently lack well-defined boundaries (Donald Borror pers. comm.). My study was initiated to determine the pattern of song variation within a single population of White-eyed Vireos. I studied a population of *Vireo griseus griseus* at Gainesville, Alachua County, Florida. This population is apparently nonmigratory, although individuals are quite secretive in winter. This vireo has a patchy distribution in northern Florida, reflecting the occurrence of preferred second-growth habitat. My initial hypothesis was that intrapopulational variation would, like the continent-wide pattern, be more or less continuous. I set out to compare song repertoires of neighboring birds within habitat patches with those of more distant males. Observations of the vocal repertoire and territorial behavior, with notes on the ontogeny of song, are presented elsewhere (Bradley 1980).

## TERMINOLOGY

Because studies of avian vocalizations often employ terms in varying ways, it is important to define here the terms I used. Thus:

*Element*—a single short burst of sound energy that appears as one continuous mark on an audiospectrogram and lasts less than 0.1 s in White-eyed Vireos.

*Song motif*—a single "song" lasting about 1 s and composed of many elements, perceived by a human listener as one "word" or utterance. White-eyed Vireos sing many such motifs with a pause of a few seconds between each motif. Within the repertoire of one individual there were several to many distinct song motifs, each with a relatively invariant structure. This term is similar to the "song pattern" of some authors.

*Song bout*—one behavioral sequence of singing. It consists of a series of song motifs delivered at a rate of 10–20 per min for a few minutes. Song bouts are variable in length but usually last less than 30 min.

*Discrete song*—the "typical" species-specific song of territorial male White-eyed Vireos. Each song motif is about 1 s long.

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*Rambling song*—A distinct, rarely heard form of singing in which a male sings more or less continuously for several seconds to minutes. Rambling song is described in detail elsewhere (Bradley 1980).

#### METHODS

During the spring and summer of 1977 and the spring of 1978, 61 territorial individuals were captured using nylon mist nets, measured, color banded, and released. Each bird was banded with a unique combination of colored plastic bands and a U.S.F.W.S. aluminum band. These individuals were subsequently observed and their songs tape recorded. The local distribution of color-banded territorial males was mapped, and the song repertoire of each male was recorded and analyzed. Each male was recorded on about 3–10 different visits. On later visits I attempted to record what I perceived as previously unrecorded “new” motifs.

Most tape recordings were made using a Nagra III open-real recorder and a Sennheiser 804 unidirectional microphone. Some additional recordings were made with a Superscope C-105 cassette recorder and a Sennheiser K2U unidirectional microphone. Recordings were analyzed on a Kay Elemetrics 7029A Sonagraph using the wide-band filter on the 80–8,000 Hz scale. Tapes made during this study have been deposited in the Bioacoustics Archive, Florida State Museum, Gainesville, Florida.

Each male's song repertoire was described in detail. Each song was analyzed with the audiospectrograph and the resulting tracing described using a letter-coding system (Fig. 1, Table 1). All of the audiospectrograms were examined, and elements deemed similar were assigned a two-letter code. While this subjective method of element classification may introduce an unconscious bias, I believe it is justified for two reasons. First, the choice of “similar” was relatively easy to make due to the invariable nature of specific elements. Second, all songs were analyzed in the same fashion, so any bias should be randomly assigned. In some cases multiple-element combinations were given one code when they were consistently used as a unit (e.g. FB, DB, Fig. 1). The repertoires of 40 territorial males (approximately 2,200 songs) were analyzed in this way.

Computer analysis was then used to compare the repertoires of the males. The Beldings Program Series employed for this analysis was written by David Bradley (Bradley and Bradley in press). These programs use dendrogram trees that describe the pattern of interelement relationships in such a way as to produce a dissimilarity matrix between the element types. I generated the dendrogram used here from my gestalt impression of element structure based on audiospectrograms of the elements. To construct the dendrogram, I arranged the elements so that similar elements formed “clusters.” These clusters were placed in a larger cluster near groups of other elements that had a generic similarity, and so on. When the tree was complete, the difference between any two elements was measured by observing the “level” at which the elements were combined together in a cluster. This method is similar to that used for the computation of cophenetic values (Sneath and Sokal 1973). Once interelement relationships had been quantified, the raw dissimilarity between any two motifs was computed as a weighted average of all the distances between pairs of elements that occur at corresponding positions in the song. Thus, an element that occurs at the beginning of one song will be compared primarily with those elements that occur near the beginning of the other song and to a lesser degree with the later elements. The final intermotif measure is, then, an overall dissimilarity of the element sequences of the two motifs being compared.

Following this, I combined the data from each song in a particular vireo's repertoire and compared the resulting group of motifs with the repertoires of the other males in the population. A new dissimilarity matrix was then produced that indicated the relative dissimilarity or “distance” between any two males' song repertoires. This distance is analogous to the “phenetic distance” between songs described by Payne (1978).

Finally, these “song distances” were compared to the spatial arrangement of the singers' territories. A direct correlation measure was applied to the generated song-distance values and the linear distances between the centers of the various males' territories. Another comparison was made between neighbors and non-neighboring individuals within the population. A similar technique was employed by Payne (1978). Variables studied that are not normally distributed are presented with a median and range instead of mean and variance.

#### RESULTS

The discrete songs of White-eyed Vireos probably function in territorial establishment and defense. Discrete song may also serve to advertise the presence of male vireos to females, but another type of song, designated the “rambling song,” is used

TABLE 1. Coded listings of the song repertoires of two males.

Male number	Song number	Song pattern	Song length (s)
7701	1	HL CA KE TC	0.50
	2	HL CA KE TC CE QU IC	1.06
	3	AG HL HE SD	0.78
	4	ID CB KQ FA QC TE	0.94
	5	IC FC PA TC	1.16
	6	SC HG ID HK CJ JA SD	1.20
	7	SC GB HK QP AE FC KP	0.96
	8	CA KN EB IB FC QA SB	0.56
	9	CC BE IC AC HK QN SD	1.40
	10	CC JC GA FB CS AF	0.90
	11	IC CC FB CQ HE SD	1.30
7702	1	CC FE DB CP QU	0.66
	2	CF MA CO QU TD	0.90
	3	KM HG GB QG SC	0.98
	4	CA MA CQ QG SD	1.00
	5	DF MB QC TD	0.92
	6	CA EA ID FB QG TE	0.96
	7	BD DD LB	1.00
	8	CC BC CB FE DB LB SD	1.22
	9	FC CC FA CQ HE TC	1.20
	10	CC BC GB FA QP AC	1.28
	11	IC AC HK QX	0.92
	12	SC JD	0.60
	13	SC UA KD KO CO JD	1.28

primarily in epigamic contexts (Bradley 1980). The rambling song is rather complex and is more or less continuous, combining elements and longer portions from the discrete song repertoire with various other call notes.

The typical song repertoire of a male White-eyed Vireo is complex. The males sampled in this study used from 1 to 14 different motifs, with a median of 5 motifs ( $n = 40$  males). I believe that most males use about 10 different motifs and that the low calculated median reflects insufficient sampling. A listing of the coded song repertoires from two males appears in Table 1. The number of element types contained in the repertoire varies directly with the number of songs recorded. There is no apparent asymptotic "limit" to the number of elements used. For the sample of 40 males, the median number of different elements per repertoire was 17, with a range of 5–47. I named 150 different element types from these 40 birds. The mean length of a motif was 1.02 s ( $s^2 = 0.06$ ,  $n = 213$  motifs). Each motif was composed of about 6 (1–9) separate elements. The song motifs were arranged in song bouts usually lasting from 5 to 15 min.

The variability within the song repertoire of an individual was large (Fig. 1). When the average calculated "distance" among songs within one bird's repertoire was compared to the average distance between all of the songs in the population, no significant difference was found. In this sample the mean distance measure within repertoires was 0.180 (0.0–0.243), and that measure between repertoires of all males was 0.179 (0.08–0.282). Thus, the song repertoire of any individual male was just as variable as a group of songs from the population as a whole.

Song is acquired very early in White-eyed Vireos. Young males sing typical discrete songs by the end of their first summer. The young males begin to sing subsong and make the transition to rehearsed song while still occupying their natal territory within 1 month of fledging. In fact, there is some evidence that young males help their fathers defend this territory late in the breeding season (Bradley 1980).

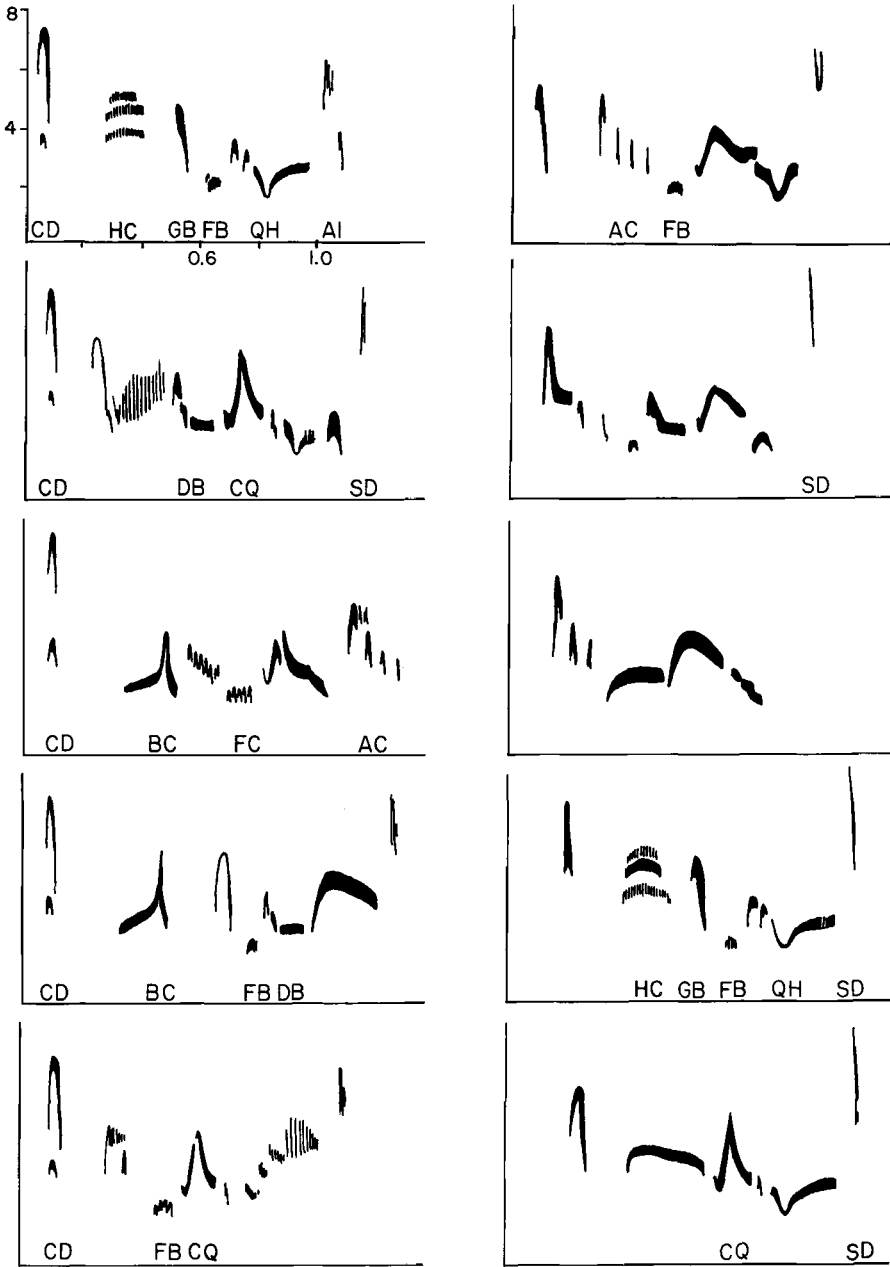


Fig. 1. The uppermost left tracing represents a sonogram of one song of White-eyed Vireo 77-06 (U.S.F.W.S. number 1320-54237). Frequency is on the ordinate in kHz, time on the abscissa in seconds. The lettered coding scheme is presented below the element structure. The other nine sonograms represent the other nine songs in this male's repertoire. Some additional element names have been labeled to illustrate the coding method.

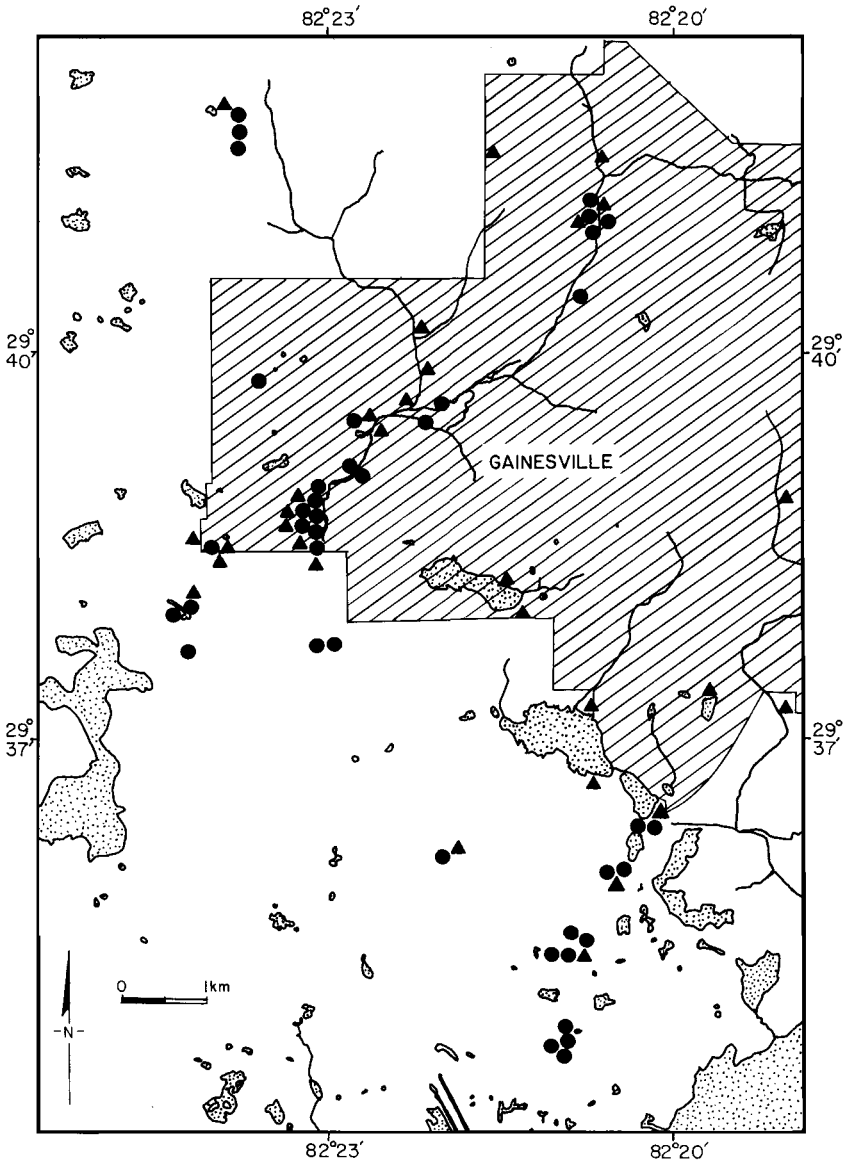


Fig. 2. A map of the White-eyed Vireo males located during 1977. The dots represent territories of color-banded males whose song repertoires have been analyzed for this paper; triangles indicate territories of other males studied. Bodies of water are stippled. The corporate limits of Gainesville are indicated by the hatched area.

In the Gainesville area, the White-eyed Vireo is found in second-growth forest edge and other disturbed habitats. The patchy nature of this habitat provides a wide variety of territorial situations. Some males occupy lone territories surrounded by unsuitable habitat. Others live in larger habitat areas with many neighbors (Fig. 2). In these crowded situations I could hear as many as seven or eight different territorial males from one place, although it is possible that the vireos could not hear all of the neighboring birds that I heard—a recent study of the Blue Jay (*Cyanocitta cristata*),

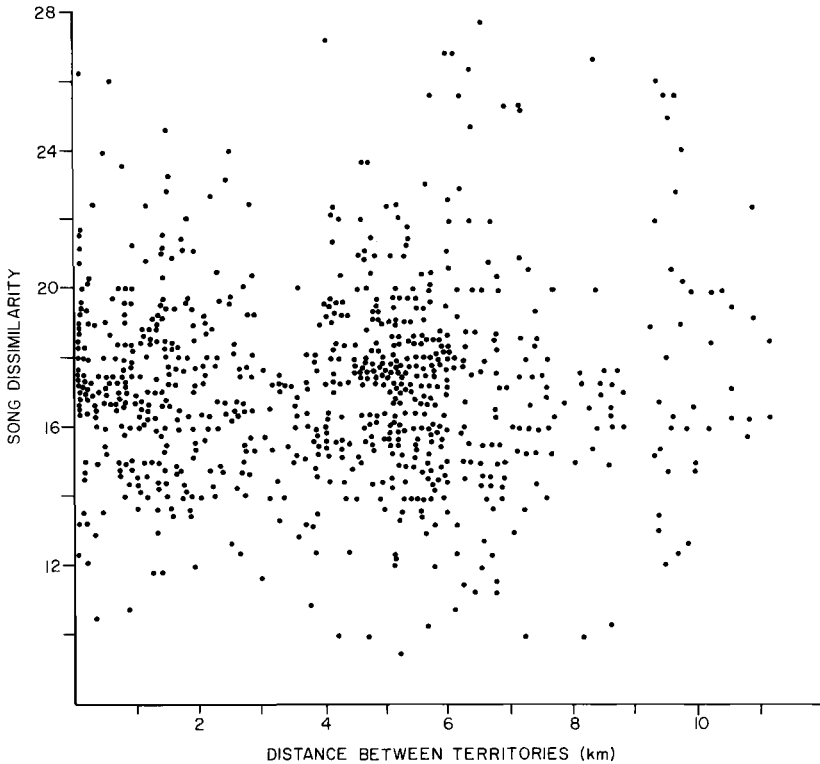


Fig. 3. A plot of the data comparing the song dissimilarity measure created by the Beldings program (ordinate) against linear distance between territories in kilometers (abscissa). There is no discernable relationship between these two variables ( $r = -0.002$ ).

for example, demonstrated that jays were not as sensitive to low level (distant) sounds as humans (Cohen et al. 1978). The distribution of territorial males whose song repertoires were analyzed during this study is illustrated in Fig. 2, which clearly shows the clumped nature of vireo distribution in Gainesville.

Of the 40 territorial males analyzed from 1977, only six were found during the spring of 1978. Perhaps the exceptionally harsh weather during 1977-1978 caused high winter mortality. Five males were relocated on their former territories. One male moved 200 m to an area occupied by a neighboring male during 1977. Although a few young males were color banded in 1977, none was located during the spring of 1978. The song patterns of the relocated adult males did not change substantially, although some additional motifs were recorded for a few individuals. In these cases I believe that the sampling in 1977 missed the songs that were newly discovered in 1978.

Song variation within the local Gainesville population was analyzed in two ways. First, a comparison of the computer-generated song distances between individuals and the map distances between their territories indicated no correlation ( $r = -0.002$ , Fig. 3). This figure should be compared with that presented by Payne (1978: Fig. 6), which illustrates a very different pattern.

A second analysis compared songs of immediate neighbors (having some portion of a territorial boundary in common) with songs of more distant individuals. Song

repertoires of neighbors showed *more* difference than repertoires from randomly selected males in the population (Student's *t*-test,  $t = 2.19$ ,  $P < 0.05$ ,  $df = 778$ ). This result should be viewed with caution, however, as the assumption of independence of observations has been violated, leading to an overstatement of the degrees of freedom. The result is interesting and may reflect a real tendency of neighboring males to possess songs more different than expected by chance alone.

#### DISCUSSION

The fact that no correlation was found between similarity in song repertoires and distance between territories is surprising. I had previously determined that young birds learned songs very much like those of their fathers and other males near the natal territory. The young birds that I observed after dispersal late in 1977 moved less than 1 km from their natal territories. I therefore expected to find local sub-population dialect groups. Such a situation evidently occurs in the Splendid Sunbird (*Nectarinia coccinigaster*; Grimes 1974, Payne 1978). On the other hand, Payne and Budde (1979) found no relationship between phenetic song distance and inter-territorial distance in Acadian Flycatchers (*Empidonax virescens*), perhaps because young flycatchers have high effective dispersal distances. The random nature of vireo song variation in space indicates that more mixing probably occurs in the population than I observed. Such dispersal, as well as high winter mortality, might thus account for the lack of distinct dialect boundaries among populations of White-eyed Vireos.

The finding that nearest neighbors tend to have more different song repertoires than non-neighboring pairs of birds from the population was entirely unexpected. This could result in the songs of neighbors being easily recognized individually by females or other territorial males. Males of some passerines can indeed distinguish between the songs of their neighbors and respond differently to playback of these songs from appropriate and inappropriate directions (Weeden and Falls 1969, Kroodsma 1976, 1979).

When territorial male White-eyed Vireos were presented with a tape-recorded "intruder," they responded by increasing both the rate and variety of their song delivery (Bradley 1980). When a playback loop with 2 different motifs was presented to 8 color-banded males, they used an average of 5.5 different motifs in the subsequent 5-min test period. The same males averaged 1.8 motifs in 5-min control periods without a playback stimulus. In the few instances that I recorded two males engaged in a counter-singing battle, the males sang rapidly, including 2-7 different motifs, but there was no evidence that males attempted to "match" themes.

The above results run contrary to the phenomenon of motif matching described for several other species (Marler 1956, Hinde 1958, Lemon 1967, Baptista 1975, Kroodsma 1979). In Long-billed Marsh Wrens (*Cistothorus palustris*), males respond to complex playback stimuli by singing complex song sequences, another form of signal matching (Verner 1976). Kroodsma (pers. comm.) has observed motif matching in closely related Caribbean species of *Vireo*.

The singing patterns of White-eyed Vireos thus differ from published descriptions for other species, in that (1) there is no relationship between song similarity and linear distance between territories of the singers, (2) songs of immediate neighbors are more different than one might expect and (3) motif matching does not occur.

## ACKNOWLEDGMENTS

I thank Luis Baptista, Jon Barlow, David Bradley, Cary Daniels, Bill Hardy, Don Kroodsma, Dwight Moore, Robert Payne, Jared Verner, and John Wiens for reading an earlier draft of this manuscript and offering many helpful suggestions. I express special thanks to Bill Hardy for his unflagging patience with me during my tenure as research associate at the Florida State Museum. I am also indebted to David Bradley for many hours spent in computer analyses of these data.

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