SONG SIMILARITY BETWEEN NEIGHBORING AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*): A STATISTICAL ANALYSIS

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ABSTRACT.—We examined the hypothesis that territorial American Redstart (*Setophaga ruticilla*) males are geographically randomly distributed with respect to structure of the single song used predominantly before nesting. Present methods to assess the degree of similarity of song between neighboring birds are often inadequate because they do not give the level of statistical significance. We present a computer method to generate the appropriate null distribution from which the level of significance can be determined. We found statistically significant correlations between neighbors primarily in the last and penultimate discrete vocal items (phones) of the song. There were also important differences between the 2 samples. *Received 25 November 1987, accepted 29 May 1988.*

SONG sharing among neighboring birds has been interpreted as both adaptive and non-adaptive. Adaptive hypotheses assume a causal link between biological and cultural evolution (Payne 1982, 1985; Wiley and Richards 1982; Baker and Cunningham 1985; Baker and Thompson 1985; Boyd and Richerson 1985). The nonadaptive hypotheses presume that song sharing is merely a result of vocal learning between neighbors (Slater et al. 1980, Wiens 1982).

A fundamental question is how to assess the degree of similarity of song across individual species. Two standard methods prevail in the literature. One effectively matches by eye the sound spectrographic patterns; the other uses some multivariate approach based on measurable features of the song. The former method is based on an assumption of types, whereas the latter assumes song variation may be more continuous, although possibly discrete as well. The "type" approach has been used widely (e.g. Bradley 1977, Lemon et al. 1985, Slater et al. 1980), and the more continuous methods less so (e.g. Lemon et al. 1983, Cunningham et al. 1987). Either way one ends up with a map or

cluster diagram of song distributions (e.g. Payne and Budde 1979, Wiens 1982).

If the measures of song similarity correlate with distance, one has a measure of significance (e.g. Payne and Budde 1979). If, however, the distributions of song are spotty, no *a priori* correlation with distance need be expected. There is no sampling nor distribution theory associated with clustering techniques and consequently no significance tests (Sokal and Sneath 1973). Some songs are so peculiar and their distributions so limited that questions of significance of similarities are unnecessary.

Other songs may be less distinctive and thereby overlap more with others both in structure and in distribution, so that a more sophisticated analysis of similarities is necessary. One solution to this problem is to use the observed data to generate the appropriate random null model. We combined the multivariate approach with such a computer randomization procedure.

Our subjects were American Redstarts (*Setophaga ruticilla*). Males of this species, like many New World warblers, subdivide their song repertoire (1–9 songs) according to functional sit-

TABLE 1. Phone features used as variables for analysis. Not all variables were measured on each phone (4 on LP-2; 5 on LP-1; 6 on LP).

PHONE FEATURES as measured on last 3 phones of song: last phone (LP), next-to-last phone (LP-1) and third-to-last phone (LP-2)	
a) FMAX	Maximum frequency of phone (kHz)
b) MINFR	Minimum frequency of phone (kHz)
c) DUR	Phone duration, from beginning to end of phone (s)
d) INT	Duration between the measured and preceding phone (s)
e) UP	As measured on last 2 phones of song (LP-1, LP), proportion of total duration of phone spent in upward sweep in frequency (percentage)
f) INFPTS	As measured on last phone (LP), inflection points, changes in direction of frequency sweep of at least 300 Hz as seen in standard spectrogram

uations. Prior to and during the arrival of females, each male sings one particular song repetitively in preference over the others. We designate this song as the "repeat" mode. The rest of the repertoire, the "serial" mode, predominates through much of the remainder of the season, and is often used in interaction between males (Lemon et al. 1985). The detail of the repeat song varies considerably between individuals. The most common form has a series of sounds (referred to here as "phones") that sweep downward in frequency, followed by one or two different, unrepeated phones that effectively "accent" or stress the song's termination (Fig. 1). We examined the hypothesis that redstart males were randomly distributed geographically with respect to the structure of the repeat song.

METHODS

Study site and sampling procedure.—The study was located at the Huntsman Marine Laboratory (HML) and Sunbury Shores Arts and Nature Centre (SS), St. Andrews, New Brunswick (45°05′N 67°04′W). The breeding male population is composed of adults and subadults. Adult males are 2 or more years old and distinguishable from subadult males by their plumage. Birds were individually color-banded. No obvious physical boundaries divided territories within populations. Geographically adjacent males that appeared to interact frequently by countersinging and fighting bouts were considered to be socially interactive.

Songs were recorded during the breeding season (May–July) in the same areas in 1982 and 1984. We used Dan Gibson parabolic reflectors, Sennheiser microphones, and Uher 4200 stereo tape recorders, run at 19 cm/s. The recordings were reproduced as spectrograms with a Kay Elemetrics SonaGraph (model 6061B) on wide band width (300 Hz). We analyzed 40 repeat songs (Song 1, Lemon et al. 1985). We mea-

sured 15 variables that describe frequency and temporal features on the last 3 phones within a song. These phones were designated as last phone (LP), next-to-last phone (LP-1) and second-to-last phone (LP-2) in song (Table 1, Fig. 1). Data for each year were treated separately.

Reliability of sampling procedure.—The stability of individual songs was tested with a one-way multivariate analysis of variance [MANOVA (SAS 1982)] with individual birds as the treatment. To assess if variation of songs between individuals was greater than within, we compared the mean vectors of individual songs. We used a sub-set of the data recorded from 7 individual birds, 67 songs, and 15 song variables. Using Wilks's lambda as the MANOVA test criterion, variation in song characters among birds was greater than within individual birds ($F_{90,265} = 79.21, P < 0.0001$) (SAS Institute Inc. 1982). Thus we assumed stability of individual song structure in regards to testing the proposed hypothesis of song similarity between neighbors.

Analysis of song and neighbor distribution.—The hypothesis to be tested was that the song structure of a given bird was correlated with the song structure of its neighbors. We tested this by computing the correlation coefficient of song variables between a bird and its neighbors (i.e. birds with territories contiguous with those of the subject). Two difficulties must be considered. First, correlating each of the 15 variables separately greatly increases the probability of a significant result by chance alone. To reduce the possibility of a spurious significant correlation, each phone was reduced to a single descriptive variable, the first component of a principal components analysis. The first components accounted for 33–45% of sample variance. This reduced the 15 variables to 3 separate principal components, one for each phone.

All components might have been reduced to a single variable by principal components analysis (PCA) on all 3 phones combined. This alternative approach could have obscured effects of individual phones and a significant correlation resulting from the effect of components of a single phone could be negated by the noise introduced by the other phones. Of course,

the same argument applies to effects due to individual phone components. The division by phone was a compromise to reduce the problem of multiple tests. This division is objective in the sense that the phones are temporally distinct. We attached no particular significance to the use of PCA to reduce the phone components to a single variable; other methods of clustering conceivably might have been used. We consider PCA an obvious and reasonable method.

The second difficulty is that the "independent" variable, the song of bird *x*, is not independent of the dependent variable, the neighbor song, because bird *x* also occurs as a neighbor. The expected value of the regression coefficient is, in fact, negative. This can be demonstrated as follows. The distribution of birds on the x-axis is obviously the ascending ranking of birds. Consider now the first bird; all of its neighbors have larger values. Similarly the neighbors' values of the last bird on the x-axis must be less than his. For the second bird on the x-axis only 1 value at most, that of the first bird, can be less than his. Similarly, for the second-to-last bird only, the last bird can have a larger value. Thus there must be a bias towards higher values at the low end on the x-axis and low values at the high end.

This problem of lack of independence was solved by estimating, via simulation, the probability of observing by chance alone a correlation coefficient as large as or larger than that obtained from the data. We constructed 5,000 randomized sets from each data set (1982 and 1984). From these, the null distribution of the correlation coefficient was generated for each year. Each randomized data set satisfied 2 requirements. First, if bird *i* is neighbor to bird *j*, bird *j* must be neighbor to bird *i*. Second, the frequency distribution of the number of neighbors/bird must remain the same (see below). For the 1982 data set, the randomization procedure indicated that the expected correlation was approximately −0.03. Although the expected value of the correlation is negative as predicted, the bias is small.

To demonstrate how a randomized data set was produced, we consider a sample that comprised 4 birds: 2 with only 1 neighbor each, and 2 with 2 neighbors each. The neighbor relationships can be specified by the 4 × 4 matrix (*n* × *n* for *n* birds):

		Neighbor to bird *i*			
		1	2	3	4
	1	·	x_1	0	0
Bird *i*	2	x_2	·	x_3	0
	3	0	x_4	·	x_5
	4	0	0	x_6	·

where x_i is the value (principal component score or metric in the case of individual phone components) between neighboring birds as shown, and 0 indicates that birds are not neighbors. The row designation 1,
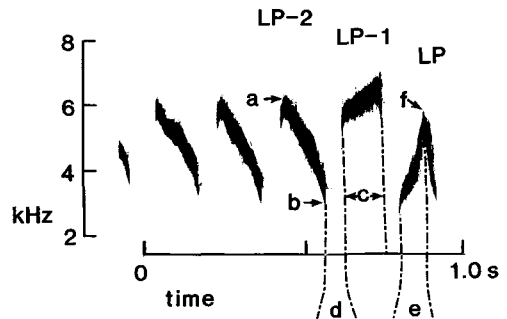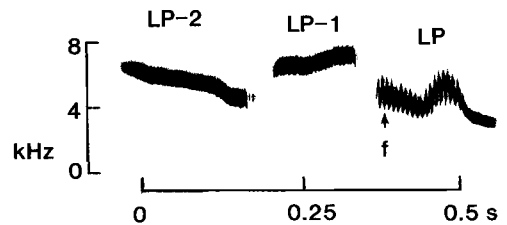

Fig. 1. Spectrograms of phone variables used in analysis. Phones are designated as last (LP), next-to-last (LP-1) and second-to-last (LP-2). A) A complete American Redstart song used in repeat mode and showing the typical accented ending. Measured variables are a = maximum frequency; b = minimum frequency; c = duration of phone; d = interval between measured and preceding phone; e = proportion of total duration spent in upward sweep in frequency; f = number of inflection points, changes in direction of frequency sweep of at least 300 Hz. B) Last 3 phones of a different song at ½ speed. Last phone showing many inflection points (f). Variables a–f measured on LP, a–e measured on LP-1, a–d measured on LP-2.

2, 3, 4 is now randomized, giving, for example, 4, 2, 1, 3:

		Neighbor to bird *i*			
		4	2	1	3
	4	·	x_1	0	0
Bird *i*	2	x_2	·	x_3	0
	1	0	x_4	·	x_5
	3	0	0	x_6	·

The rows are finally reclassified in order and the entries within the matrix moved accordingly (e.g. "old" bird 4 becomes "new" bird 1) to produce the randomized set:

TABLE 2. Correlations between neighbors using the first principal component of LP-2, LP-1 and LP.

Principal compo-nent	1982 Correla-tion between neigh-bors	P	1984 Correla-tion between neigh-bors	P
LP-2	0.0082	0.425	0.2637	0.034
LP-1	0.3749	0.005	0.2665	0.031
LP	0.2722	0.028	0.0782	0.238

TABLE 3. Correlations between the first principal components of the last 3 phones. Lower diagonal values refer to 1982 data ($n = 34$); upper refer to 1984 data ($n = 40$). Significant correlations indicated by asterisks ($P < 0.05$).

	LP-2	LP-1	LP
LP-2	1	0.279	0.097
LP-1	0.484*	1	−0.468*
LP	0.724*	0.587*	1

Neighbor to bird i

		1	2	3	4
	1	.	x_4	x_5	0
Bird i	2	x_3	.	0	x_2
	3	x_6	0	.	0
	4	0	x_1	0	.

Several significant correlations between neighbors may be due to the 3 variables themselves being correlated. We examined this effect by an analysis of residuals. Suppose two variables, say X and Y, generate significant correlations between neighbors. Further, suppose that X and Y are themselves correlated. To examine the influence of X, we regress Y on X and compute the residuals $[Y' = Y - (a + bX)]$, where a and b are the intercept and slope of the regression of Y on X. Because the variables are standardized, b is equal to the correlation coefficient between Y and X and $a = 0$; i.e. $Y' = Y - rX$. We then compute the correlation between neighbors based on their respective residuals, Y'. This "partial" correlation indicates the extent to which the 2 significant correlations between neighbors results from a common source.

When significant correlations between neighbors were obtained, we undertook to locate which of the 15 variables accounted for most of the variance by examining all 15 correlations. It must be stressed that this stage of the analysis was designed not to establish the significance of the correlation between neighbors, but rather to determine which components generated this significance.

RESULTS

Neighbor distribution and associated song structure.—We obtained a significant correlation between neighbors for the first principal component of the penultimate phone (LP-1) in both years (Table 2). From the 1982 data we also obtained a significant correlation between neighbors for the first principal component of the last phone (LP), while from the 1984 data the

second-to-last phone (LP-2) yielded a significant correlation.

The first principal components of all 3 phones in the 1982 data were correlated with each other (Table 3). To assess this effect on the correlation between neighbors, we proceeded with a residual analysis as described in the Methods. To isolate independent effects, we regressed LP-1 on LP-2, and LP on LP-2, and repeated the analysis on LP-1' and LP'. The correlation between neighbors was increased for both LP-1' and LP' (Table 4). In 1982, there was a substantial increase in the correlation between neighbors for both LP-1 and LP after correcting for the correlation with LP-2.

The residuals LP-1' and LP' in the latter analysis also were correlated significantly ($r = 0.392$, $P < 0.001$). To assess the extent to which these correlations influenced the separate correlations between neighbors of LP-1' and LP', we proceeded in the same manner as with LP-2. We used a regression of LP-1' on LP', and vice versa, and analyzed the residuals (LP-1" and LP"). There were only minor decreases in the two resultant correlations (Table 4), which indicated that the correlations obtained from LP-1 and LP neighbors were not due to collinearity between these variables.

In the 1984 data, phones LP and LP-1 were correlated significantly (Table 3). To examine the influence of LP-1, we regressed LP on LP-1 and recomputed the correlation between neighbors using the residuals (LP'). To remove the effects of LP, we regressed LP-1 on LP and likewise recomputed the correlation between neighbors using the residuals (LP-1'). In both cases the correlation was reduced to an insignificant level (Table 2). Therefore, for 1984 we cannot separate effects that are specific to only one phone.

The first principal component scores of the penultimate phones (LP-1) gave significant correlations between neighbors in both years. For

TABLE 4. Correlations between neighbors from the residual values of the first principal component of LP-2, LP-1, and LP. Primes indicate the residuals obtained from $Y' = Y - rX$ where Y and X were 2 of the principal components, and r was the correlation between X and Y. Double primes indicate the analysis based on the residuals of the regression of Y' on X'.

Year	Y	X	Correlation between neighbors using Y'	P
1982	LP-1'	LP-2'	0.464	0.001
	LP'	LP-2'	0.400	0.004
	LP-1"	LP"	0.438	0.002
	LP"	LP-1"	0.381	0.005
1984	LP-1'	LP'	0.133	NS
	LP'	LP-1'	−0.071	NS

TABLE 5. Correlations between neighbors for the 15 original variables.

Variable[1]	Correlation between neighbors		P	
	1982	1984	1982	1984
LP-2				
FMAX	0.164	0.202	NS	NS
MINFR	0.031	0.130	NS	NS
DUR	0.292	0.166	0.021	NS
INT	0.047	−0.114	NS	NS
LP-1				
FMAX	0.015	0.160	NS	NS
MINFR	0.202	0.112	NS	NS
DUR	−0.072	0.099	NS	NS
INT	0.097	0.211	NS	NS
UP	0.567	0.324	0.0002	0.015
LP				
FMAX	0.086	0.007	NS	NS
MINFR	−0.142	−0.089	NS	NS
DUR	0.353	−0.001	0.009	NS
INT	0.059	−0.015	NS	NS
INFPTS	0.058	0.062	NS	NS
UP	0.084	−0.056	NS	NS

[1] Variables described in Table 1.

the 1982 data set, the between-neighbor correlation obtained using the last phone was independent of factors that it had in common with the penultimate phone. However, we cannot demonstrate this for the significant correlation between neighbors obtained using the last phone in the 1984 data.

Variables contributing to significant neighbor/song correlations.—To determine the source of the significant correlations between neighbors' songs, we examined the contribution of each of the 15 original variables. In each phone, no more than a single variable produced a significant correlation (Table 5). In the case of LP-1, the correlation was greater in both years than that obtained from the respective first principal component or its residual value. Similarly, in the case of the duration of LP for 1984, the correlation was also increased. These results indicate that the correlation between neighboring birds depended primarily upon these single variables. The other phone variables tended to obscure the independent effect of single variables in the principal component analysis and reduced the correlation between neighbors.

Although we found a significant correlation between neighbors for the first principal component of LP-2 in 1984 (Table 2), no single component of LP-2 correlated significantly, though FMAX approached significance ($P = 0.072$). One variable of LP-2 (duration) in 1982 was also significant (Table 5). Duration was highly correlated to both significant variables in the LP-1 and LP: UP of LP-1 ($r = 0.60$, $n = 40$, $P < 0.001$) and duration of LP ($r = 0.486$, $n = 40$, $P < 0.002$).

As before, we tested for the independent importance of LP-2 by computing the residuals from the multiple regression of duration of LP-2 on UP of LP-1 and duration of LP which yielded the equation: $Y = 0.56X_1 - 0.43X_2$, where $Y =$ LP-2, $X_1 =$ percent time up of LP-1, and $X_2 =$ duration of LP ($r = 0.74$, $P < 0.001$). The resulting correlation between neighbors was not significant ($r = 0.0902$, $P < 0.2$), and demonstrated that the original apparent significance of LP-2:DUR resulted from the correlation of LP-1:UP and LP:DUR. These latter 2 variables were uncorrelated ($r = 0.092$, $n = 40$, $P > 0.2$), indicating that LP-1 and LP incorporate different components, as previously found.

In summary, UP of LP-1 in both 1982 and 1984, and DUR LP in 1982, yielded significant correlations between neighbors independently. In addition, UP yielded a higher correlation alone than when combined with other variables in a principal component.

Graphic distribution of neighbors and songs in 1982.—The actual neighbor distribution with respect to percent time in upward moving frequency of LP-1 for 1982 is depicted in Fig. 2. For ease of presentation, the values of the entire population were divided into 6 arbitrary categories ranging from 0–100% time spent in UP. The distribution of categories is bimodal, and
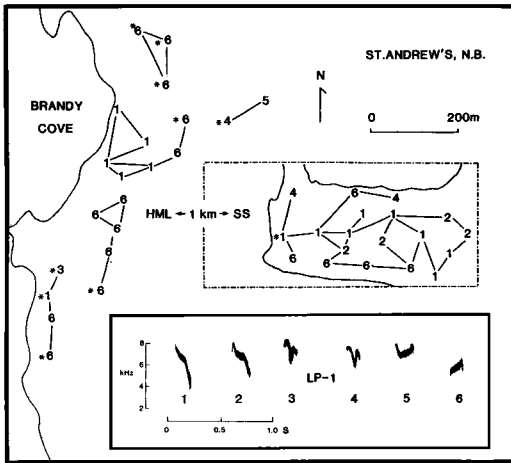
Fig. 2. Map showing location of neighboring red-starts coded by value of LP-1:UP (second-to-last phone: percentage of time spent in upward moving frequency) at two areas, HML and SS at St. Andrews, N.B. in 1982. Solid lines between values connect socially interactive neighbors. Solid bordered inset depicts representative spectrograms of categories 1–6 of phone variable LP-1:UP (see text). Dashed bordered inset shows subarea SS. Yearling males are starred (*).

Fig. 3. Individual spectrograms showing last 3 phones of repeat song of HML neighborhoods coded A–E in 1982. In the center is a "map" showing relative geographic location of birds, where each number is the coded value of variable LP-1:UP, as in Fig. 2.

the majority of individuals fall either in categories 1 or 6. Minimum frequency of phone category 1 is readily distinguishable from minimum frequency of phone category 6. Note that the most common categories 1 and 6 occur with comparable frequencies in both subareas, HML and SS (Fig. 2). The last 3 phones of each individual song in the HML area are shown in Fig. 3, where it is evident that neighboring males typically shared very similar last 2 phones (neighborhoods "A," "B," "D"), although with differences between neighborhoods being evident. The small map aids in directing attention to LP-1 of each male.

DISCUSSION

The method we used allowed us to determine that the neighbor associations by song were other than random; those parts of the song that yielded these significant associations; and the variables which were the bases for the significance of the song parts. An analysis based on types and some clustering technique would not have permitted the last.

We found consistent nonrandom associations of male American Redstarts based on the features of the next-to-last phone (LP-1) in the song.
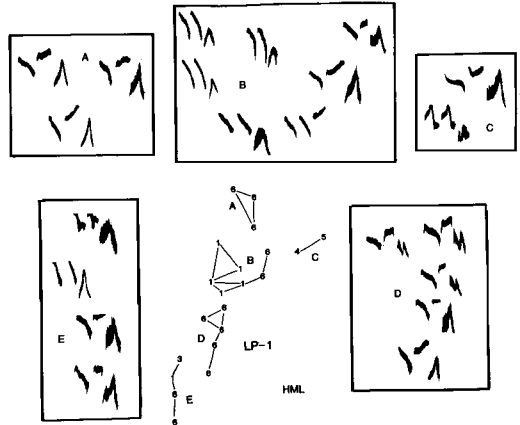
This was attributable to percent of frequency sweep in upward direction (UP). There was a range of variation of LP-1 phones such that, at one extreme, some are swept entirely downward in frequency; at the other extreme, others are entirely upward, with still others in between (Fig. 2, Fig. 3). For 1982 we found a significant correlation of neighbors based on the last phone as well, related to its duration. Some striking groupings are illustrated (Fig. 3, boxes D and E). In some cases not shown in the figures, a few males [roughly 5% (Lemon et al. 1983)] simply repeated the same phones throughout the entire song without adding the unrepeated accents at the end.

In spite of the similarities, there were discrepancies between samples from the years, particularly in the significance of the last phone (1982 vs. 1984). Also, there was a discrepancy between the correlation obtained for LP-2: significant in 1984 but not 1982. Why the differences occur between the 2 years is not clear, but it must be related in part to how the similarities are achieved originally. Part of the answer probably would come from the interplay of copying at some stage of life and by geographic movement at other times. It is relevant that the correlation between the first principal components of the last 3 phones changed dramatically between the 2 years, even reversing in sign (Table 3).

We made no attempt to separate contributions of yearlings or subadult males, although

these males are indicated in the figures. Clearly, they participated in some of the song neighborhoods. The significant associations we found were not based on larger "neighborhood" groupings within the study area itself. For example, the extremes of variation of LP-1 occurred in both subareas (Fig. 2).

The high similarity of the endings of the songs implies that the details of this portion of the song are evident to a perceiving redstart. It was particularly evident to us that even the last phone was often similar. Yet the difference in the rhythm of the song induced by next-to-last phone (LP-1) had easily detectable differences at a distance, even if the details of the phones were not apparent. Where LP-1 was a frequency upsweep, it extended the ending; otherwise the repetition of LP-1 and LP-2 before the last phone led to a seemingly quicker and more abrupt end.

These songs described here often prevail early in the season at the time of mate attraction. They may assist females in visiting neighborhoods of males with whom they have had previous breeding experience. Experimental playback of model songs to territorial males shows maximal responses to songs with or without the peculiar "accented" ending (Date and Lemon ms), so these accents are not essential to species identification by males. If we broadly define accenting as the ending of a song with a non-repeated phone when preceded by repeated ones, then the feature occurs in several American warblers, especially in *Dendroica, Parula*, as well as *Setophaga*, but not others such as *Vermivora, Oporornis* (Lemon et al. 1983). The *Parula* case is interesting because the actual terminal phone is often identical to some used by redstarts. These "accented" and often low frequency phones may be particularly useful for long-distance signaling (Lemon et al. 1981).

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