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SONG DIFFERENCES AND MAP DISTANCES IN A POPULATION OF ACADIAN FLYCATCHERS

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Songs may vary among both local birds and local populations (Borror 1961, Borror and Gunn 1965). The variation among birds may allow birds to recognize each other as individuals. The variation among populations has sometimes been described in terms of "dialects," with neighboring birds having similar songs but populations no more than a few km away having quite distinct songs (Lemon 1966, 1975, Marler 1970, Harris and Lemon 1972, Baptista 1975, Mundinger 1975, Verner 1976). In a few species local geographic variation is less regular and may involve a few neighbors sharing similar songs, but other birds having no songs very similar to those of their neighbors (Borror and Gunn 1965), and a bird may share a song with only 1 neighbor (Thompson 1970, Kroodsma 1974). Few studies have sampled intensively a large proportion of the singing birds in a single locality and have described the microgeographic pattern of variation in song. The possible importance of song similarities in social behavior (Payne 1978), in the genetic differentiation of populations (Nottebohm 1969, Thielcke 1970), in adaptation of song to the physical features of the habitat (Nottebohm 1969), and in marking the structure and dispersal of bird populations (Baptista 1975) all make it desirable to investigate the variation in song on a local level. Here we describe individual variation and the microgeographic pattern of song similarity in a population of Acadian Flycatchers (*Empidonax virescens*). The population lives in a relatively homogeneous, linear habitat, the bottomland forest bordering the Potomac River in Montgomery County, Maryland. As the habitat is similar along the transect, the main effect separating the singing birds is simple linear distance.

The problem of relative similarities and differences in song structure among birds within local populations and between more remote assemblages of birds may be met usefully by applying multivariate statistical techniques. We compared measures of time and pitch in the songs of Acadian Flycatchers in relation to map distance. This avoids a subjective view of similarities as "dialects." We take the empirical approach that the associations of individuals in nature are unknown to us, but that we can recognize associations such as groups with similar songs by using the descriptive techniques of population phenetics (Sneath and Sokal 1973).

STUDY AREA AND METHODS

Acadian Flycatchers are common singing birds in the deciduous riverine forest along the Potomac River. Birds were recorded with a Uher 4000-L tape recorder and a Sennheiser MKH-805 directional microphone between 05:20 and 09:00 on the mornings of 1 and 2 July 1975. Map positions were determined for each bird from landmarks and mileage markers along the Chesapeake and Ohio Canal towpath, where the recordings were made. Birds were recorded in sequence, and birds on neighboring territories were distinguished by walking from the first to the second while both were singing.

Acadian Flycatchers give several rather simple vocalizations; the ones used in the comparisons here were the "advertising song," a territorial song transliterated as "*tee chup*" by Mumford (1964). We include the "dawn songs" recorded at the earliest times of 3 individuals (nos. 26, 27, 29), as this song ("*seet tee chup,*" or with additional introductory "seet" notes, as described by Mumford 1964) ends with the same pattern as the advertising song. Songs were analyzed with a Kay Elemetrics "Vibralyzer" 6030A at a wide band setting for maximal temporal resolution and a frequency range of 8 kHz. Audiospectrograms of 20 birds were sufficiently clear to allow measurement of frequency and time characters. The clearest song of each bird was chosen for measurement. In addition, audiospectrograms were produced for 10 consecutive songs of 1 bird to measure the variability of an individual.

For comparing the songs of flycatchers with each other, the measurements for each song were subjected to several univariate and multivariate analyses. In the multivariate analysis, correlation coefficients were computed for each pair of birds using the profile of data of 11 song characters for each bird, and phenetic distances for each pair were then computed as $D = 1 - r$, where r is the correlation coefficient of the pair. A phenogram was then derived from the resulting distance matrix to determine whether birds that are geographic neighbors tend to occur in clumps of similar songs. We determined x- and y- map coordinates for each bird from a map and then computed the map distance between every pair of birds. This distance is the shortest distance each bird would travel to visit each of the other flycatchers. As the curves of the river arc around some unsuitable unforested habitat, we also compared the phenetic song distances with the trail distances, where trail distances in miles were recorded directly from the C & O towpath markers and from local maps. In addition, the eigenvectors of standardized song characters were derived from a matrix of correlations in a principal component analysis, and the 2-dimensional PC ordination values were plotted for each bird to describe overall tendencies for neighboring birds to have similar songs. The multivariate techniques applied in the study have been used widely in numerical taxonomy and population phenetics and are discussed in Sneath and Sokal (1973), Cooley and Lohnes (1971), and Anderberg (1973).

RESULTS

Map locations of the 20 flycatchers are shown in Fig. 1. Birds were recorded mainly in 2 areas, from Edwards Ferry at mile marker 30.8 on the towpath, measured from the south end of the canal, downstream to mile 28.6, and from mile 17.5 just below Watts Branch downstream past Swains Lock to the Limekiln Branch above the Great Falls parking lot at mile 14.8. Elevation along the entire section is about 60 m above sea level,

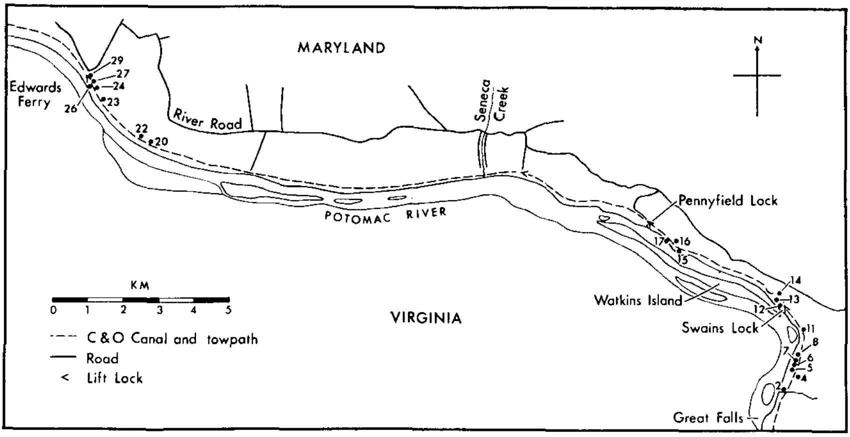

FIG. 1. Localities of Acadian Flycatchers recorded along the C & O Canal, Montgomery County, Maryland. Map after Clague 1963.

and the forest bordering the Maryland side of the river and both sides of the towpath is continuous in this section.

The song characters used in analysis included (1) frequency inflections on calibrated audiospectrograms and (2) temporal intervals. The beginning and end of notes rapidly rising or dropping in pitch were often unclear, and these notes seemed to start and end at a wide variety of frequencies. Marler and Isaac (1960) noted this result in another species and attributed it to differences in loudness as a function of distance. To avoid measurement error due to loudness, the temporal intervals of flycatcher song were measured at points along the intersection of the audiospectrogram figures and the 4 kHz calibration. The points of inflection where pitch could be measured with confidence (characters 1–6) and the temporal characters (7–11) are illustrated in Fig. 2, with representative songs of Acadian Flycatchers.

All song characters were variable in the population (Table 1). The temporal characters appeared to be more variable among birds than did the pitch characters, as the coefficients of variation ($\mathrm{CV} = \mathrm{SD}/\mathrm{mean}$) are generally higher for the temporal characters (Table 1). Variation in a single bird's "*tee chup*" also is evident for all song characters (Table 2). Note that the CVs are uniformly lower for all 11 song characters of a single individual (bird 14) than for the sample of songs from 20 different birds. The calculated variance within this 1 bird was significantly less than the variance among the local birds ($F \geqslant 4.67$, $P < 0.05$) for 8 of the 11 song characters (exceptions were characters 3, 4, and 6). Data from 5 songs of

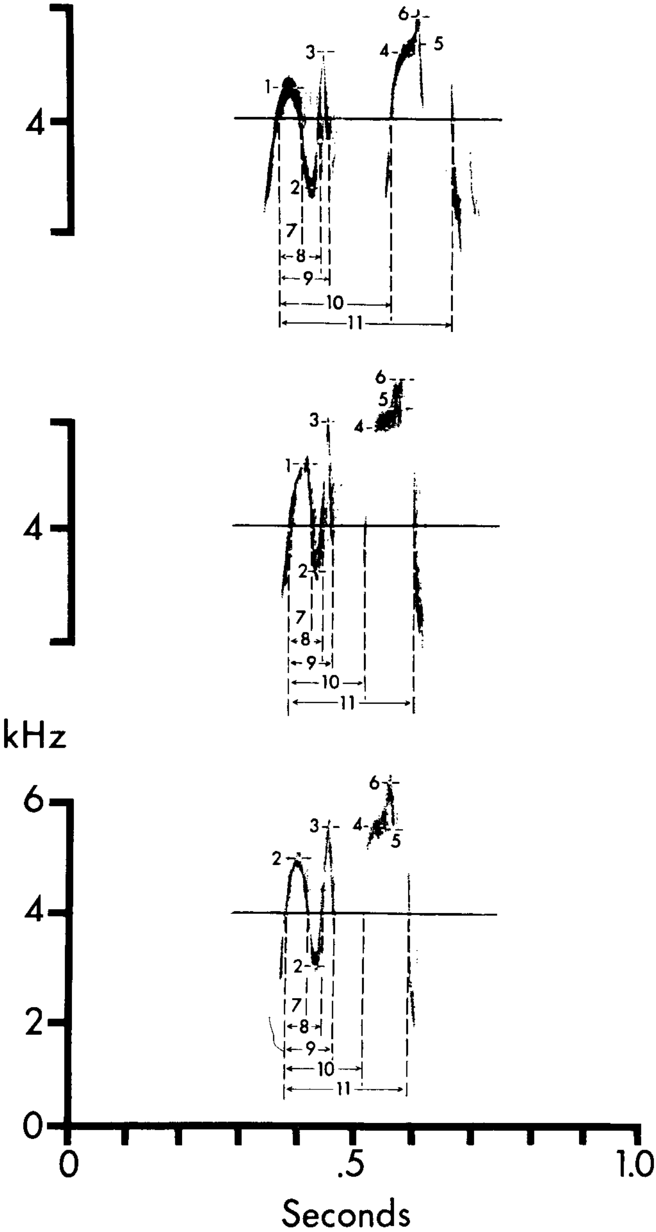

FIG. 2. Audiospectrograms of songs of 3 Acadian Flycatchers (nos. 14, 15, and 16) illustrating the 11 song characters measured.

TABLE 1

VARIATION IN 11 SONG CHARACTERS IN A POPULATION OF ACADIAN FLYCATCHERS

Variable and units	N	Min.	Max.	Mean	SD	CV
1 kHz	20	4.7	5.4	5.07	.208	.041
2 kHz	20	2.7	3.8	3.26	.373	.115
3 kHz	20	5.2	6.2	5.62	.278	.049
4 kHz	20	5.0	6.0	5.52	.271	.049
5 kHz	20	4.7	5.8	5.47	.270	.049
6 kHz	20	5.8	6.6	6.13	.231	.038
7 msec	20	90	150	116	17.5	.151
8 msec	20	125	205	165	24.5	.150
9 msec	20	165	260	214	22.5	.105
10 msec	20	320	560	387	69	.177
11 msec	20	550	830	638	92	.144

bird 7 and 6 songs of bird 5 also were examined and it appeared that the song characters were consistent within a bird in those smaller song samples as well. The results of Tables 1 and 2 suggest that the songs of an individual Acadian Flycatcher are less variable than are the songs of local flycatchers in general, and that much of the difference in song among individual flycatchers is in the temporal characteristics of the song. This appears to be the first quantitative study that shows individual song differences among the tyrannid flycatchers. Perhaps an observer or an Acadian Flycatcher

TABLE 2

VARIATION IN 11 SONG CHARACTERS IN 1 INDIVIDUAL ACADIAN FLYCATCHER

Variable and units	N	Min.	Max.	Mean	SD	CV
1 kHz	10	4.4	4.7	4.58	.103	.022
2 kHz	10	2.6	2.8	2.68	.063	.024
3 kHz	10	4.9	5.5	5.16	.190	.037
4 kHz	10	4.9	5.4	5.09	.152	.030
5 kHz	10	5.1	5.5	5.27	.125	.024
6 kHz	10	5.7	6.1	5.88	.140	.024
7 msec	10	100	125	116	8.3	.072
8 msec	10	190	210	197	6.3	.032
9 msec	10	220	250	236	8.3	.035
10 msec	10	495	575	531	22.9	.043
11 msec	10	755	860	805	28.8	.036

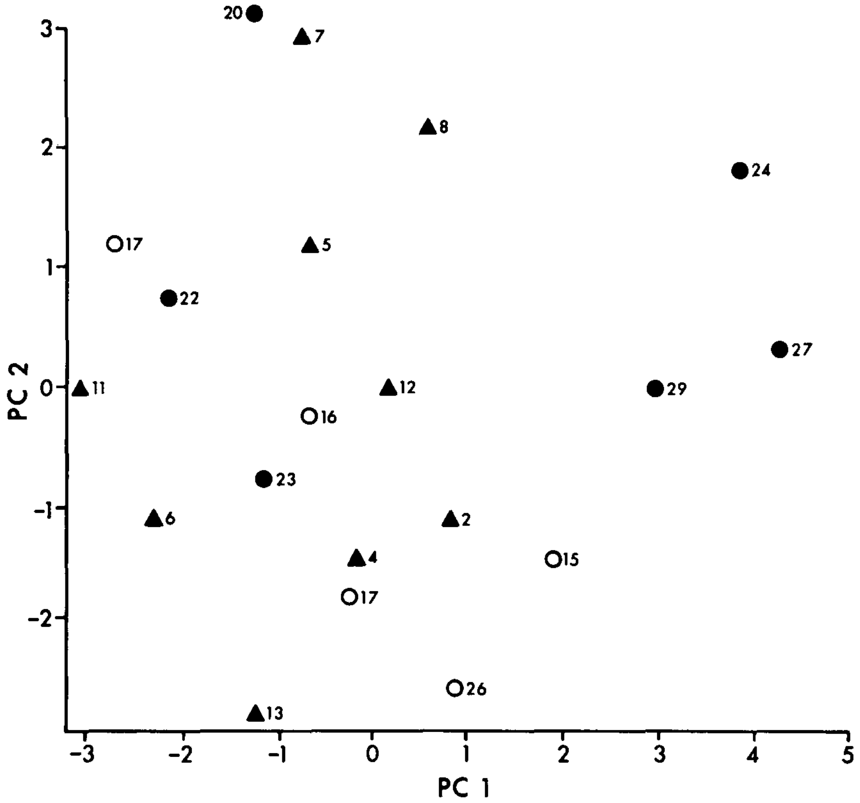

FIG. 3. Principal component analysis of the songs of 20 Acadian Flycatchers. Numbers refer to the individual birds shown in Fig. 1; triangles represent birds at the west end of the transect near Edwards Ferry, open circles are birds in the east-central part, and closed circles are birds at the east end near Great Falls.

could recognize a singing individual flycatcher, though the songs do sound similar.

We tested all the song characters to find whether any one was correlated with the map position of the bird along the towpath. No song character was significantly correlated with distance ($r_p \geqslant 0.39$, $P > 0.05$). Thus no song characters vary in a gradual way along the river in the area where we recorded the flycatchers.

A principal component analysis was completed for the 20 flycatchers to determine whether any natural clustering of birds from the ends of the transect was apparent. The results (Fig. 3) indicate no tendency for birds

TABLE 3

EIGENVECTORS OF 11 SONG CHARACTERS IN A PRINCIPAL COMPONENT ANALYSIS

Song character	Eigenvectors		
	PC 1	PC 2	PC 3
1	.358	.254	.209
2	.378	-.214	.028
3	.448	.096	-.044
4	.388	.142	.208
5	.311	-.149	.154
6	.376	-.096	.053
7	-.067	.485	.240
8	-.254	.466	.031
9	-.016	.546	.141
10	.118	.210	-.673
11	.236	.187	-.593
Component	4.29	2.98	1.68
Total cumulative variance	39.0%	66.1%	81.3%

to have distinct songs in the areas of Edwards Ferry, Swains Lock, and Great Falls. There is no tendency apparent for flycatcher song to form local "dialects" within distances of 4–8 km, nor is there a tendency for any dialect differentiation among birds 20 km apart. As with the individual song characters, the principal component results suggest no simple gradient in song variation along the river from Edwards Ferry to Great Falls. Analysis of the principal components results (Table 3) shows that the song characters with high eigenvalues on PC 1 are the pitch characters, those with high values on PC 2 are temporal characters 7–9, and those with high values on PC 3 are temporal characters 10 and 11. Hence even the clear interpretation of PC 1 as pitch and PC 2 as time does not allow a simple separation of flycatcher songs into local neighborhoods of similar song character combinations.

A phenogram or cluster tree derived from the matrix of correlation coefficients of standardized song characters and constructed using an unweighted averaging algorithm gives similar results (Fig. 4). Some neighboring birds were closely linked in the song phenogram, but this result was not general, nor were the birds for which we used the "dawn song" associated in a cluster, these instead were mixed among the other birds. This result is taken as justification for including these 3 birds in the analysis. Birds on adjacent territories show no strong tendency to have the most similar songs, and birds from the main areas along the river are not

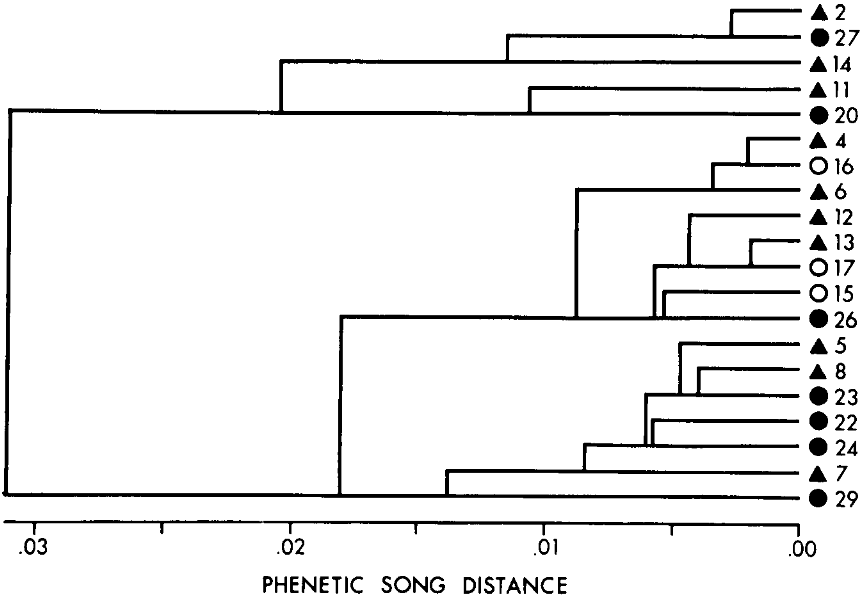

FIG. 4. Distance phenogram from a correlation matrix of 11 song characters of 20 Acadian Flycatchers clustered by unweighted pair-group averages of the standardized characters. The cophenetic correlation coefficient is .772.

closely associated in the figure. Although the cophenetic correlation coefficient is reasonably high (Sneath and Sokal 1973), a phenogram is a linear representation of a more complex distance matrix. The song phenetic distance values of the matrix were thus compared with the map distances of the territorial singing birds. If neighboring birds tended to have similar songs, whether song variation over a larger area were graded or were discontinuous as in a mosiac, one would expect to see a clustering of points in the lower left corner of the figure. As seen in the scatter diagram, there is no tendency for increasing song distance (or difference) with increasing map distance. There is no tendency for birds that are close neighbors, even birds on adjacent territories, to have songs more similar than birds at much greater distances. Substituting Euclidean map distances for the trail distances had little effect on the results. In Fig. 5 the intensity of points for low song phenetic distance (or, high song similarity) is about the same for birds near each other along the river as for those separated by several km, indicating that birds in a local neighborhood and within hearing distance of each other are no more similar in song than are those birds living farther apart.

To test whether birds on neighboring territories tended to have songs

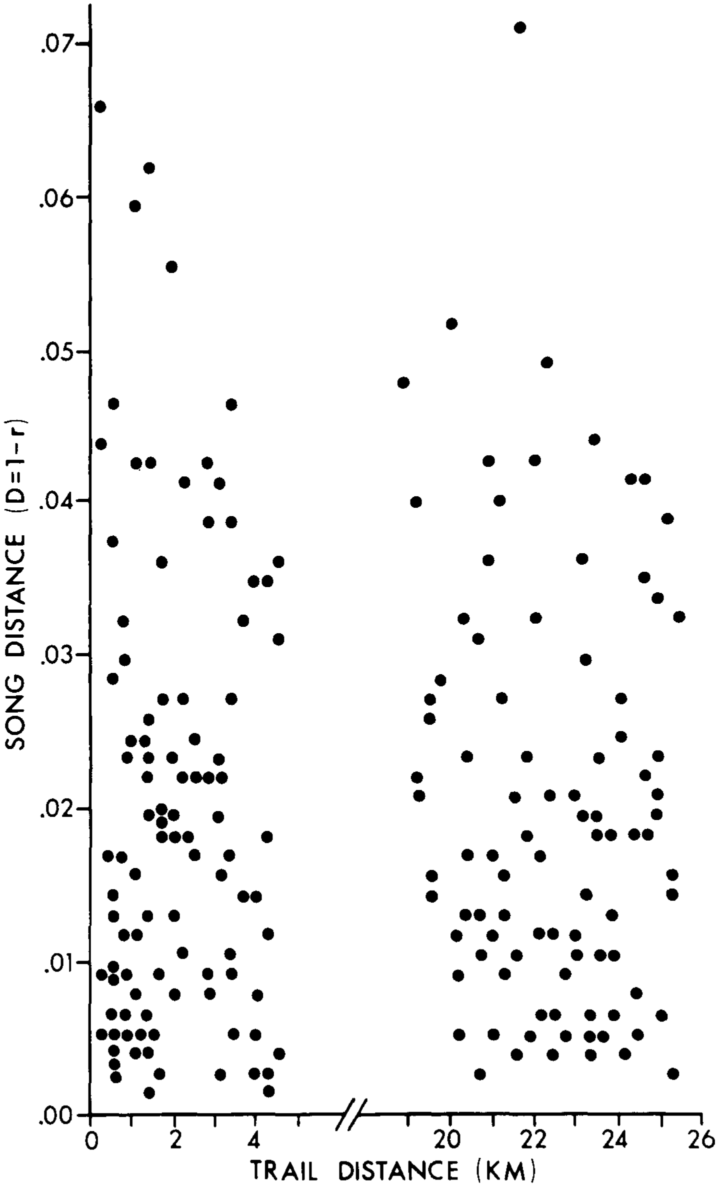

FIG. 5. Scatter diagram of microgeographic distances and phenetic song distances between Acadian Flycatchers. Note the lack of any tendency for the less remote birds to be more similar in their songs.

more similar to one another than birds not on neighboring territories, we compared the mean phenetic song distances of the 9 couplets of birds that were tape recorded within 100 m of each other with the 181 remaining phenetic song distances. Acadian Flycatchers have territories approximately 100 m across (Mumford 1964, Walkinshaw 1966), so birds recorded within 100 m are likely to be territorial neighbors, and in fact they were observed to be territorial neighbors in the field. The mean phenetic song distance of territorial neighbors was .0274. Analysis of the rank-order scores of the distances with a Mann-Whitney U-test ($U = 865$, $z = .314$, $P = .377$) shows that the mean phenetic distances in songs of adjacent and nonadjacent birds are not significantly different. Hence birds on adjacent territories do not have songs more similar to each other than to other birds in the local area.

DISCUSSION

Within the 30-km study area along the Potomac River, the Acadian Flycatchers show no evidence of local song dialects, song gradients with distance, or song similarities among birds on neighboring territories. A lack of behavioral differentiation in these local populations may be explained in several ways. First, some birds that have local dialects or have song sharing among neighbors and in which song development has been studied experimentally, are known to learn some features of their songs (Marler 1970, Rice and Thompson 1968, Dittus and Lemon 1969). Although local song variation does occur in some birds other than the songbirds (D. W. Snow 1968, B. Snow 1970, Mirsky 1976), it is unknown whether the pre-dispersal or post-dispersal songs heard by these birds affect the form of their songs. Perhaps the tyrannids such as the Acadian Flycatchers do not copy any particular song variant that they hear earlier in their lives.

Second, most birds with local dialects are nonmigratory but at least some birds disperse and then learn the songs of other adults in their new areas (Kroodsma 1974, Verner 1976). Acadian Flycatchers migrate to southern Central America and northern South America (A.O.U. Check-list, 1957). Adults usually return to the same locality in their breeding range year after year (Bird Banding Laboratory records). In Michigan, Walkinshaw (1966) found that nearly half of the banded, territorial Acadian Flycatchers returned to the same territory in successive years. Population structure in a genetic sense, however, is affected by the dispersal of young from the place of birth to the place of breeding in the adult years. Walkinshaw (1966) found no local returns for Acadian Flycatchers banded as young. The recoveries in the files of the Bird Banding Laboratory include only 2 birds ringed as a young in one year and recovered in a later year. One bird was recovered on 6 May in the year after hatching more than 160 km from the place of banding. The early date of recapture suggests that the bird may have been migrating, though the recapture was north of the site of banding. The second bird was recovered one BBL distance unit (a unit equals a block extending 0.1 degree on a side), and the recovery was within 16 km from the site of banding in the year after banding, suggesting a tendency to return to the area near the birthplace, though not to the same territory area of the parents. With only 2 banding recoveries, no general conclusions can be made about effective dispersal distance, but the lack of local returns in Walkinshaw's study suggests that Acadian Flycatchers usually do not return to the place of hatching, and that the distances of effective hatching-to-breeding dispersal are commonly greater than 1–2 km.

The function of the song in most dialectal birds or birds with song similarities among neighboring males includes territorial advertisement, as in the *Empidonax* flycatchers. Perhaps the individual differences in songs of the flycatchers are behaviorally significant in the recognition of neighboring individual males or in the recognition by females of the mates of earlier years or of the same year. Walkinshaw (1966) found that the same pairs formed in successive years, often on the same territories, even when the territory boundaries changed from year to year. However, we know of no experimental studies designed to test whether either the territorial males or their mates respond differently to the songs of different individual Acadian Flycatchers. The absence of song gradients with distance in our study area is consistent with the view that the birds all belong to a single effective population that extends across many social units of neighboring, territorial birds.

A similar analysis of phenetic song distance and microgeographic distance in another species, the Splendid Sunbird (*Nectarinia coccinigaster*), has shown a local similarity in song among neighbors where song and map distances are related only among birds that live closer than about 1 km (Payne 1978). This species is tropical and apparently nonmigratory. Quantitative analysis of song variation among other species of birds and its relation to the map distance among the birds may lead to a better understanding of the significance of local variations in the songs of birds.

SUMMARY

Tape recordings of the advertisement songs of 20 Acadian Flycatchers located within 30 km of each other along a continuous belt of lowland forest on the C & O Canal in Montgomery County, Maryland, were examined. Time and frequency measurements indicated that the songs of an individual are significantly less variable than the songs of different individuals. Songs were subjected to multivariate statistical analyses for detection of behavioral differentiation of local populations. No pattern of local song dialects or of song matching by neighboring territorial males was found in these flycatchers. Phenetic distances between songs were not related in any simple manner to the microgeographic map distances between the birds. The results are consistent with a pattern of effective dispersal of the young from their place of birth to their place of breeding and with a view of the birds as comprising a very large effective population. We suggest that multivariate phenetic analysis of bird songs may help provide a common basis for comparing patterns of geographic variation in bird songs.

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