The Structure of Song and Its Geographical Variation in the Scarlet Tanager (Piranga olivacea)

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ABSTRACT: This paper describes variation in songs of scarlet tanagers in the N-central parts of the U.S.A., using both the traditional comparison of figure types, and a comparison of multivariate and univariate scores of frequency and temporal characteristics. The song is usually composed of 4-7 figures, its duration is 1.5-4.0 s, and its main sound energy is concentrated in the 2-5 kHz range. Each male possesses an average of 10 figure types, and his songs differ in the sequence of their figures. Many of the figure types are shared by individuals from localities hundreds of miles apart. In this respect scarlet tanagers have no dialects. However, individuals in Michigan share significantly more figure types with birds in their own region than with others.

Multivariate and univariate statistics reveal significant differences in frequency and temporal variables among individuals within a locality, among localities within a region, and among regions. Multiple stepwise discriminant analyses support these findings and show the differences in the contribution of the different variables to the variance. It is suggested that males establish their song characteristics when they are 1 year old and after dispersal from their natal site, and that the variation in frequency and temporal characteristics might relate to ecological factors.

INTRODUCTION

In songbirds, variation in songs has been investigated at different levels: within individuals, among individuals within a population and among populations. Song characteristics that vary among individuals can be used by birds for individual recognition such as discrimination of neighbors and strangers (Weeden and Falls, 1959; Emlen, 1971). Characteristics of songs that vary geographically are those from which birds can choose to recognize members of their own population, especially in species that have dialects (Lemon, 1967; Milligan and Verner, 1971; Harris and Lemon, 1974; Petrinovich and Patterson, 1981; McGregor, 1983). Song features that are common across the geographical distribution range of the species can be the basis for recognizing members of the species (Thompson, 1969; Emlen, 1972; Shiovitz, 1975; Beletsky *et al.,* 1980).

Traditionally, variation of songs has been investigated by visual comparison of the morphology of figures as they appear on sound spectrograms (sonagrams). The variation in the morphology of figures was suggested to function in recognizing neighbors and population members in species with "dialects" (Shiovitz and Lemon, 1980). Recently it was suggested that in addition to selection for individual recognition some ecological factors such as the acoustical characteristics of the habitat (reviewed by Wiley and Richards, 1978), body size (Bergmann, 1976) and interaction with other species sharing the same habitat (Cody, 1969; Brown, 1977) can explain geographical variation of song characteristics, especially variation in frequency and temporal characteristics and frequency-amplitude patterns. Therefore, a study of variation in songs should include quantitative measurements of these characteristics in addition to comparison of shape of figures. The variation could be described by comparing values of single variables using univariate statistical methods or by comparing values of a combination of variables (some of which are correlated), using multivariate techniques. Multivariate techniques are important because they are more objective means

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of examining an overall variation of a group of variables, but also because it is possible that birds perceive a complex structure of the song rather than breaking it down to discrete variables. The latter techniques were used for description of variation of songs of some avian species (Morgan *et al.*, 1976; Goldstein, 1978; Payne, 1978; Payne and Budde, 1979; Martindale, 1980a; Chew, 1981; for discussion of the application of these methods to the study of avian sounds *see* Sparling and Williams, 1978, *but also* Martindale, 1980b).

The main purpose of this paper is to describe the variation of song features in the scarlet tanager (*Piranga olivacea*) using both approaches described above (comparison of figure types as well as quantitative comparison of frequency and temporal characteristics) at three levels: among individuals in a locality, among localities within a region and among regions (groups of localities). Another purpose is to examine the usefulness of different statistical methods in describing geographical variation in songs. This was part of a larger study of the relation of geographical variation in song characteristics to habitat features, body size and interactions among closely related species in North American tanagers. Investigation of variation in song characteristics has not been done in the tanager group (Thraupinae). Singing behavior and songs of some tropical tanager species (Willis, 1960, 1972) and the scarlet tanager (Prescott, 1965) were described for the most part without spectrographic analysis.

MATERIALS AND METHODS

I recorded 912 songs of 59 males in four regions in the N-central part of the U.S.A. in 1979 and 1980: Michigan, Ohio, Indiana-Illinois and Tennessee-Alabama (Table 1 and Fig. 1). They were recorded with a UHER 4000 IC tape recorder and a UHER M517 microphone mounted on a 60-cm parabolic reflector. Sonagrams of these songs were produced with a Kay Elemetrics Sound Spectrograph model 6061B (in the wide band mode).

TABLE 1.—Localities and numbers of birds and songs recorded in each

Region	*Locality*	*No. of birds*	*No. of songs*
Michigan		*18*	*333*
	Pontiac Lake and Highland Recreation Areas (PNT)	10	187
	Stony Creek Metropark (STC)	1	16
	Waterloo Recreation Area (WTL)	7	130
Ohio		*15*	*181*
	Hocking Hills State Park (HKN)	5	61
	Fort Hill State Memorial (FHL)	7	93
	Fort Ancient State Memorial (FAT)	3	27
Indiana-Illinois		*13*	*176*
	Turkey Run State Park (Ind.) (TRN)	5	68
	Ferne Clyffe State Park (Ill.) (FRC)	5	68
	Beall Woods State Park (Ill.) (BLW)	3	40
Tennessee-Alabama		*13*	*222*
	Great Smoky Mountains National Park (Tenn.) (SMK)	8	144
	Bankhead National Forest (Ala.) (BNK)	5	78

Two types of analysis were performed: (1) Figure types were identified and compared visually from the sonagrams, (2) the following frequency and temporal characteristics were measured and calculated from the sonagrams with a digital plotter Tektronix 4662 used as a digitizer and a Data General Micronova Computer: song duration, number of figures in the song, highest frequency of each figure, lowest frequency of each figure, figure duration and interval between figures. Values for the following variables were computed for each song and used in the statistical analysis: song duration, number of figures in the song, maximum frequency, minimum frequency, frequency range, average maximum frequency of figures, average minimum frequency of figures, average frequency range of figures, average duration of figures and average interval between figures.

Statistical procedures. — In order to look for possible grouping of subjects (individual songs, or mean values of song for birds or populations) I performed principal components analysis (PCA). This analysis reduces the large number of variables to a smaller number of entities called principal components, and places the set of subjects in a multidimensional space. The importance of each component can be measured by the proportion of the total variance it explains. PCA does not test any statistical hypothesis. It is a tool for presenting the multivariate data, and can give rise to hypotheses that may be tested by other means. I examined the possibility that there are significant differences between groups of subjects by Kruskal-Wallis tests for each variable, and by multivariate analysis of variance (MANOVA) (the multivariate analog of the univariate analysis of variance) for all the frequency and temporal variables. Multiple stepwise discriminant analysis (MSDA) was performed to reveal

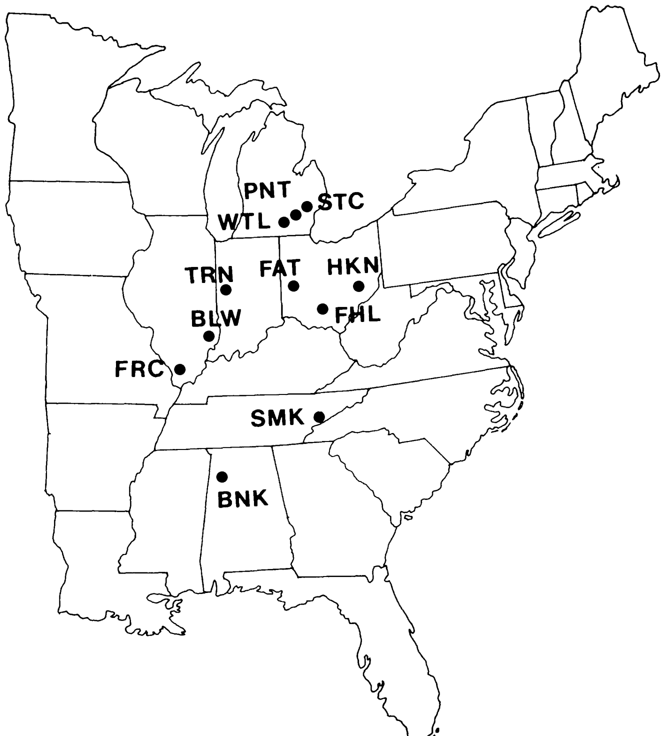

Fig. 1. — A map of the localities in which male scarlet tanagers were recorded in this study (abbrev. as in the Appendix)

the order of importance of variables in separating groups of subjects from each other. This multivariate technique maximizes differences between the groups and computes a sequence of discriminant functions to which variables are added in a stepwise manner, according to their respective ability to separate the groups. MSDA also verifies the distinctness of the preidentified groups by classifying individual subjects among the original groups.

All multivariate and univariate methods were performed with MIDAS, the computer statistical package of the University of Michigan.

RESULTS

Structure of the song. —The song is usually composed of 4-7 figures, its duration is 1.5-4.0 s, and its main acoustic energy is concentrated in the 2-5 kHz frequency range. A figure is usually a continuous unit of energy as appears on the sonograms (in some songs it is broken, as the second figure in Fig. 2 a,b,c). Figures are rarely repeated within one song. The first figure in the song is shared by most birds (64%) and is simple and short in duration. The first part of the song is usually stereotyped among an individual's songs. Each male possesses an average of 10 figure types (SD, 3.0). The reader can get some idea of how figure types were classified by examining Figure 2. According to my classification each song in Figure 2 is composed of several different figure types. The first three figure types in song b appear in the same order in song c. The fourth figure in song c (from Michigan) and the second figure in songs d, e, f (from Tennessee) are considered to be one type. Songs of each male differ in the last part of the song or their sequence or both. In this respect the scarlet tanager song resembles those of the rose-breasted grosbeak *Pheucticus ludovicianus* (Lemon and Chatfield, 1973), and the sedge wren, *Cistothorus platensis* (Kroodsma and Verner, 1978). In Figure 2 the third and the fourth figures in song d change positions in song e. Song e also includes two figure types that are not present in song d. Another type of change occurs in songs a and b. All the last three figures in song a differ from the last three in song b. The first four figures in song b appear in the same order in song c but another figure type is inserted between the third and the fourth figures. The pattern of singing

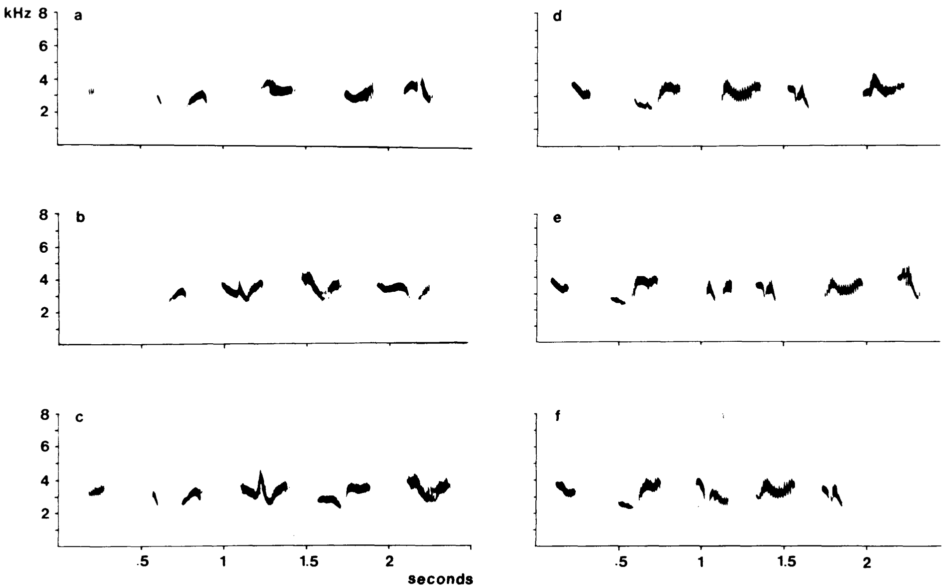

Fig. 2.—Sonagrams of three songs of a male scarlet tanager from Michigan (a,b,c) and three songs of a male from Tennessee (d,e,f)

different songs is not clear from examining my sonagrams. Scarlet tanagers do not sing a bout of songs consisting of one type and then switch to another type like song sparrows *Melospiza melodia* (Harris and Lemon, 1972), nor do they switch to another type after each song like fox sparrows *Passerella iliaca* (Martin, 1977). Analysis of hundreds of songs from each of several individuals is needed to reveal the actual pattern of sequencing figure types.

About half of the figure types are shared by more than one individual and I refer to them when I describe the variation in songs. Many of the others are less common in the individual's repertoire than the figures that are shared with other birds. Some figure types are more common than others. Each of 33 types is shared by more than 10% of the birds, 10 types by more than 20%, six by more than 30%, four by more than 40% and one (the first figure) by more than 50%. Figure 3 presents a cumulative graph of the number of new figure types vs. the number of songs of four individuals. According to this figure, the sample of songs that is sufficient to cover a bird's repertoire varies from 3-21 (average of 10.2). I was able to analyze, on the average, 15.5 (maximum 20) songs per individual.

Variation of songs among individuals within a locality.—To study this variation, I analyzed mainly 187 songs of 10 males from Pontiac Lake Recreation area in Michigan. Individuals of this population differ from each other in the number of types they possess (9-14), the number of types shared with others (7-13), and the number of types not shared with others (0-4). The range of figure types shared by each pair of males in this locality is 1-9. These numbers depend on the sample size. Seventeen of the 59 males recorded in this study compose seven groups of neighbors (2-3 birds in each group). In each of three of these groups (two in Michigan and one in Illinois), individuals share more types with each other than with others in their locality.

The left column of Table 2 presents the results of the Kruskal-Wallis tests that were performed to examine the possibility that the 10 individuals in Pontiac Lake Recrea-

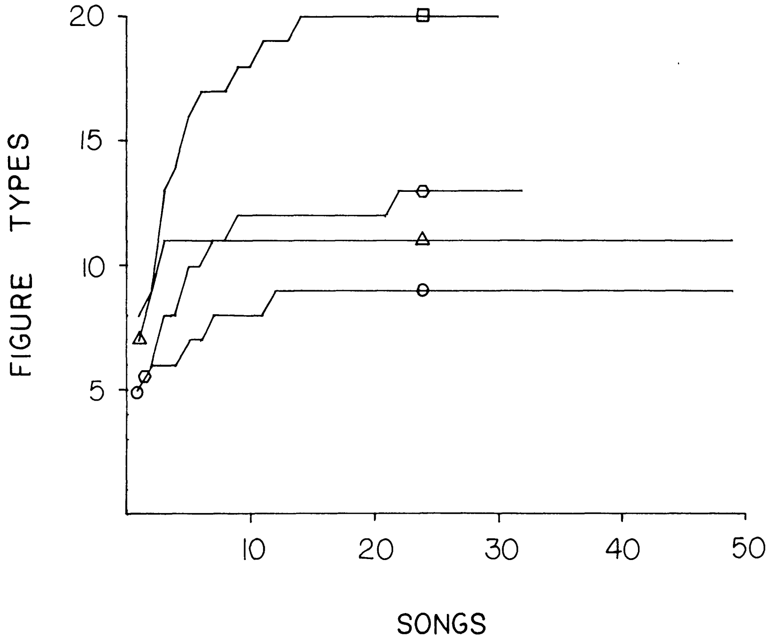

Fig. 3.—A cumulative plot of number of new figure types vs. number of songs in four scarlet tanagers

tion Area differ significantly from each other in each of the frequency and temporal characteristics measured and in the number of types of figures per song. These individuals differ significantly from each other in all the variables. Frequency range (but not average frequency range of a figure) and number of figures per song were eliminated from the statistical analysis because they were highly correlated to other variables. Multivariate analysis of variance also shows significant differences among the 10 individuals ($p < 0.0001$). The left column of Table 3 presents the order of importance of variables in separating the 10 individuals according to the multiple stepwise discriminant analysis, the variables that were excluded by the program as not significant in separating the individuals, and the percent of correct classification of songs to the 10 individuals. Seventy percent of the songs were classified correctly (to the right individual) by the program.

Variation of songs among localities within a region. —The geographical distance between localities within a region varies as well as the number of birds recorded in each locality (Fig. 1, Table 1). The results of the comparison of sharing figure types probably reflect sample size. In this analysis, only localities with at least five birds were included (8 out of 11). Table 4 shows what percentage of their figure repertoire is shared by individuals from each locality with individuals in other localities in their region. Also shown in this table are the results of Kolmogorov-Smirnov tests that examined the possibility that individuals of each locality share figure types more among themselves than with individuals of the other localities. Two localities showed this trend. The distance between these two localities and others in their region are much greater than among localities in other regions.

Principal components analysis results for the Ohio region are presented in Table 5 and Figure 4. The figure shows projections of individual birds on the first three components, and the table shows loadings of song variables on the three components. The figure suggests differences between localities within this region. FHL individuals are separated from HKN individuals by an imaginary vertical plane that passes diagonally from near the PC1-PC2 intersection (on the left) to near their intersection on the right. Therefore, they are separated by PC1 and PC2. Frequency characteristics load most on PC1 and temporal characteristics more on PC2. Within other regions there is no separation between localities (*see* Shy, 1982). Multivariate analysis of variance demonstrates significant differences between localities in each of the four regions ($p < 0.0001$). This is supported by the univariate Kruskal-Wallis tests that show significant differences between localities within each region in most of the variables (Table 2).

TABLE 2.—Results of Kruskal-Wallis tests of scarlet tanager songs within a locality (PNT), between localities within each region, and between regions[1]

	PNT	Michigan	Ohio	Ind-Ill	Tenn-Ala	Regions
SONGDUR	0.0001	0.0024	0.0001	0.0003	0.0001	0.0001
MAXFREQ	0.0001	0.0047	0.0125	n.s.	n.s.	0.0001
MINFREQ	0.0001	0.0001	n.s.	n.s.	0.0045	0.0001
AVMAX	0.0001	0.0001	0.0012	0.0114	0.0003	0.0001
AVMIN	0.0001	0.0001	n.s.	0.0001	n.s.	0.0001
AVRANGE	0.0001	n.s.	0.0321	0.0001	0.0003	0.0001
AVDUR	0.0001	n.s.	0.0001	0.0017	0.0001	0.0024
AVINT	0.0001	0.0001	0.0001	n.s.	n.s.	0.0001
NUMTYPE	0.0001	n.s.	0.0001	0.0008	0.0001	0.0001

[1]Results are given in p values; SONGDUR-song duration; MAXFREQ-maximum frequency of the song; MINFREQ-minimum frequency of the song; AVMAX-average maximum frequency of a figure; AVMIN-average minimum frequency of a figure; AVRANGE-average frequency range of a figure; AVDUR-average duration of figures; AVINT-average interval between figures; NUMTYPE-number of figure types in the song

About 75% of the songs were classified correctly to their own localities within each region (Table 3).

Variation of songs among regions. —The number of figure types shared by each pair of regions is not associated with the geographical distance between them. However, individuals in Michigan share significantly more types of figures (in percent) among themselves than with individuals in other regions (Kolmogorov-Smirnov tests, $p<0.01$). Males from other localities do not show this characteristic.

Principal components analysis that was performed for average values of the 11 localities did not indicati groupings of localities according to regions (*see* Shy, 1982). However, both multivariate analysis of variance ($p<0.0001$) and Kruskal-Wallis tests ($p<0.0001$ in all but one in which $p<0.0024$, Table 2) show significant differences among the four regions in all the variables tested. Only 54.5% of the songs were classified correctly to their own region by multiple stepwise discriminant analysis, but this is twice as likely as would be the case if the songs were distributed equally among the regions (25%).

DISCUSSION

Variation in figure types. —Although the general structure of the song is similar among scarlet tanager males, there are significant differences among them in the possession of certain figure types as well as in frequency and temporal characteristics, as was demonstrated by the analysis of songs of the 10 males from one locality in Michigan. Male scarlet tanagers may be able to recognize each other individually by the specific

TABLE 3. —Multiple stepwise discriminant analysis of scarlet tanager songs within a locality (PNT), among localities within each region, and among regions[1]

	PNT		Michigan		Ohio	
	Variable	p	Variable	p	Variable	p
Included	AVINT	0.0001	MINFREQ	0.0001	AVINT	0.0001
	AVMIN	0.0001	AVINT	0.0001	AVDUR	0.0001
	AVDUR	0.0001	MAXFREQ	0.0004	AVMAX	0.0008
	AVMAX	0.0001	AVMAX	0.0001	SONGDUR	0.0001
	SONGDUR	0.0001	AVDUR	0.0351	MINFREQ	0.0001
	MINFREQ	0.0001			AVRANGE	0.0031
	MAXFREQ	0.0120				
Not included	AVRANGE		SONGDUR		MAXFREQ	
			AVMIN		AVMIN	
			AVRANGE			
Classification		70%		76%		75%
	Indiana-Illinois		**Tennessee-Alabama**		**Regions**	
	Variable	p	Variable	p	Variable	p
Included	AVMIN	0.0001	DURATION	0.0001	AVINT	0.0001
	AVDUR	0.0001	AVDUR	0.0001	AVMAX	0.0001
	SONGDUR	0.0001	AVRANGE	0.0001	AVMIN	0.0001
	MINFREQ	0.0012	MINFREQ	0.0067	MINFREQ	0.0001
	AVINT	0.0001	MAXFREQ	0.0143	SONGDUR	0.0001
	AVRANGE	0.0086			AVDUR	0.0001
					MAXFREQ	0.0371
Not included	MAXFREQ		AVMAX		AVRANGE	
	AVMAX		AVMIN			
			AVINT			
Classification		76%		73%		55%

[1]Levels of maximum and minimum inclusion are 0.05 and 0.1, respectively; abbreviations as in Table 1; percentage figures show correct classification of songs to the original groups by the discriminant functions

figure type repertoire each of them possesses and also by the specific sequence of those figures (as the first part of the song is more stereotyped within individuals than the last). Since males differ significantly in a combination of frequency and temporal characteristics, they can use at least some of them for individual recognition also. This is speculative and only behavioral experiments can test which of the individual characteristics is important in individual recognition. Matching of song types can help neighbors recognize each other (*see* discussion in Krebs and Kroodsma, 1980), but males within some groups of neighboring scarlet tanagers sing loudly against each other without matching their songs. It seems that if individual recognition takes place in this species, matching is not essential to the recognition process.

Geographical variation in songs among contiguous groups of birds can be gradual,

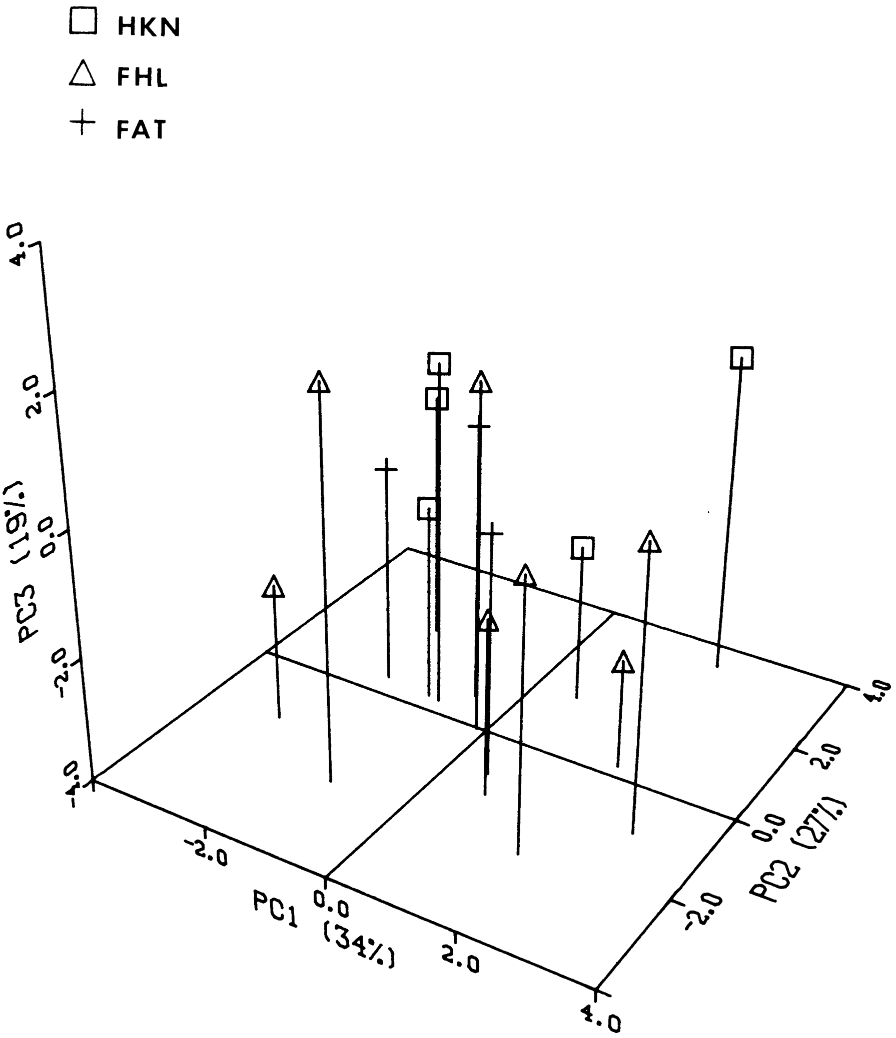

Fig. 4.—Projections of song characteristics of scarlet tanagers from Ohio on the first three principal components (the amount of the variation accounted for by each component is given in parentheses)

rapid over a restricted contact zone, or sudden with a sharp boundary (Krebs and Kroodsma, 1980). Scarlet tanagers do not have a set of figure types restricted to a small area, so in this respect they have no dialects (Lemon, 1975; Payne, 1973:137). The distribution of scarlet tanager figures more closely resembles species like the indigo bunting *Passerina cyanea* (Shiovitz and Thompson, 1970), in which many figure types are shared by birds in large areas of their distributional range. Geographical variation in figure types is detected in small distances but not on a large scale. Only in two localities do individuals share more figure types among themselves than with individuals in other localities in their region. Also, only in Michigan individuals shared significantly more types of figures with each other than with individuals in other regions. These findings may reflect the closer spacing of individuals in Michigan than in other regions sampled. These findings might reflect also distances among localities within each region (Fig. 1). The two localities that were significantly different in song characteristics from other localities in their own regions were also much more distant from these localities. Wiens (1982) found that whereas there is a tendency for the songs of distant populations of the sage sparrow *Amphispiza belli* to differ more than those in nearby locations, some nearby locations share many song elements and patterns and some do not.

Assuming that scarlet tanagers learn their songs like most songbirds that have been studied so far (Krebs and Kroodsma, 1980), then the distribution of figure types within and between localities raises the question of how they learn their songs. The fact that there are no dialects and that some neighbors have similar songs and some do not might be explained by suggesting that males establish their song characteristics in a place other than their natal site in their first breeding season when they are 1 year old. This was found in other birds (such as the indigo bunting, Rice and Thompson, 1968; Thompson, 1970; Payne, 1981) with a similar pattern of geographical variation in figure types. Neighbors that do not share much of their figure repertoire are probably

TABLE 4. — Mean percentages of figure types shared by male scarlet tanagers from each locality with other localities in their region[1]

Region	Locality	% shared	p
Michigan	PNT	63	n.s
	WTL	63	n.s
Ohio	HKN	58	n.s
	FHL	41	n.s
Ind-Ill	TRN	53	0.05
	FRC	69	n.s
Tenn-Ala	SMK	49	0.05
	BNK	72	n.s

[1]Abbreviations as in Table 1

TABLE 5. — Loadings of variables on the first three principal components within the Ohio region[1]

	PC1	PC2	PC3
MAXFREQ	.549	.012	.736
MINFREQ	.458	.034	.141
AVMAX	.549	.097	.103
AVMIN	.417	.154	.116
AVINT	.000	.419	.528
SONGDUR	.012	.621	.020
AVRANGE	.428	.000	.046
AVFIG	.052	.578	.268
AVDUR	.356	.265	.245

[1]AVFIG-number of figures in the song; other abbrev. as in Table 2

males that dispersed after their song characteristics were established. It is also possible that males learn their songs only in their natal site and that those that share their songs might have established their territories near their father or a neighbor from the previous year. However, it seems less likely that males will be able to establish their territories right next to the male from which they learned the song in the previous or the same year (as suggested by Thompson, 1970). The learning period of songs in scarlet tanagers might be affected by environmental factors such as the photoperiod in the time of hatching and the amount of song heard during the hatching year, as in marsh wrens *Cistothorus palustris* (Kroodsma and Pickert, 1980). Scarlet tanagers nest in Michigan from late May until late July. Many first nesting attempts are unsuccessful and, therefore, hatching time may vary among individuals. Raising a second brood is probably uncommon (Prescott, 1965). Most of the young are probably exposed to song to some extent in the hatching year, since singing occurs throughout the breeding season (Bent, 1958; Prescott, 1965; Shy, pers. observ.). The various learning mechanisms of song mentioned here, and nestling and adult mortality were suggested as possible explanations for distribution of song types in other birds (*e.g.*, Wiens, 1982). These alternatives could be examined only by raising birds in isolation and by tracing bird and song dispersal in the wild.

Variation in frequency and temporal characteristics. — Geographical variation in frequency and temporal characteristics is more pronounced than geographical variation in figure types. At all levels of comparison (between individuals in one locality, among localities within a region, and among regions), there are significant differences between groups in song variables. Are some variables more important than others in separating the groups in each level of comparison? When each variable is examined separately (Table 2), and differences are maximized by multiple stepwise discriminant analysis (Table 3) almost all variables show significant differences between individuals in one locality and between regions. The variation pattern in song characteristics among localities within a region is more complicated; regions differ from each other in the importance of particular variables for separating localities. This might be due to differences in distances between localities within each region, and in the extent to which localities are isolated from each other.

In some cases in this study there is much overlap in the principal components space between groups among which significant differences were found by multivariate analysis of variance and Kruskal-Wallis tests. One should not conclude that principal components analysis is not useful in describing variation in bird songs for the following reasons: This technique predicted differences between song groups more successfully in some of the studies mentioned in the Introduction; also, in interpreting the data it is important to know that there could be much overlap in the multivariate space, although the differences between song groups may be significant. Description of geographical variation in songs, using different methods and approaches, as done in this study, should be continued until we have more information on the specific variables or a combination of them that are perceived by birds when listening to songs of others.

The fact that frequency and temporal characteristics vary geographically in the scarlet tanager suggests that ecological factors might be involved in shaping some song characteristics of this species (Wiley and Richards, 1978). The relation of variation in song features to habitat characteristics in the scarlet tanager and the summer tanager is discussed elsewhere (Shy, 1983).

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