

SONG REPERTOIRES AND SONG SHARING BY AMERICAN REDSTARTS

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ABSTRACT.— We studied the extent to which male American Redstarts (*Setophaga ruticilla*) share songs in their repertoires. Examining samples of songs from three locations in New Brunswick, Canada, we found significant heterogeneity in the frequencies of the different songs across the locations. The extent to which neighbors shared songs related to increasing repertoire size (mean 4.4 songs/adult male). In the relatively larger sample at St. Andrews, neighboring adult males shared significantly more song types ($P < 0.05$) than did adult males chosen at random. However, this result applied only to individuals with intermediate-sized repertoires (four songs). Subadult males at St. Andrews shared as much with neighboring adult males as did adult males among themselves. In the small, island population at Back Bay, adult males shared noticeably more songs than at St. Andrews. We attribute the difference in degree of song sharing to demographic aspects, including patterns of settlement, interacting with tendencies to copy songs. Therefore, any so-called “dialects” in songs of American Redstarts seem more as “epiphenomena” resulting from competition between males rather than as indications of local adaptations of males.

The geographic distribution of similar patterns of sound used in bird song is often considered to reflect one or a number of selective pressures. These include preference for males adapted to local environments and identified by particular song patterns (Baker 1975, Baker et al. 1981); the competitive interactions of males for gaining advantage either through mimicry of superiors (Payne 1981, 1982) or by improving their competitive status in direct aggressive encounters between males (Hinde 1958, Lemon 1968); and the effects of selection on acoustic features of the song by environmental factors (Richards 1981). Alternatively, distributions of bird songs may reflect only the effects of chance with no direct selection involved (Slater et al. 1980). Patterns of song similarity are known to vary considerably across species (Mundinger 1983), consequently a single functional basis for the distribution of bird songs need not apply.

In this study, we examined the distribution of songs of American Redstarts (*Setophaga ruticilla*) resident in coastal New Brunswick. Although islands are common along the coast of New Brunswick, there appear to be no major boundaries to dispersal for this migratory species. Relative to other warblers (Parulidae), this species has moderate-sized repertoires averaging somewhat over four songs per male. We investigated: (1) whether song types were

shared to a significant degree among three close sites; and (2) whether sharing was significantly greater between immediate neighbors on contiguous territories than between non-neighbors. In order to make these comparisons, we first established a classification of the songs and considered the problem of repertoire size on the extent of song sharing.

Having made these comparisons, we then examine the results in light of the hypotheses cited above. Although this study in itself is not sufficient for the elimination of any of the hypotheses, nonetheless the results point to the use of the songs in competition between males (see Discussion).

METHODS AND MATERIALS

LOCATION OF SAMPLES

This study is based on tape recordings of songs made at Back Bay, New Brunswick, in May and June, 1979, and at or near St. Andrews, N.B., May through July in 1980, 1981, and 1982 (see Fig. 4). At St. Andrews, the study was performed on properties of the Huntsman Marine Laboratory; Fisheries and Oceans, Canada; St. Andrews Golf Course; and Sunbury Shores Arts and Nature Centre. The first three properties combined (designated HML) were 40 ha in size; the last (designated SS) was 10 ha. At Back Bay (BB), the birds studied

were resident on a 5-ha property of D. B. McMillan at Leavitts Head. These sites lie within the Maritime Lowlands Ecoregion (Loucks 1961) dominated by spruce-balsam (*Picea-Abies*), but include numerous deciduous elements.

Songs were recorded by Uher 4000 or 4200 tape recorders at 19 cm/s using Dan Gibson parabolic reflectors and Uher or Sennheiser microphones. In the last three years, birds were banded, both with an aluminum numbered band and with three plastic colored bands. In 1979, they were number-banded and individually marked with temporary wing tags.

Measurements of "phones," which we defined as individual sounds continuous in time, were made from sonagrams (Kay Elemetrics), and were used for principal components analysis (PCA) and discriminant analysis. The measures were: maximum and minimum frequencies, band-width in octaves, number of inflection points of change in direction of frequency sweep, initial sweep direction, span of longest frequency sweep, rate of longest frequency sweep, percentage time in down sweep. Multivariate statistical analysis was achieved by using the Statistical Package for the Social Sciences (Nie et al. 1975).

We designate males of one-year age-class as "sub-adult" (=SY, or second year) and two-year-olds or older birds as "adult" (=ASY, or after second year [North American Bird Banding Techniques 1977]).

SAMPLING OF REPERTOIRES

Repertoires were sampled in relation to the way in which they are given: repeating one particular song type over and over, and then proceeding through the remainder of the repertoire in serial fashion with little repetition. The former pattern is most frequent early in the season before the females arrive. As a result, one would have to record each bird on at least two occasions to get both repeat and serial modes. In practice, however, we recorded the serial modes on at least two occasions and a maximum of ten different days. We tape recorded hundreds of individual songs, subsequently identified in real-time studies using a Ubiquitous Spectrum Analyzer (Federal Scientific). The recurrence interval, that is, the number of switches between successive songs before the same type recurs (Slater 1983), is related to the number of types in the repertoire and to their relative frequency of use (Lemon et al., unpubl. data). Since American Redstart song repertoires are small, a single recording session of a few dozen songs normally records all types. We noted only four changes in repertoire, two possibly in response to playback

and two from one season to the next. Otherwise, the repertoires we recorded in different years were highly stable, although the frequencies of the different songs varied between samples in some cases.

DEFINING TYPES OF PHONES AND SONGS

Our aim was to relate the song repertoires of different individuals one to another. Our initial problem was that of determining whether we were dealing with continuous or discrete variation across individuals.

The term "repertoire" implies a catalogue of discrete types. There is substantial evidence that song birds organize their singing around types (Isaac and Marler 1963, Lemon and Chatfield 1971). We found this to be the case in American Redstarts. We wanted to know whether the classifications of types used by the birds themselves could be used by researchers. Hence, our initial question was whether types were recognizable across different individuals. Since variation naturally arises, the distinction between types so evident in individual birds may fade when applied to many. Therefore, a researcher needs an operational definition of types.

In our samples, each male American Redstart had one to eight song types easily recognizable throughout a breeding season, and even from year to year where applicable. In some examples, it was apparent that the phones used in a particular song by one individual were used by others in combination with other phones, thereby yielding different song types. Consequently, this led us to the initial approach of classifying the individual phones to type, and then typing the songs by their phone permutations. Taking examples of 409 phones from a number of birds and measuring eight variables noted earlier, we anticipated that a principal components analysis (PCA) would separate phones into natural groups. This approach was only moderately successful, owing, perhaps, to the amount of information available for such an approach. A more complete description of phones, such as that used by Bertram (1970), Miller (1979), or McGregor and Krebs (1982), might have helped. But successive phones within a song can vary considerably (Fig. 2h, n), and, consequently, variances of different measures from the phones of one individual may be just as great as those from across individuals, although this was not the usual case. Furthermore, when we bypassed the PCAs and made a subjective classification by three observers on our total sample of songs, including those of 1982, we had over 45 phone types producing 88 song types.

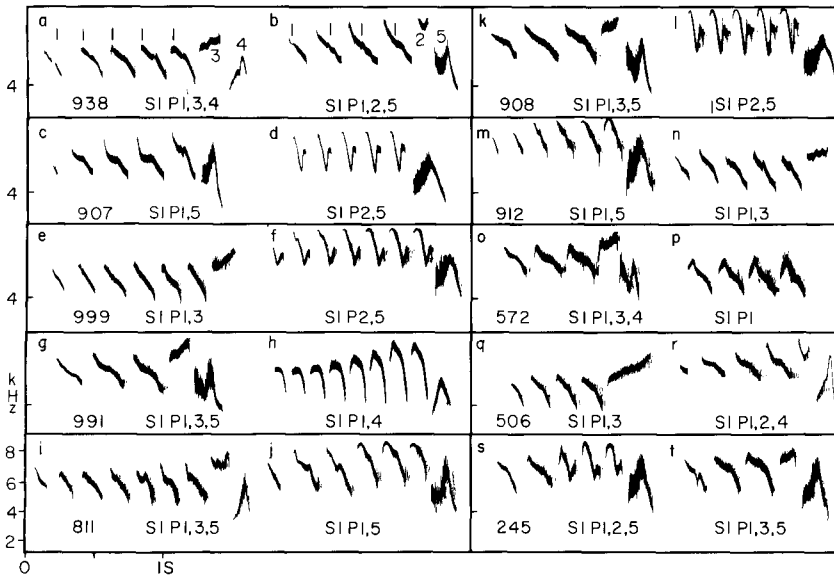


FIGURE 1. Examples of song 1 sung by male American Redstarts, showing the variety both within each phone type and in phone combinations. These examples were also chosen to illustrate examples of two distinct versions of song 1 in each of 10 males. Symbols: in Fig. 1a, 938 identifies bird, S and P designate song and phone types.

Such high numbers indicated that a classification of songs based initially on phones was too finely tuned for practical purposes. Therefore, this initial approach emphasized the differences rather than the similarities between individuals. Obviously a compromise was needed.

Instead of beginning with a catalogue of phones, we began our final classification with the entire songs. Although we faced much the same problem as before, we ignored many differences between songs. Consequently, we reduced the number of song types, and, secondarily, phones, by about one-half from the original classification.

Nonetheless, problems of sorting arose so that the following guidelines were followed:

(1) Generally we tried to lump rather than to split. Consequently, some rather different "looking" songs or phones were placed together because variation appeared to be continuous across the particular group as a whole: song 6 (Fig. 2h-k) is an example. Subsequent classifications might find it useful to make further separations. Although lumping did lead to economy between birds, individuals sometimes sang two versions of what we considered the same song: song 1 (Fig. 1) is an example.

(2) Since most American Redstart songs consist of repetitions of the same phone, changes of phone type at the end of the song were often ignored as far as song classification was concerned. These changes seem to result either from modifications or "drift" of the previous phones in the song as in Figure 1h, or through the addition of obviously entirely dif-

ferent phone types, especially the last one or two in the song. The aural effect is to "accent" the endings of these songs: songs of class 1 (Fig. 1) are the most common example. These songs have in common repeated phones with most emphasis on the downward frequency sweep. Terminal phones classed 3 and 4 in song 1 sometimes occurred; they were not used in song classification, however, although we recognize them as particular phone types.

(3) As noted, some birds combined phones into a song type, when otherwise these phones were sung alone in separate songs. Where these combinations occurred, they were designated as new song types. Figures for many of these are not shown since few occurred.

Once the songs were sorted, we returned to classify the phones subjectively, again applying the rules against splitting. Also, we considered two-part combinations as phones (Fig. 3r, t), so as to avoid having to designate the subparts as separate items. Measuring the eight features of the phones noted earlier, we then applied discriminant analyses to ascertain the reliability of our classifications. These consistently gave 85% or more correct classification of phones to type. We concluded that the same would have applied to the songs had such a method been applied to them.

ANALYSIS OF PATTERNS OF SONG SHARING

Elementary statistical considerations imply that the likelihood of sharing a given number of songs by two males will depend upon the repertoire size of each male. Clearly, the maxi-

imum number of shared songs is limited by the smaller repertoire size of the two males in any pair. Consider the relative probability that a particular male, whose repertoire size can be represented as R_i , sings a particular n -plet (as in "triplet") of songs (that is, $n = 1, 2, \dots, R_i$). The total number of n -plets for a particular value of n is given by the expression:

$$U_i = \binom{R_i}{n}. \quad (1)$$

This value represents the number of possible combinations of n songs that can be contained in a repertoire of R_i songs. For simplicity, let the probability of occurrence of any one n -plet in the population-wide pool of songs be the same as that of any other n -plet. If there are N songs in the pool, then the total number of n -plets is:

$$V = \binom{N}{n}, \quad N \geq R_i \geq n. \quad (2)$$

The probability that any given n -plet is one particular combination of interest is just V^{-1} . Therefore, the relative probability that the repertoire of male i contains the n -plet of interest is:

$$U_i V^{-1} = \binom{R_i}{n} \binom{N}{n}^{-1}. \quad (3)$$

Thus, the joint probability that two males, i and j , share the n -plet of interest is:

$$P_{ij} = U_i U_j V^{-2} \\ = \binom{R_i}{n} \binom{R_j}{n} \binom{N}{n}^{-2}. \quad (4)$$

Equation (4) reduces to the expression:

$$P_{ij} = \frac{R_i! R_j!}{(R_i - n)! (R_j - n)!} \cdot \left[\frac{(N - n)!}{N!} \right]^2. \quad (5)$$

What, then, is the dependence of the probability of sharing upon repertoire size? Our first step is to reduce the complexity of equation (5) by introducing the notion of relative probability, P_{ij}' . The term in square brackets in equation (5) is a constant in comparisons between n -plets of the same size, say $n = m$, irrespective of repertoire size (providing $R_i, R_j \geq m$). Therefore, we can examine sharing as a function of repertoire sizes alone by restricting our attention to trends within the set in which n -plet size is fixed at $n = m$. The

relative probability of sharing is defined by the expression:

$$P_{ij}'(m) = \frac{(R_i)(R_i - 1) \dots (m + 1)}{(R_j)(R_j - 1) \dots (m + 1)}. \quad (6)$$

In the simplest case, where $R_i = R_j = Q$, equation (6) becomes:

$$P_{ij}'(m) = Q^2(Q - 1)^2 \dots (m + 2)^2(m + 1)^2. \quad (7)$$

Dependence upon repertoire size can be given by the ratio of the relative probability for repertoire sizes of Q to the analogous probability for $R_i = R_j = Q + 1$:

$$P_{ij}'(m, Q + 1) / P_{ij}'(m, Q) = (Q + 1)^2. \quad (8)$$

Probabilities of sharing increase by this factor as repertoire sizes increase, which indicates that expected levels of sharing in large repertoires are much greater than those levels for smaller repertoires.

These considerations imply that we should treat repertoire pair-sizes (R_i, R_j) separately. Unfortunately, this constraint reduces the sample sizes of information for neighboring males in any one pair-size. Nevertheless, song sharing should increase as repertoire size increases, so that any pooling of data that may be undertaken between pair-size classes must establish homogeneity between data for such classes.

An important question about song sharing is: do immediate neighbors share significantly more songs than non-neighbors? This question can be addressed in the following way. The appropriate neutral models are song sharing patterns of non-neighbors: (1) in the same sample area (i.e., both males are in HML, or both males are in SS—we term these non-neighbor combinations as local non-neighbors); and (2) in different areas (i.e., one male from HML and one from SS—disjunct non-neighbors). The repertoires of every possible pair of non-neighboring males (both local and disjunct pairs) can be compared to establish the number of common songs in their repertoires. The result, then, may be entered into the appropriate class (e.g., local, $R_i = 7, R_j = 4$; or disjunct, $R_i = 6, R_j = 5$; etc.). We recognized only two classes of sharing: (A) share none or only one song; and (B) share two or more songs. This classification was necessary for two reasons. First, most males in the population use song "1" as the repeat song, so that the sharing of just one song between two repertoires essentially is the "ground-state" and indicates little information (see Results). Second, there were insufficient data to treat higher modes of sharing ($n = 3, 4, \dots$) as separate classes, so these were pooled with information for sharing of two songs.

TABLE 1. Phone sequences in song 1 of 39 subadult male and 67 adult male American Redstarts, color-banded and tape-recorded at St. Andrews and Back Bay, N.B. Phone 1 is always repeated in each song; others not so.

Phone sequence	Example in Fig. 1	n		
		Subadult male ²	Adult male ¹	Total
1	p	0	5	5
1, 2, 4	r	0	3 (3) ²	3
1, 2, 5	s	2	2 (1)	4
1, 3	q	3	3 (1)	6
1, 3, 4	o	8	11	19
1, 3, 5	t	12	20 (1)	32
1, 4	h	2	11 (1)	13
1, 5	c	9	6	15
2, 4	—	1	1	2
2, 5	d	2	5	7
		39	67	106

¹ Excludes three birds counted as subadults only.

² The Back Bay individuals are indicated in brackets, but are also included in the totals.

³ Comparing subadult male versus adult, $\chi^2 = 6.95$, n.s., 5 df. Certain sequences were grouped to permit sufficiently high expected values, these groupings being (1; 1, 2, 4; 1, 2, 5; 1, 3) and (2, 4; 2, 5).

RESULTS

CATALOGUE OF SONGS AND PHONES

Most American Redstart males organized their total repertoire of songs into two modes: the repetitive or repeat mode, in which a particular song was sung several times in succession; and the serial mode, in which the remaining songs in the total repertoire were presented in sequence, with little or no successive repetition of each. We found two individuals who used a song from serial mode and repeated it for long periods in addition to the usual repeat song, but these instances seemed exceptional.

Song 1 was the most commonly used in the repeat mode and was given by adult males especially early in the breeding season, and by the later-arriving subadult males that were easily distinguishable by plumage (Sherry 1979, Procter-Gray and Holmes 1981). Song 1 was characterized by repeated phones that were mainly inflected downward in frequency (Fig. 1). Two types of phones were so designated as having these features, phones 1 and 2. Phone 1 might or might not have an initial frequency upsweep; phone 2 had a terminal upsweep. A principal components analysis based on eight measured features (see Methods) suggested that the phone 1s might also be separable into two groups, one of higher and the other of lower frequency: examples are shown in Figure 1b, c. Yet when many examples were placed out for viewing, the observers could not detect a clear separation, so we did not attempt to apply one.

Song 1 was frequently and strikingly marked by a terminal accent achieved by use of phones 4 and 5 especially, each sung alone or preceded

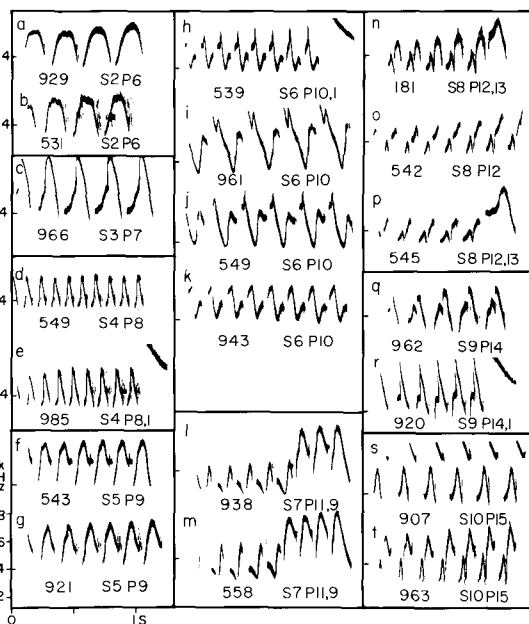


FIGURE 2. Examples of redstart songs, numbered 2 to 10. Symbols as in Figure 1.

by phone 3. Such accented songs were those by which many naturalists would identify the American Redstart. Phone 5 differed from 4 in having a vibrato imposed upon the carrier frequency. Some songs lacked phones 4 and 5 and ended with a high accent from phone 3, markedly different from the other two.

A summary of the composition of song 1 from all tape recorded songs (Table 1) shows that the frequency distributions of subadult and adult males were not significantly different. Only 5% of these songs were sung without any accenting in that they lacked phones 3, 4, or 5, and all were by adults. Nearly 90% ended with the accent of phones 4 or 5, but only 5% ended in phone 3. Sequence 1, 2, 4 occurred at Back Bay but not at St. Andrews.

Ten adult males in the sample had duplicate versions of song 1 (Fig. 1). Where these occurred, one version was sung in the repeat mode, whereas the other was included in the serial mode. The occurrence of these duplicates suggested at first that our method of classification was in error, but the two versions were distinct within individuals.

The remainder of the common songs were usually repetitions of a single phone (Figs. 2, 3); a notable exception was song 7. Other exceptions were those with a terminal accent, some involving a high frequency phone 1 (Fig. 2e, h, r). Other examples of accents were by phone 13 in song 8 (Fig. 2n, p). Phones designated 10 in song 6 (Fig. 2h-k), and of 12 in song 8 (Fig. 2n-p), were variable. A number of

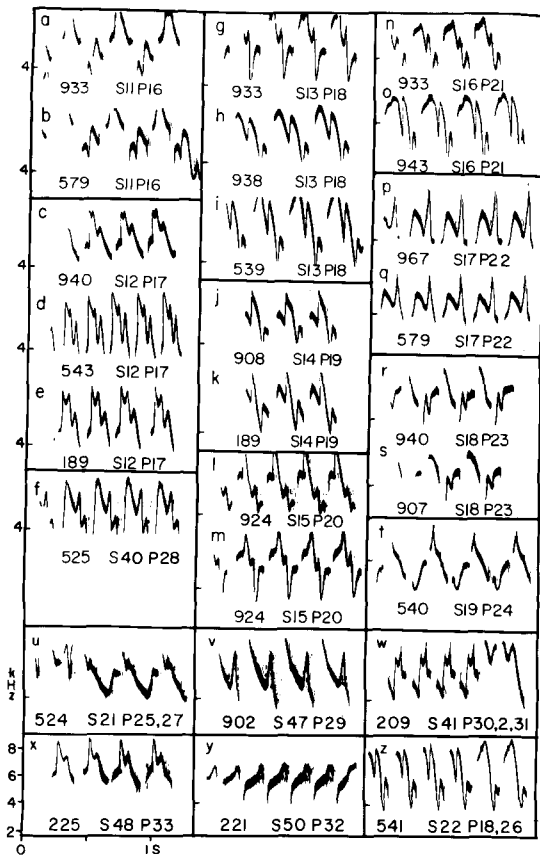


FIGURE 3. Examples of redstart songs, numbered 11 to 19 and higher (not all song types are shown). Symbols as in Figure 1.

songs combined phones otherwise used separately in the songs just considered. These songs were uncommon and we have not shown them.

Male American Redstarts frequently used phones which have an inverted U appearance in sonagrams, being simple up-down sweeps of frequency; examples are phones 6 to 9 and 11 to 13 (Fig. 2). A discriminant analysis on these phones had no trouble separating them by the designated types, yet certain cases presented difficulties. In songs at Back Bay (Fig. 7), songs b, h, and m had a terminal phone similar to those in the preceding song, but this phone was more similar to the type 7 noted earlier in Fig. 2c, and was so designated. Phone 7 at Back Bay resembled phone 4 in songs a, g, i (Fig. 7). As with song 1, duplicate versions of songs 12, 13, 18 occurred in three birds.

When subadult male American Redstarts are developing their songs, they apparently copy songs in a manner somewhat analogous to what we followed in classifying the songs, i.e., there is considerable uncertainty of what is an appropriate type to match. This aspect is illustrated in recordings made in early June, 1981 from an unbanded individual. Evidence in-

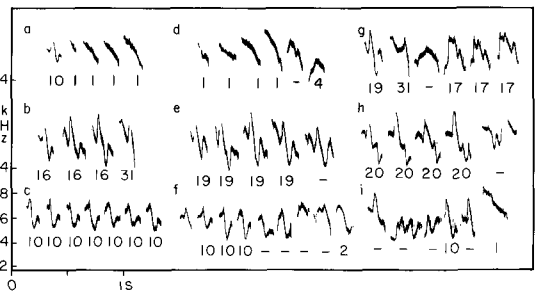


FIGURE 4. A series of songs recorded from a subadult male redstart in early June, 1981, showing more variability than in songs of adults shown earlier.

cludes: (1) graded change in successive phones of either the same or different types as the songs progress (Fig. 4c-g); (2) various combinations of different phones in songs a, b, f, g, h, i. Even the most common song, type 1, was highly variable (Fig. 4d). Some of these results might also be consistent with an interpretation of low motivation early in the singing season, but they are typical of song development in other species where learning is evident (Lemon 1975).

REPertoire SIZES

Only a single song type was recorded from many subadult males and only one song type was recorded from male 587 both as subadult and adult. Table 2 summarizes data from all males where the repertoires were noted, excluding individuals considered improperly sampled. It includes individuals whose repeated song 1 was noted but not recorded on tape. Since we noted many subadult males singing only one song type, their mean value was much lower than that of adults and the coefficient of variation much higher. No significant differences were noted in repertoire size among the three sample sites.

SONG IN REPEAT MODE

Song 1 was the predominant song used in repeat mode by both subadults and adults (Table 3). Nonetheless, other songs were used in this mode. Although song 2 was used by four males, it did not seem to be preferred. Song 2 phones seemed simple to us, merely up-down in frequency, but the other songs were sometimes quite complex, so phone structure did not seem relevant.

Of the 16 birds that did not use song 1 in the repeat mode, three (adult 909 and subadults 222 and 225) also had a different version of the song in the serial mode.

LOCAL DISTRIBUTION OF SONGS

We determined whether the songs were distributed locally relative to our three sample

TABLE 2. Number of songs per subadult and adult male color-banded American Redstarts in all areas. Data include cases where song 1 was only identified aurally.

	Songs per individual								Total	Mean	SD	C.V.
	1	2	3	4	5	6	7	8				
Subadult	22	4	7	5	4	1	1	1	45	2.49	1.85	74.3%
Adult	1	2	14	30	17	9	3	2	78	4.40	1.30	29.6%

We designate probabilities by convention: n.s., $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.
Subadult male versus adult: $\chi^2 = 49.94^{***}$, 5 df. Data of songs per individual of 6, 7, and 8 were combined for the test.

areas by using data from the BB samples of 1979, and for the HML (1982) and SS (1982) samples (Fig. 5). HML and SS were 1 km apart, and SS was about 17 km from BB.

Distributions of the songs were complex. Song 1 was sung by most birds in all three locations (Fig. 6a). Song 13 (Fig. 6b) and song 18 (Fig. 6d) also occurred in all three locations, but were proportionately more frequent at BB. Song 9 (Fig. 6c) occurred at HML and SS only, song 2 (Fig. 6e) at HML and BB plus one individual at SS. Song 16 occurred commonly at SS, in one bird at BB, but not at HML.

Testing for heterogeneity, using a χ^2 test, we found that the HML and SS samples differed significantly (Table 4). To perform this test, it was necessary to group the data to eliminate cells with expectancies of less than five. This grouping was done by lumping data for all songs where the row total was eight or less (song types: 3, 7, 8 . . .). The result seems conservative because the largest entries were essentially the same in both sites, these being the entries for song 1 and the combined entries just noted, thereby counteracting any difference between sites. A comparison across the three sites presented the combined problems of the large number of songs absent at BB, while some common at BB were not so in at least one of the other sites. Consequently, it was impossible to satisfy a condition of the χ^2 test that no more than 20% of the studied cells have expected values less than five (Cochran 1954). Instead, we combined the data in cells where the song types were absent at BB (song types: 3, 6, 7 . . . [Table 4]) and applied a Kendall Coefficient of Concordance across the table. The resulting coefficient, W , was not significant, thereby indicating that the samples were different, a view consistent with the HML-SS comparison.

SONG SHARING BY NEIGHBORING ADULT MALES AT ST. ANDREWS

For the larger area at St. Andrews, we examined the extent of sharing of songs by neighbors known to counter-sing from contiguous territories. This selection gave the analysis a more functional focus, since we felt that males tended to interact with particular neighbors rather

than to patrol the periphery of the entire territory.

The null hypothesis was that neighboring males do not share significantly more songs than either local or disjunct non-neighbors. Therefore, the appropriate comparison is between data for neighbors and for non-neighbors.

Our first step was to determine whether song sharing related to repertoire size (explicitly to the smaller repertoire), as predicted by our assumptions and arguments noted in Methods. This relationship (Fig. 7) was found to be so, both for neighbors (dashed line) and for non-neighbors (solid line). Next, we determined whether patterns of sharing by local non-neighbors (i.e., both birds in HML, or both in SS) differed from patterns of disjunct non-neighbors (i.e., one bird in HML and the other in SS). We employed a multiway-G analysis for independence to simultaneously explore the effects of repertoire size and location (i.e., local versus disjunct pairings). Sharing was found to be independent of whether the pairs of males were local or disjunct ($G_1 = 1.160$ n.s.), so that data for sharing in local non-neighbors (HML and SS) could be pooled. Since song sharing depended upon repertoire size (i.e., $[R_i, R_j]$), no general pooling could be undertaken with respect to repertoire size ($G_{11} = 56.256^{***}$).

By inspection, we noted that variation in sharing rose systematically in relation to rep-

TABLE 3. The number of individual males (n) in subadult and adult age classes using particular songs in the repeat mode in all areas.

Song	Subadult		Adult	
	Song	n	Song	n
1	35	(81.4%)	1	66 (84.6%)
2	2		2	2
8	1		7	3
10	1		9	2
12	2		12	1
18	2		14	1
Total	43		18	1
			23	2
			39	1
			49	1
			Total	78

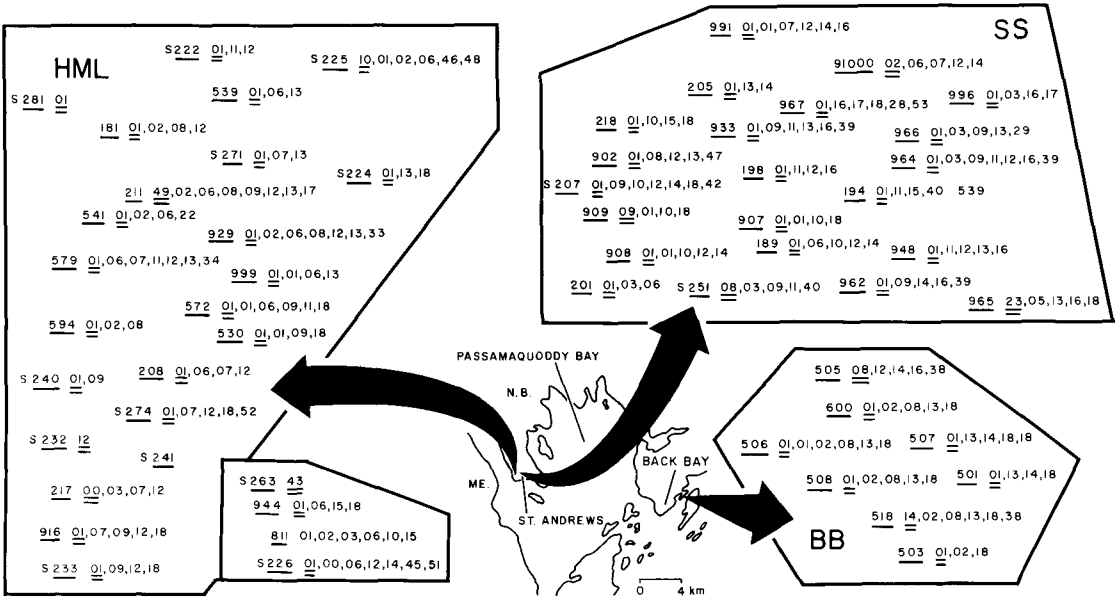


FIGURE 5. Maps showing location of males and their song repertoires used in analysis of song sharing by location and by neighbor. HML and SS data from 1982; BB data from 1979. One underline, e.g., 222, identifies male. Two underlines, e.g., 01, identify repeat song. Numbers preceded by S indicate subadults.

ertoire size (Table 5): relatively little sharing occurred between pairs when (R_i, R_j) were both small, more sharing occurred in intermediate-sized repertoires, and still more was evident in the largest repertoires. To avoid this heterogeneity, we produced three homogeneous data sets by partitioning the repertoire pair sizes (Table 5). Such a pooling was desirable

because data were insufficient to examine sharing in neighbors if the expanded data set was retained. The partitioning of repertoire pair-sizes into three homogeneous subsets is perfectly acceptable in a statistical sense. The inclusion of adjacent pair-sizes (e.g., 4,4 into the intermediate group, or 4,5 into the small group, or 4,7 into the large group, or 5,5 into the

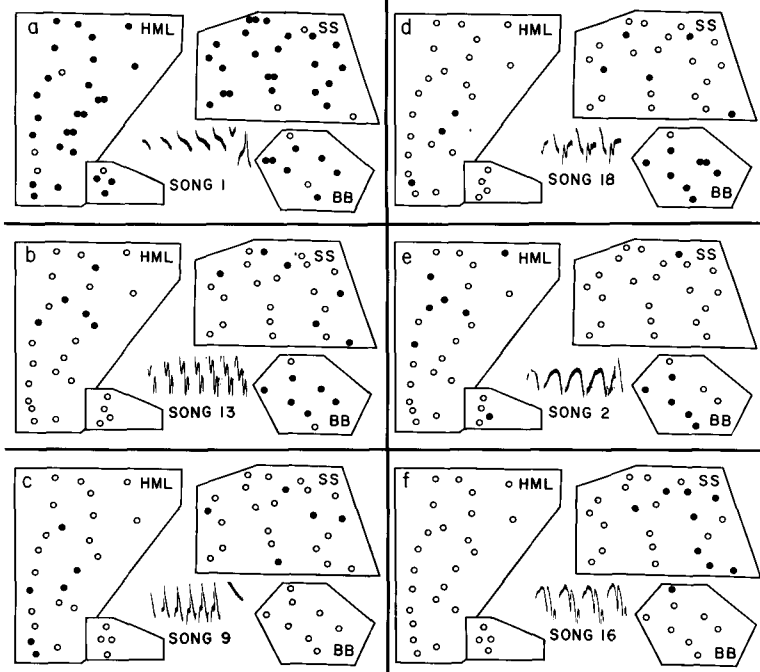


FIGURE 6. Occurrence of certain songs in birds at the three study locations, HML, SS, BB. Outlines of map areas as in Figure 5. Black dot indicates presence in particular male redstart, open dot indicates absence. Refer to Figure 5 for details of repertoires.

TABLE 4. Frequencies of song types in the three areas of HML, SS, and BB (see Fig. 5). Data omit song types found in one bird only.

Song type	Area ^{1,2}		
	HML	SS	BB
1	25	22	7
2	7	1	5
3	2	5	0
6	12	3	0
7	6	2	0
8	4	2	5
9	6	7	0
10	2	6	0
11	3	6	0
12	12	9	1
13	7	6	6
14	1	7	4
15	2	2	0
16	0	9	0
17	1	2	0
18	7	6	8
38	0	0	2
39	0	2	0
Total	18	97	38

¹ Testing for heterogeneity, HML and SS, results in $\chi^2 = 16.7^*$ (8 df). Test combines data for song types of combined frequencies of HML and SS of 8 or less.

² Comparing across the three samples, Kendall $W = .38$, $P > 0.5$ (7 df). To avoid the large number of ties, we combined entries where no songs were present at BB.

intermediate group) created significant heterogeneity (Table 5). This did not mean that the groupings were meaningful in any functional sense, but it allowed sufficient pooling of neighbor-sharing to make some reasonable conclusions.

In comparisons of song sharing in neighbors and non-neighbors (Table 6A, B), we assumed that sharing by neighbors was homogeneous in the same way as non-neighbors, so that partitions based on the ample data for non-neighbors also applied to information for neighbors. Neighbors did not appear to share more songs than expected by chance in either small or large repertoires (Table 6A). For intermediate repertoires, neighbors shared significantly more songs than non-neighbors at the 5% level. Therefore, this analysis reveals that one of three such groupings of repertoire size (intermediate) showed significantly more sharing than would be expected by chance, but not greatly so.

Our conclusions concerning song sharing do not appear to depend upon our use of just two categories: 0 or 1 songs; and ≥ 2 songs. Assuming that each category (small, intermediate, large) represents a homogeneous data set, then the average number of songs that were shared by neighbors was not significantly different from the average number shared by non-neighbors in either the large or small repertoire categories (Table 6B). Neighbors shared significantly more songs, however, than did non-

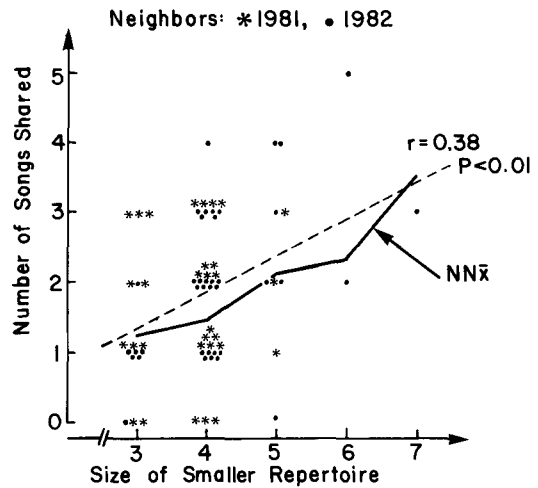


FIGURE 7. Relationships between song sharing and size of smaller repertoire in pairs of neighbors and of non-neighbors. Information for each pair of neighbors in 1981 ($n = 31$) and in 1982 ($n = 39$) is shown, as are the regression line (dashed line) and correlation coefficient that are based on these data. The solid line (NN \bar{x}) links mean values derived for the appropriate groupings of non-neighbor pairs of males whose individual data points are not shown in the figure (total $n = 459$).

neighbors in the intermediate repertoire category (Table 6B).

SAMPLE COMPARISONS VERSUS NEIGHBOR COMPARISONS

The data used in comparing the three samples (Local Distribution of Songs) were relative frequencies of each song type in each area. The data just considered (on sharing of songs at St.

TABLE 5. Occurrence of song sharing in non-neighbor pairs of adult male American Redstarts at St. Andrews in 1982 (data pooled for areas, see text). By dividing repertoire pair sizes into three classes (small, intermediate, large), homogeneous subsets were constructed to aid comparison with data for neighbors.

Repertoire pair size (R _i , R _j)	Number of pairs of non-neighbors sharing		G-analysis	
	0, 1 songs	2 songs	df	G
Small repertoires				
3, 4	43	14		
3, 5	26	14		
3, 6	15	4		
4, 4	45	15	3	1.89 n.s.
Intermediate repertoires				
4, 5	57	38		
4, 6	18	26		
4, 7	17	16	2	4.48 n.s.
Large repertoires				
5, 5	14	19		
5, 6	15	21		
5, 7	8	22		
6, 7 and 7, 8	2	10	3	4.42 n.s.

TABLE 6. Comparisons of song sharing between immediate neighbors and non-neighbors (data pooled for local and disjunct categories) in adult male redstarts at St. Andrews in 1982. Repertoire pair-sizes are pooled in accordance with the homogeneous data set (see Table 4). Part (A): G-analysis for homogeneity to discern whether the proportion of pairs of neighbors sharing 0, 1 song, or 2 songs differs from the analogous proportion in pairs of non-neighbors. Part (B): comparisons of average numbers of songs shared between pairs of neighbors and pairs of non-neighbors in the small, intermediate, and large repertoire pair size classes.

(A)			
Nature of pairs	Pairs sharing		G-analysis (all 1 df)
	0, 1 song	2 songs	
Small repertoires			
Neighbors	9	3	0.017 n.s.
Non-neighbors	129	47	
Intermediate repertoires			
Neighbors	4	11	4.10*
Non-neighbors	92	80	
Large repertoires			
Neighbors	1	8	2.57 n.s.
Non-neighbors	39	72	

(B)			
Nature of pairs	Shared songs	df	t-test
	$\bar{x} \pm SD (n)$		t
Small repertoires			
Neighbors	1.08 \pm 0.51 (12)	186	0.85 n.s.
Non-neighbors	1.22 \pm 0.64 (176)		
Intermediate repertoires			
Neighbors	2.13 \pm 0.92 (15)	185	2.56*
Non-neighbors	1.51 \pm 0.86 (172)		
Large repertoires			
Neighbors	2.78 \pm 1.48 (9)	118	1.729 n.s.
Non-neighbors	1.91 \pm 0.99 (111)		

Andrews) were distributions of numbers of songs shared between males, whether those males were local non-neighbors or disjunct non-neighbors. The results obtained in these two comparisons were seemingly contradictory because different questions were being asked. The sample comparisons examined global similarity of distribution of males that sang each song type. If 20% sang song 2 at HML, then we expected that 20% of males at SS sang that song also. Two major differences were encountered when considering the data on song sharing. First, it did not matter whether two males shared, for example, songs 3 and 16 or songs 9 and 24, for each couplet was considered as sharing irrespective of the actual types. From this viewpoint, sharing data were more heterogeneous than were the sample data. Second, the sharing analysis did not consider just how different the "unshared" elements were. For example, males might not share songs 7, 12, 18, and 39, or not share songs 2, 10, 11, and 33; what is not shared does not matter to sharing analyses but it does to the sample comparisons. Overall, then, high sample similarity may be associated with high neighbor sharing but not necessarily vice versa.

In any event, if the sample heterogeneity did

affect song sharing in any way, this would be to emphasize sharing by local neighbors relative to sharing of non-neighbors overall, making it easier to show greater sharing between neighbors. However, our rather weak or absent trend in this direction contradicts this.

HIGHER SHARING AT BACK BAY

At Back Bay, it was particularly striking that most male redstarts (excluding 503 and 505) had very similar repertoires (Fig. 5), although some neighbors such as males 505 and 600 shared only song 8. Often, even the fine detail of the phones was remarkably similar, as was the case in the songs of immediate neighbors, 506, 508, and 600 (Fig. 8), although male 506 had an additional version of song 1. In particular, we noted similarities across the males in the endings of songs 1, 2, and 8.

Because of the small size of the BB sample (8 males), we could not analyze the data on the basis of groups of minimum repertoire size. However, the following comparisons are noteworthy: mean songs shared by contiguous pairs—BB: 2.99 ± 1.54 ; HML + SS: 1.83 ± 1.11 ; mean size of smaller repertoire of a pair—BB: 4.33 ± 0.70 ; HML + SS: 3.99 ± 0.79 . So, BB had an average of one song more shared

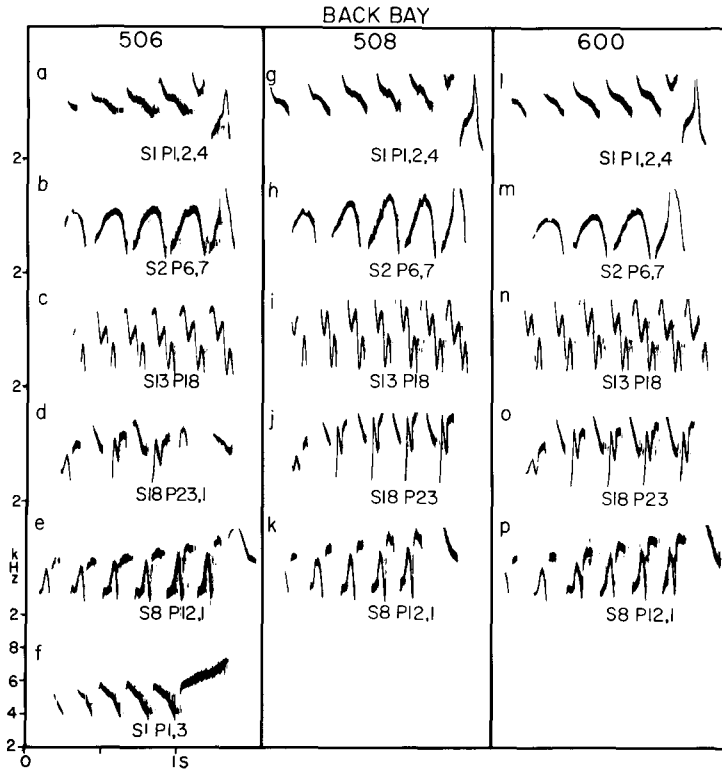


FIGURE 8. Song repertoires of three neighboring male redstarts at Back Bay, showing the strong similarity in repertoire and detail of phones.

in slightly larger repertoires. Even the raw data (Fig. 5) differ between the two areas.

SONG SHARING BETWEEN SUBADULTS AND ADULTS

If subadult males develop songs through copying adult males, as suggested earlier (Fig. 4), then subadult males might be expected to share as many songs with adult males as adults do among themselves. We examined the repertoires of 11 subadult males at St. Andrews that possessed repertoires of three or more songs from 1980 to 1982. These 11 birds formed 12 neighbor pairings with adult males (one subadult was associated with two adult males). Owing to the dependence of sharing upon repertoire size, we allocated each subadult-adult pairing to the appropriate repertoire size-class (i.e., small, intermediate, large). The numbers

of songs shared between subadults and their neighboring adults did not differ from the numbers shared between adult males in any of the repertoire size classes (Table 7).

DISCUSSION

Adult male American Redstarts in three small localities in southern New Brunswick averaged over four songs each, ranging from one to eight. Generally, one song was sung repeatedly (usually song "1," of which most versions were "accented"). The remaining songs were usually sung serially with little or no immediate repetition. Most subadult males had the same repeated song as the adults, but many did not sing the serial songs while holding their first territories, which were often of a transitory nature (Lemon et al., unpubl.). The overall frequencies of songs were significantly different

TABLE 7. Information on song sharing between neighbors when: (1) one male is a subadult and the other is an adult; and (2) each is an adult male. To facilitate comparison, we present data for pairs in which each male sang at least three songs (i.e., most subadults sing just one song, so that no information can be gained from considering pairs in which they occur). Data obtained at St. Andrews from 1980 to 1982.

Size of repertoires	Subadult-adult pairs	Adult-adult pairs	Mann-Whitney <i>U</i> -test	
			df	<i>U</i>
Small	1, 1, 2, 2, 2, 2	0, 1, 1, 1, 1, 1, 1, 1, 1, 2, 2, 3	6,12	50 n.s.
Intermediate	3, 3, 4	1, 1, 1, 1, 2, 2, 2, 2, 2, 2, 3, 3, 3, 3, 4	3,15	38 n.s.
Large	2, 4, 4	0, 2, 2, 2, 3, 3, 4, 4, 5	3,9	15.5 n.s.

across the three localities. Some songs occurred almost exclusively in one or two of the localities, seemingly without preference. Others were widespread and occurred in all three, the most widespread being the repeated song 1.

A particularly striking feature was the relatively low degree of song sharing by neighbors at St. Andrews (HML and SS) on one hand, and the high sharing at Back Bay (BB) on the other. As shown in Figure 7, at St. Andrews, seven of 70 pairings (10%) shared no songs at all, indicating that at least one partner of a male pair did not have even song 1. Twenty-two of 70 (31%) shared only one song, which most often was song 1, usually in repeat mode. The remaining 60% had two or more songs shared, and, again, most often one of these was the repeat song 1. Consequently, in the serial mode, more commonly only one song or none was shared. At Back Bay, on average, one song more was shared in pairings of neighbors than at St. Andrews, and several shared most of the repertoire.

Several hypotheses have been proposed to explain the distributions of similar songs geographically. We will not review all the literature here, but we will mention a number of relevant points.

(1) Distribution of songs is essentially random. Slater et al. (1980) argued that song types in chaffinches (*Fringilla coelebs*) have frequencies which fit a neutral allele model: the distribution of songs is merely the outcome of random events involved when the songs are copied by young males as they disperse. It is possible that samples of songs of American Redstarts, taken over larger areas, would fit such a model. We have not yet attempted such an analysis. Some songs are local in distribution (Fig. 7), in a manner which does not appear random. If not, it could be for a number of reasons.

(2) Song types may be preferred because they reflect individuals with special adaptations to the local environment. The songs are learned, but the other adaptations are genetic. This interpretation has been made especially in relation to crowned sparrows (*Zonotrichia* spp.; e.g., Baker 1975, Baker et al. 1981). Two arguments militate against this interpretation in our redstarts. Our sites were not separated by strong geographic barriers and movement between them was highly probable; although we have returns from a few banded nestlings, thereby suggesting choice of nesting ground is not random. Nevertheless, subadult males often make major moves between their initial territory, chosen in their first breeding attempt, and those selected later (Lemon et al., unpubl.

data). Secondly, the distribution of songs seems to be independent of the total repertoire. We cannot sustain an argument that local adaptations may be related to particular song types or to combinations thereof. In *Zonotrichia*, where such an argument is made, individuals usually have only one song type. Further, assuming that song type reflects quality of singer, and since songs are learned, the higher quality songs could often be acquired by "cheaters."

(3) Song types may be individually selected on the basis of their acoustic features. The songs of some birds appear to contain elements which vary in their transmission qualities (Morton 1975, Richards 1981). Consequently, birds may use this information in assessing the distance of the singer. This feature may apply to the accented song of the American Redstart relative to other songs. However, we doubt that the distribution of most of the serial songs would be affected in this manner. On the other hand, there may be strong selection for resolution of types. If types are important, then, they must be distinguishable. As we have noted, many of our recognized types are similar. The fact that individuals have two versions of the song 1 indicates that the singers are capable of high resolution of detail. We emphasize that perception is related to, but still different from, transmission.

(4) Young males may gain reproductive status by mimicking older males, as Payne (1981, 1982) suggested in Indigo Buntings (*Passerina cyanea*). The physical distribution of males in that species differs from that in American Redstarts (see below). Although first-year male redstarts may copy songs of their adult neighbors, we found no direct evidence that this constitutes mimicry, in the sense of "pretending" to be the birds they copy. They may be copying their prime competitors.

(5) The geographic pattern may be the result of copying and demographic considerations, based on pressures on the males to compete directly against their neighbors, especially as adults. If the observed difference in song similarity is typical of neighboring American Redstarts on mainland New Brunswick or islands off the coast, this suggests that local similarities of repertoires, or "dialects," are epiphenomena (Wiens 1982) resulting from the interaction of several features, such as the following.

Subadult males arrive later than adult males (Lemon et al., unpubl.), which contributes greatly to their acquisition of territories around the periphery of the breeding areas chosen by adult males. Differences in breeding areas of the two age-classes have been known in American Redstarts (Howe 1974), but may not be

universal (Sherry 1979). Many of the subadults at St. Andrews return a second year (as shown by our bandings) and breed in the areas of adults, creating a centripetal movement of males. At St. Andrews, which is larger than Back Bay, the number of males is high and, consequently, much mixing of individuals of various song experiences probably occurs. The small area at Leavitts Head at Back Bay simply cannot accommodate large movements or numbers of birds to the degree possible at St. Andrews.

We have noted subadult males singing as if uncertain which phones they were trying to present (Fig. 4), a feature characteristic of other birds when developing song. Therefore, it seems probable that sharing often reflects instances in which subadult males initially copy songs from neighbors on the breeding ground during the first summer. The following year, many former subadult males return to the same territories to reside adjacent to adults or possibly even new subadults. This interpretation recognizes song stability once learning has occurred. Alternatively, owing to the strong centripetal effect, some individuals may develop some of their serial repertoire during their second season. Although serial repertoires seem to change little once recorded, a few exceptions do occur (Lemon et al., unpubl.); but, perhaps more importantly, it is possible that many males do not sing serial repertoires until their second year on the breeding ground. If so, they might copy adult neighbors directly.

Although most males of whatever age share a version of song 1, generally they reflect a degree of individuality, as shown in Figure 1. We have noted instances where song 1 of more than one neighbor is remarkably similar, such as that of neighboring males illustrated in Figure 8. These high similarities occur either by chance, males somehow having selected a neighbor with a similar song, or by active adjustment of song 1 to match in detail the pattern of a neighbor. This point remains to be examined, but we think that adjustment of the song is the most probable.

Finally, let us consider whether song repertoires are culturally stable strategies (CSS); that is, the CSS is a strategy which is learned and cannot be bettered in the population. This term is the cultural equivalent to the genetic evolutionary stable strategy (Maynard-Smith 1982). Song repertoires would seem to be a CSS in the case of small island populations, should high similarity of song there be found general. The fact that the song sharing on the mainland is less evident, however, suggests that a CSS is either unattainable there because of

demography, or it occurs on the mainland only among very small groups of individuals (neighborhoods). Further, it may be that song repertoires are used in rather different ways in the two circumstances.

As in other warblers, American Redstarts tend to use their repertoires in relation to location within the territory. The repeat song, usually song 1, is used either before arrival of females, or later, in parts of the territory where males are least in contact with one another. The serial songs are used more after females arrive and seemingly in situations of countersinging between males. This division of the repertoire would seem to aid neighboring males in assessing each other's ability to guard some resource (i.e., resource holding potential, RHP), the serial songs being used in a "probe" situation (Maynard-Smith and Price 1973). We have no evidence, however, of any significant matching of song types when countersinging, as has been noted in other song birds (Hinde 1958, Lemon 1968, Krebs and Orsdol 1981). Size of song repertoire in Great Tits (*Parus major*) relates directly to lifetime fitness (McGregor et al. 1981), but that may not be the case in American Redstarts.

Where much less sharing of songs occurs, the repertoire might be used to indicate individuality. Although most neighboring American Redstarts at St. Andrews share some songs, the repertoires of most neighbors differ. After listening to them sing for a period of time, a person can identify individuals and one supposes that the birds may do the same. Individuality of pattern may be particularly important in assessment of RHP, for one can relate his past experiences of conflict to known adversaries (Barnard and Burk 1979). Much of the defense of territory occurs after initial establishment; that is, it seems related to the fact that nesting is associated with high predation throughout the season. Consequently, males are often required to defend their areas against neighbors' intrusions as females seek new nest sites. Therefore, assessment of RHP would seem particularly advantageous to individuals with known neighbors, in contests that are often symmetric.

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