

GEOGRAPHIC VARIATION OF SONG FORM WITHIN AND AMONG CHESTNUT-SIDED WARBLER POPULATIONS

BRUCE E. BYERS

Department of Biology, University of Massachusetts, Amherst, Massachusetts 01003, USA

ABSTRACT.—Chestnut-sided Warbler (*Dendroica pensylvanica*) song repertoires include both accented-ending (AE) and unaccented-ending (UE) songs, and the two song categories are used in different behavioral contexts. To determine if the song categories also differ in patterns of spatial distribution, I analyzed local geographic variation in song form within a Massachusetts population and also compared songs from this local population with songs from other geographic regions. I found that: (1) UE repertoires of individuals were more similar to those of nearby individuals in the local population than to those of more distant birds; (2) most UE song types and song elements tended to cluster on groups of adjacent territories; and (3) UE songs from geographically distant sites tended not to match types from the main study site. In contrast, my findings indicate that: (1) AE-repertoire similarities were not significantly related to local interindividual distances; (2) AE song types were dispersed at random over the local area; and (3) nearly all AE song types from distant sites were identical to the AE types found at the main study site. The contrast between variable, geographically clustered UE songs, and stereotyped, geographically dispersed AE songs suggests that the two song categories serve different communication functions. Received 21 December 1994, accepted 28 June 1995.

THE STUDY OF GEOGRAPHIC VARIATION has long played a prominent role in evolutionary biology, because "the foundation of most evolutionary theory rests upon inferences drawn from geographic variation" (Gould and Johnston 1972:457). Analysis of morphological or biochemical variation over geographic space is a classic and productive approach to questions of phylogeny and evolutionary mechanism. Behaviors also can vary geographically, and such variation in behavioral expression can likewise serve to reveal biological processes and mechanisms. For example, analysis of geographic variation of bird songs has been used to examine indirectly the process of cultural evolution (e.g. Lynch and Baker 1993), the functional significance of song forms (e.g. Rothstein and Fleischer 1987), and mechanisms of song development (e.g. Marler and Pickert 1984).

The interplay of song function, song development, and geographic variation of song form is especially intriguing among the North American wood-warbler (Parulinae) species whose song repertoires are partitioned into discrete categories. In these species, songs from different categories are used in different contexts (for review, see Spector 1992) and may follow different developmental pathways (Byers and Kroodsma 1992). One might expect that such differences in communication function and

mode of song acquisition would be reflected in differences in geographic variation. Indeed, evidence of such intercategorical differences has been found in patterns of macrogeographic song variation in the Blue-winged Warbler (*Vermivora pinus*) and the Chestnut-sided Warbler (*Dendroica pensylvanica*; Kroodsma 1981). In particular, the form of these parulines' first-category songs (sensu Spector 1992) appears to be more stereotyped across regions than is the form of second-category songs.

Any such pattern of macrogeographic song variation must arise from processes that occur on a local level. If one wishes to infer the causes of patterns that are apparent at larger scales of organization, one must first try to understand how variability is created in populations of interacting individuals. As a step towards gaining that understanding, I analyzed geographic variation in song form within a local population of Chestnut-sided Warblers, and compared songs from that population with those of birds from other geographic regions.

METHODS

Microgeographic variation.—My analysis of local geographic distribution of song forms was designed to determine whether the spatial distribution of song types and song element types was structured. This

assessment was based on a sample of 62,335 songs recorded over three breeding seasons (1988–1990) from 80 different color-banded individuals, 17 of which were recorded over two years, and 3 of which were recorded in all three years. All recording was done at a 2-km² study site in the Savoy State Forest, Town of Florida, Berkshire County, Massachusetts (42°40'N, 73°3'W). Within the mostly forested study area, Chestnut-sided Warblers were concentrated on two power line rights-of-ways that provided shrubby habitat suitable for breeding. All recorded song elements (defined operationally as discrete sounds represented by continuous traces on a sonagram) and songs were classified into types by a visual comparison of printed sonagrams. The classification of songs into types was confirmed by a naive observer.

Prior analysis of the relationship between sampling intensity and recorded repertoire size (Byers 1995) suggested that most, but not all, of the song types occurring in the study area were included in the sample. Measured repertoire sizes for accented-ending (AE) songs were not dependent on sampling intensity, but sample size did affect measurement of unaccented-ending (UE) repertoire sizes. Thus, recorded AE repertoires were probably complete for almost all birds, but some rarely-sung UE types of the least-intensively-sampled birds were probably omitted from the sample.

Repertoire similarity was defined as the extent to which song types were shared between repertoires, and was measured as $2s/(r_1 + r_2)$, where s is the number of types shared by two birds and $r_1 + r_2$ is the sum of the two birds' repertoire sizes (McGregor and Krebs 1982). Values were calculated for all possible pairs of individuals in each of the three study years, and separate values were calculated for AE and UE song-type repertoires so that comparisons between the two song categories could be made. To determine if patterns of microgeographic variation were different when songs were analyzed at a finer level of structural detail, I also calculated similarity values for repertoires of introductory song elements of UE songs.

Analysis at this second level of song organization was undertaken because different levels of analysis might reveal different aspects of song-pattern distribution. For example, although measurement of similarities between repertoires of individual song elements ignores the information on sequential organization that is incorporated in measurements of similarity among whole-song types, it can detect new information on similarities between songs that share some, but not all elements. UE introductory elements in particular were chosen for the analysis because certain UE introductory-element types can occur in multiple song types and, in theory, could be culturally propagated and distributed independently of whole song types. Almost all AE song-element types, in contrast, are strictly bound to particular AE song types, so a separate analysis of AE elements would

have added no additional information to the existing analysis of AE songs.

Geographic distance between individuals was measured as the number of territorial boundaries crossed by the most direct path between two birds. The distance between immediate territorial neighbors was assigned a value of 1, between neighbors once-removed a value of 2, and so on. Geographic distance thus was encoded in a minimum-path connectivity matrix (Sokal 1979) designed to incorporate a distance metric that had biologically interpretable meaning.

The study area was divided by an area of unsuitable habitat (forest) that contained no Chestnut-sided Warblers. Birds on opposite sides of this divide were not connected by any direct series of contiguous territories, so distances between them were assigned an arbitrarily high distance value of 30 (the maximum measured value between any two birds within an area of contiguous territories was 17), as suggested by Sokal (1979) for situations in which some elements of a connectivity matrix lack connections.

I assessed the relationships between geographic distance and the three similarity measures (AE songs, UE songs, and UE introductory elements) with Mantel's randomization test (Manly 1991). This test provides a method for determining the statistical significance of the association between matrices of pairwise distance or similarity measurements. For each pair of matrices in the analysis, I calculated the matrix correlation and tested the significance of the correlation by direct comparison with a randomization distribution (i.e. with an empirical distribution generated by calculating the correlation on 1,000 random permutations of one of the matrices). The SIGNAL software package (Beeman 1993) was used to compute the randomization tests.

After this assessment of the overall relationship between distance and repertoire similarity, I examined the contribution of individual song types and song elements to the overall microgeographic distribution of types. In particular, each type of AE song, UE song, and UE introductory element that was sung by more than one bird in a given year was tested for evidence of spatial autocorrelation. Spatial autocorrelation was measured by a join-count statistic (Sokal and Oden 1978, Cliff and Ord 1981) that compared the observed number of joins (in this case, the number of territorial boundaries) separating unlike songs or elements to the number expected under a null hypothesis of no spatial autocorrelation (i.e. of random spatial distribution). The join-count statistic was constructed by analyzing joins between territories on which a particular song or element type occurred and those on which that type was absent. For example, if song type X were being analyzed, a map was drawn on which the territories of all birds that sang type X were shaded, and those territories that lacked X were left unshaded. Boundaries (joins) between shaded and unshaded territories were counted, and the count was

TABLE 1. Chestnut-sided Warbler AE songs from distant sites tended to match local songs, but UE songs did not. Each song in a sample of 224 songs from distant sites was classified as matching or not matching any of the songs in a library of 246 local songs recorded 1988–1990.

Sample	Proximity (km)	No. songs		Matches (percent of songs)	
		AE	UE	AE	UE
Minnesota 1990	1,600	17	15	82	47
Ohio 1951–1959	850	12	19	92	0
Ohio 1960–1972	850	12	27	92	0
Ohio 1973–1984	850	11	15	73	0
Virginia 1990	650	14	1	86	0
Maine 1953–1962	300	24	9	88	0
New Hampshire 1977	150	1	0	100	NA*
Maine 1977	300	2	0	100	NA
Leverett, Massachusetts 1989	60	6	9	100	22
Shelburne, Massachusetts 1990	40	7	7	100	29
Charlemont, Massachusetts 1989	10	7	9	100	33
Total		113	111	89	13

* Not available.

compared to that expected by chance alone, given the total number of joins on the map and the observed frequency of type X among the study population. Thus, the join-count statistic can be viewed as a measure of whether a type is more (or less) clustered in space (i.e. is involved in fewer or more shaded-unshaded joins) than is expected by chance. Clustering is identified, however, relative to a quite conservative standard, because shared songs on nearby, but non-contiguous territories are not detected. Only direct connections between like types are counted by the statistic.

Macrogeographic variation.—Variation in song form over larger distances was assessed by comparing AE and UE songs recorded at distant sites to the collection of song types recorded at the main study site in 1988, 1989, and 1990. The songs of the main study site were represented by a library of 246 printed sonagrams of 154 different song types from both song categories. Types sung by several members of the local population were represented by multiple sonagrams so that the range of within-type variation was incorporated.

Distant sites were represented by printed sonagrams of 224 different songs recorded at sites whose proximity to the main site ranged from 2 km to about 1,600 km (Table 1). Songs recorded in the Itasca region of Minnesota in 1990 and in the Clinch Mountain National Wildlife Refuge, Virginia, were provided by collaborators. The remaining distant songs used in this analysis were obtained from the collection of the Borror Laboratory of Bioacoustics, and included songs from Ohio, Maine, and one from New Hampshire. Recording dates of the Borror tapes ranged from 1951 to 1984.

To compare local and distant songs, a naive observer was asked to classify each distant song as either a "match" or "no match" to each local song, or as not matching any local song. Criteria for a match were

specified to include the form (shape) and sequence of song elements, but not the number of repetitions of any element. If the entire song did not match, the observer was asked to determine if any individual song elements of the distant song were also found in the local library.

In addition, a separate pool of AE songs drawn from two different regions was analyzed to determine if AE song form was tied to the geographic origin of songs. The analyzed sample consisted of unlabeled sonagrams of 208 different AE songs, of which 123 were recorded in Berkshire County, Massachusetts, in 1986 and 1987, and 85 were recorded in Shenandoah National Park, Virginia, in 1987. I determined, by visual inspection, the song type of each sonagram. The sonagrams were also classified by two naive observers who were familiar with bird songs and with the concept of song types. These observers were asked to sort the sonagrams into groups of the same type, although no definition of "type" was supplied.

RESULTS

Microgeographic variation.—The relationship between repertoire similarity and local geographic distance differed strikingly between AE and UE songs (Table 2). AE-repertoire similarities were not significantly associated with geographic distance, and birds separated by small distances were no more likely to share AE types than were birds separated by larger distances. In contrast, similarity between the UE repertoires of individuals at the main study site was significantly related to the distance between birds in all three years, and similarity between UE introductory element repertoires was sig-

TABLE 2. Matrix correlations (*r*) between repertoire similarity and interindividual distance within a population of Chestnut-sided Warblers, showing that repertoires of UE songs and UE introductory elements are more similar among geographically closer birds, but that repertoire similarity and geographic distance are not related for AE songs. Two-tailed significance of associations was tested with Mantel's randomization test.

Year	<i>n</i>	AE songs	UE songs	UE introductory elements
1	34	-0.0023	-0.168**	-0.0411
2	42	0.0025	-0.314***	-0.1640***
3	27	-0.0015	-0.400***	-0.1984***

P* < 0.01; *P* < 0.001; others *P* > 0.05.

nificantly related to interindividual distances in two of three years.

The contrast between the local distribution patterns of AE and UE songs also was apparent in the analysis of individual song types and song-element types. AE song types appeared to be dispersed at random over the study area (Table 3). The normalized join-count statistics for all AE types tended to cluster around zero, and no type had a statistically significant value in any year. Thus, no AE type was either significantly clustered or over-dispersed (e.g. alternating or checkerboard pattern) relative to chance expectation.

I also did not find any evidence of clustering when only predominant AE types were considered. Individual Chestnut-sided Warblers use only one (or rarely two) of the AE types in their repertoires for most AE singing (Byers 1995), and these predominant songs might have exhibited a pattern of distribution that was masked when other, less frequently sung types were included in the analysis. Even when uncommonly sung types were excluded from the analysis, however, the join-count statistic for each AE type remained nonsignificant and generally near zero. The predominant AE type of a male thus typically did not match the neighboring males' predominant AE type.

Many UE song types, however, did cluster geographically (Fig. 1). UE types were very likely to have negative join-count *z*-scores, indicating clustering of songs in space, and values for many types were highly significant. The clustering was most pronounced among types that were shared by more than five birds, and was weaker in year 3 than in the prior two years.

TABLE 3. Lack of spatial patterning among accented-ending songs within a population of Chestnut-sided Warblers, as shown by nonsignificant values of standard normal deviate (*z*) of the join-count statistic for each type (all *P* > 0.05).

Song type	Year 1		Year 2		Year 3	
	<i>n</i> ^a	<i>z</i> ^b	<i>n</i>	<i>z</i>	<i>n</i>	<i>z</i>
All songs						
AE-1	11	0.53	18	0.63	6	-0.24
AE-1a	9	1.28	9	-0.62	6	0.11
AE-2	25	-0.63	24	-0.67	14	-0.41
AE-3	6	-0.54	12	-0.23	15	0.47
AE-4	9	0.09	14	-0.62	13	1.24
Predominant songs only^c						
AE-1	6	-0.10	11	1.14	5	0.18
AE-1a	5	-0.55	7	-1.07	2	0.90
AE-2	18	-0.45	14	0.12	8	0.11
AE-3	4	0.36	8	-0.22	9	-1.58
AE-4	3	0.20	5	-0.39	3	1.29

^a Number of individual Chestnut-sided Warblers singing each accented-ending song type.

^b Negative values of *z* indicate that a type was more clustered than expected by chance; positive values that a type was more evenly dispersed.

^c Most birds used a single AE type for 70% or more of AE singing. A few individuals (two in year 1 and three in year 2) used two copredominant types.

A similar pattern was observed among UE introductory element variants (Fig. 2). Again, variants used by several individuals were likely to be clustered. For variants of many elements, clustering was pronounced, indicating that neighboring males were copying the fine structure of each others' songs.

Macrogeographic variation.—AE songs from the distant sites usually matched very closely the song types found at the main study site (Table 1). Regardless of the spatial or temporal distance between sites, almost all of the AE songs from distant sites were of one of the five forms identified at the local site (Fig. 3).

The few distant AE songs that did not precisely match a local type were clearly related to local AE types. Of the 13 AE songs classified as not matching closely, 11 differed only subtly from songs in the local library, and were clearly variants of the 4 main AE types (Fig. 3; G, K, O, H, L). Although these variants did not occur in the local library, they matched AE songs recorded at diverse locations in 1962 and 1963, and archived at the Cornell Laboratory of Ornithology. For example, Kroodsma (1981), working with these archived tapes, published sonagrams of: an AE-2a song recorded in Wis-

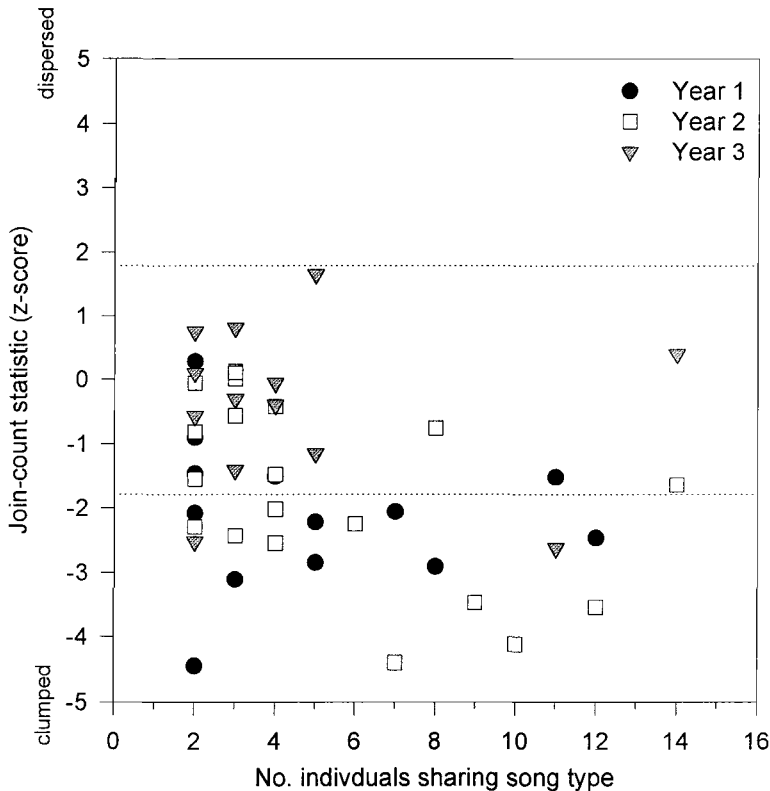


Fig. 1. Spatial clustering of unaccented-ending song types. Negative values of z indicate that type more clustered than expected by chance; positive values that type more evenly dispersed than expected. Values above 1.96 or below -1.96 (dotted lines) indicate $P < 0.05$.

consin; AE-2b songs recorded in Michigan, New York, West Virginia, and New Hampshire; and AE-1b songs from Maine, New Hampshire, New York, Maryland, Ohio, Virginia, Tennessee, and North Carolina.

Only a single exception was found to the overall correspondence in form between the AE types in the local and distant samples. AE songs recorded from two territorial neighbors in Minnesota (AE-5; Fig. 3; P) did not match any song in the local library. These songs did not appear to be variants of any of the main AE song types, and were the only AE songs in the distant sample that had no introductory song elements in common with the local sample.

The general stereotypy and invariance of form among AE songs was confirmed by the separate examination of AE songs from Massachusetts and Virginia. The two naive observers both classified the songs into four types, and assigned songs to types without respect to geographical

origin. All identified song types were identical to the main AE types found at my main study site in western Massachusetts. The types were so distinctly different from one another that the two independent observers were in 100% agreement in the songs that were assigned to each group.

Unlike AE songs, UE songs from distant sites usually did not match types from the main study site (Table 1). Nonmatching songs constituted the large majority of UE distant songs, most remote sites had no matching UE types, and the few samples that contained matching UE songs had more nonmatching than matching types. UE type matches did occur, however. I identified 14 examples of matching UE songs at four remote sites. Three of these sites were those closest to the main site (i.e. <100 km); this proximity between matched UE songs suggests that close sites were more likely to share UE types with the main site than were distant ones. The

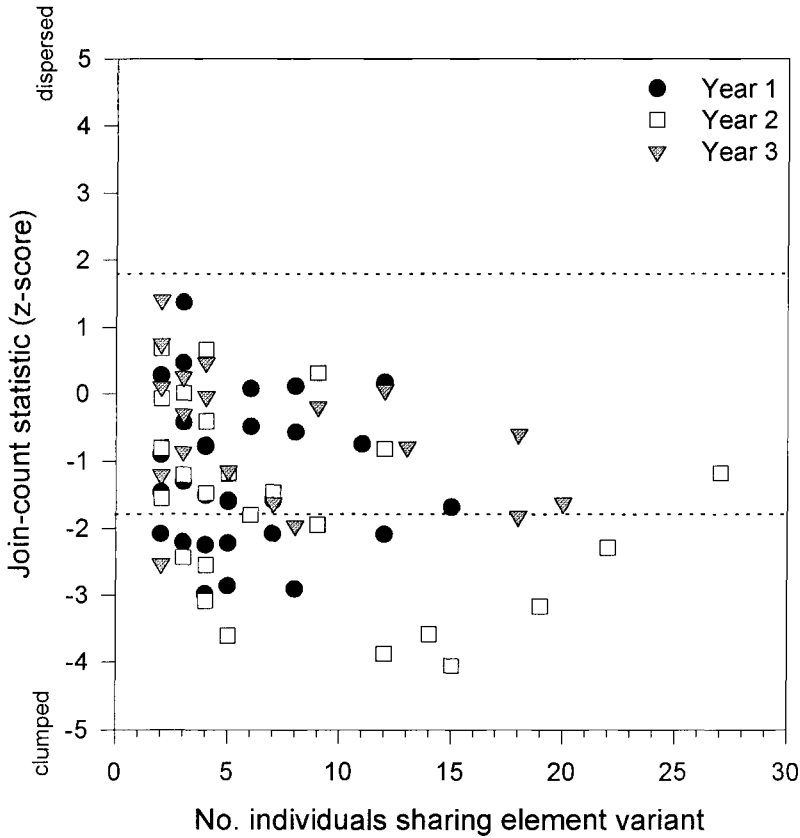


Fig. 2. Introductory elements of UE songs also cluster geographically. For interpretation of z-values, see caption of Figure 1.

fourth site with UE-type matches, however, was Minnesota, the site farthest from the main site. Despite its remoteness, the Minnesota sample had a proportion of UE song matches that was higher than the three nearby sites.

Although 97 of the 111 UE songs in the distant samples did not fully match the song types found at the main site, most of the nonmatching songs had a least one song element in common with UE songs at the main site. Matches between local and remote song elements were mostly among termination, rather than introductory, elements. In 71 of 77 cases in which matching elements were incorporated in nonmatching songs, the element match was due exclusively to one or more of the elements in a particular termination sequence. This five-element sequence, or some portion of it, formed the ending of a large portion of the UE songs recorded at the main study site, and also commonly formed the termination of UE songs in

the remote samples (Fig. 4). Matching introductory elements, in contrast, were found in only six of the nonmatching UE songs from remote sites.

DISCUSSION

Patterns of geographic variation in the form of Chestnut-sided Warbler songs differ sharply between the two categories of songs. AE song types and the elements that compose them are few in number, highly stereotyped over both time and distance, and distributed at random locally and (with some possible exceptions) among regions. UE song and song element types have a more complex distribution pattern that is characterized by a much larger number of types, a diverse and variable array of forms, local clustering of some song and element types, and widespread distribution of some element types and features of song organization. Be-

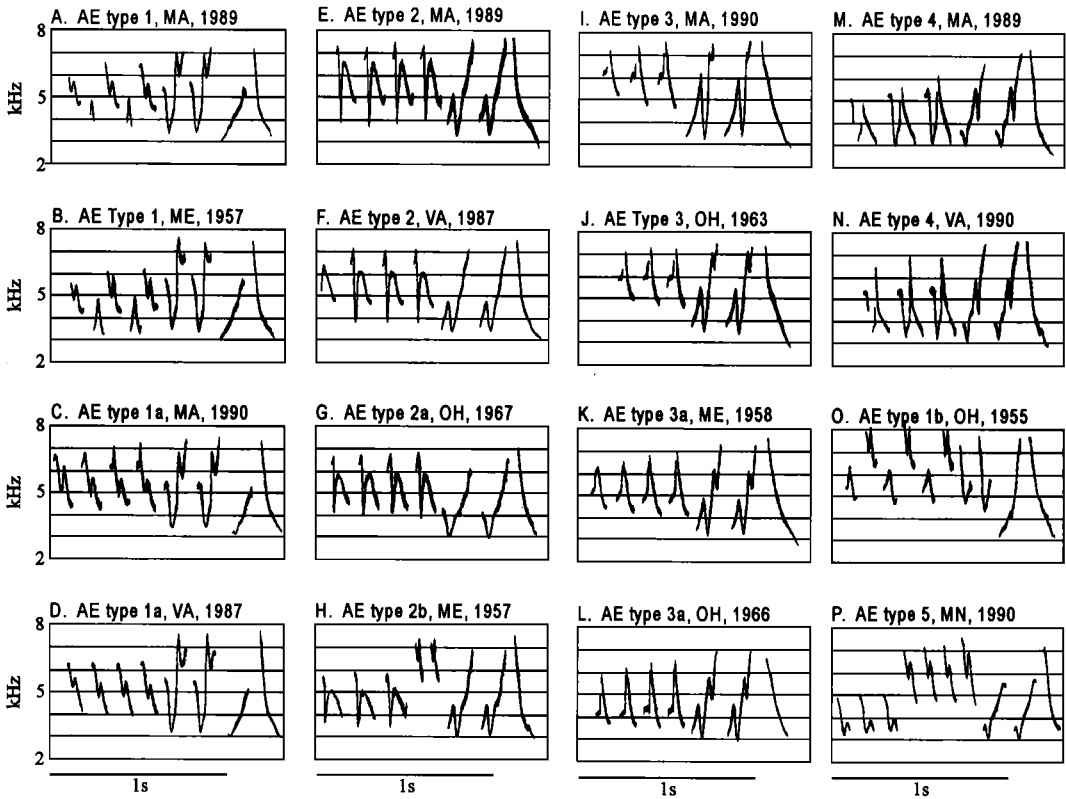


Fig. 3. Stereotypy of AE song form across spans of time and geographic distance. Examples of five Chestnut-sided Warbler accented-ending song types and their variants. Except for type AE-5, all illustrated forms were found in more than one geographic sample. Abbreviations: (MA) Massachusetts; (ME) Maine; (MN) Minnesota; (OH) Ohio; and (VA) Virginia.

cause the two song categories vary in such distinct fashions, I discuss them separately below before considering the song system as a whole.

Unaccented-ending songs.—Patterns of UE geographic variation fit easily into the continuum of different patterns documented among other species of songbirds. For example, the local relationship between song similarity and inter-bird distance that this study found for UE songs is a common phenomenon among songbirds. A literature review by Krebs and Kroodsma (1980) found 63 oscine species in which “songs of neighbors are more similar to one another than they are to the songs of more distant conspecifics.” This kind of structured microgeographic variation in song form often is interpreted as evidence of song copying, either at the natal site by young birds that subsequently breed close to the natal site (Slater and Ince 1982, Cunningham et al. 1987), or at the breeding site by adult birds (McGregor and Krebs 1989).

Extensive neighbor sharing, like that apparent in Chestnut-sided Warbler UE songs, is most likely to occur when breeding adults copy songs from their territorial neighbors. If the birds instead memorized UE songs as nestlings or fledglings at their natal site, it is unlikely that individuals would reliably settle, after a long-distance migration, as the immediate territorial neighbors of their tutors (Thompson 1970). Such predispersal song learning might, if birds returned to their natal areas to breed, lead to a microgeographic pattern in which nearby birds sang more similar songs than did distant birds, but would not generate the observed bias towards sharing with direct neighbors.

Other lines of evidence also indicate that Chestnut-sided Warblers probably acquire their shared songs and elements as adults. For example, it appears that nestlings rarely return to breed at their natal site. Of 87 nestlings banded over the course of my study, none was observed

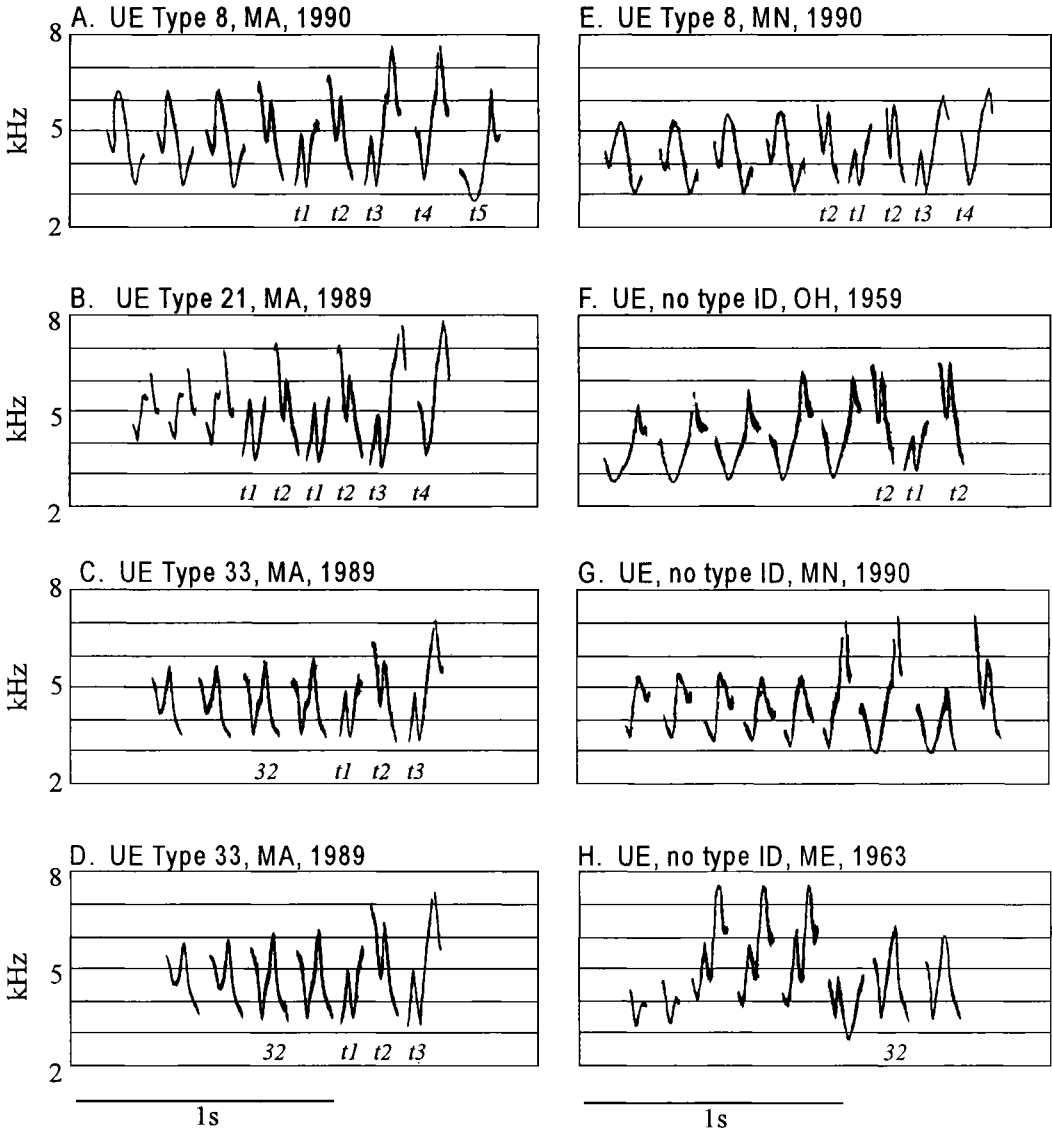


Fig. 4. Four Chestnut-sided Warbler unaccented-ending songs (A, B, C, D) from main study site in western Massachusetts, and four from other locations (E, F, G, H). Songs A and E illustrate geographically separated, yet similar songs. Songs C and D recorded from territorial neighbors, and illustrate the much more precise matching possible between nearby birds. Song elements of a standardized termination sequence that occurred in some songs in all geographic regions are labeled *t1* through *t5* in songs in which they occur. Song element 32 is labeled in songs C, D, and H to illustrate occurrence of the same introductory element in different song types taken in temporally and geographically separated samples. For state abbreviations, see caption of Figure 3.

in the study area in subsequent years; Chestnut-sided Warblers show no tendency to breed near the singers that they heard as nestlings. Also, laboratory studies (Byers and Kroodsma 1992) have shown that Chestnut-sided Warblers are at least capable of learning new songs during

their second spring (i.e. 10–12 month after hatching), and field evidence suggests that adults can add new songs to their repertoires (Spector and Byers unpubl. manuscript). Even if new arrivals to a breeding population already have some UE songs in their repertoires, the

shared portion of the UE repertoire probably is acquired after arrival.

UE song-type sharing is apparently not connected to a function, such as signaling social status (Payne 1982, O'Loghlen and Rothstein 1993) or directing signals at particular individuals (Falls 1985), that would require birds to make extensive use of their ability to match the songs of other birds. In fact, individual Chestnut-sided Warblers use shared UE songs only rarely, even during territorial conflicts. Although every UE repertoire at the main study site contained at least one song that matched another local bird, singing males generally did not use a type that their neighbors would be likely to sing. For example, relatively few birds had predominant UE types that matched those of their direct neighbors. Only 1 of 33 possible neighboring pairs in year 1 shared the same predominant UE type, 3 of 41 pairs in year 2, and 1 of 27 in year 3. Furthermore, males do not seem to reserve the shared songs in their repertoires for the kind of matched countersinging—during conflicts or when otherwise close to other males—that characterizes some other species with repertoire sharing among neighbors (e.g. Marsh Wrens, *Cistothorus palustris*; Verner 1976). For example, in singing by 10 pairs of year 1 territorial neighbors whose repertoires contained UE song types in common, both males used the same song type in only 13 of 285 samples, even though 97 of those samples also contained fighting or chasing.

Alternative interpretations of the clustered portion of UE repertoires include the possibility that use of matching songs is reserved for uncommon but important situations in which the sudden "emergence" of a matching song would be an especially potent signal. Another possibility, suggested by the observed clustering of UE element variants, is that the important functional unit for matching is actually the individual song element and that matching between different song types that contain matching elements is more common in day-to-day singing than is matching of whole songs. Alternatively, clustering might be a functionless consequence of a stochastic process in which new song components arise and spread through a population.

Although the widely scattered point samples used in my macrogeographic analyses do not allow for a precise description of regional variation patterns among UE songs, some intriguing aspects of UE-song and song-element dis-

tribution were observed. UE songs were characterized by both a general geographic variability and by some particular features that were conserved over time and distance. For example, most UE introductory elements, even those in the nearby Massachusetts samples, were unique to the geographic sample in which they occurred. Despite this regional distinctiveness, however, some introductory element types were found in more than one location and, in a few cases, whole UE songs matched across large distances (although not across long times). None of the long-distance matches, however, approached the precise matching often found within the main local study site (Fig. 4).

UE termination elements likewise combined variability with a certain degree of interregional consistency. The five elements of the standardized UE termination sequence that occurred in all geographic regions are rather variable in form, but these elements recur, with syntax (element sequence) intact, across all geographic samples, and are no more variable in form between than within samples. Although this ending sequence occurred frequently in all sampled regions, it was not universal among UE songs. Songs lacking it also occurred in all regions.

Given the overall geographic diversity of UE songs, the common threads among UE songs from diverse locales are puzzling, especially because the shared aspects are present in only a portion of the songs at each locality. The UE macrogeographic pattern thus differs from that in species (e.g. Swamp Sparrow, *Melospiza georgiana*; Marler and Pickert 1984) in which all songs share common song elements across all regions, with individuals constructing songs by variously recombining a finite set of species-universal song elements. UE songs also differ from those of species (e.g. Greenfinch, *Chloris chloris*; Güttinger 1976) in which song element forms are geographically variable, but other features of song organization remain consistent across all songs. Songs systems like those of the Swamp Sparrow and the Greenfinch allow individual song variability while preserving species distinctiveness. UE songs of Chestnut-sided Warblers might incorporate a kind of partial version of this system, in which a few universal elements and/or syntax rules are maintained within a set of more plastic elements and song construction rules. This explanation, however, is difficult to reconcile with the many UE songs

that contain neither the elements nor the syntax that are widely shared among other UE songs.

Accented-ending songs.—Structured geographic variation does not emerge among AE songs, regardless of the scale of analysis. AE songs assume the same few, geographically widespread forms across the range of the species. Similarly, AE songs lack structured microgeographic patterning; song types in local populations are distributed at random. Birds do not incorporate their neighbors' AE songs into their own repertoires and do not select a predominant AE song that matches that of their neighbors. Whatever advantage might be gained by sharing UE songs with neighbors apparently does not extend to AE songs. Chestnut-sided Warblers likewise do not appear to settle on territories or to adjust their singing such that AE matches with neighbors are avoided, as has been suggested for the Darwin's Large Cactus-Finch (*Geospiza conirostris*; Grant 1984).

The absence of geographic variation in song form is relatively uncommon among birds (Munding 1982). The songs of some species (e.g. Short-toed Treecreeper, *Certhia brachydactyla*; Thielcke 1973) do not vary within local populations, but the songs of different localities are different. Other species seem to lack any kind of local or regional patterning. Most song types of Wood Thrushes (*Hylocichla mustelina*), for example, are widespread over the breeding range of the species, among-locality variation in a song type is no greater than that within a locality, and local song sharing among individuals is not related to interindividual distance (Whitney and Miller 1987, Whitney 1989). Prothonotary Warbler (*Protonotaria citrea*) songs are geographically uniform; song forms recur with random probability among widespread geographic samples (Bryan et al. 1987).

AE songs of Chestnut-sided Warblers show the lack of geographic structure exemplified by Wood Thrush and Prothonotary Warbler songs, but are further distinguished by having only a small number of types. A similarly limited range of possible song types is found in island populations of Darwin's ground finches (*Geospizinae*; Millington and Price 1985), but the geographic scale of this system is small. The few AE song forms, in contrast, are very widely distributed (with the exception of type AE-5, so far found only in Minnesota). Thus, AE songs are perhaps more analogous to the whistle song of the Black-capped Chickadee (*Parus atricapil-*

lus), which has only a single form that is invariant over most of the range of the species (reviewed in Hailman 1989).

The persistence of particular song forms over long stretches of time and space raises questions about the mechanism for maintaining such rigid stereotypy in a culturally transmitted signal. Copying errors and innovations during song development would quickly introduce variability in the absence of some mechanism to prevent it. Thielcke (1987) suggested that song uniformity could be maintained across generations if young birds memorized all of the different adult songs that they heard and then somehow "averaged" those songs during development. Marler (e.g. 1990) has presented evidence that, even in song-development systems that require auditory experience of conspecific song, genetically controlled factors can guide and limit expressed vocal behavior. This postulated "extensive pre-encoding of information about song in the brain of naive male songbirds" (Marler and Nelson 1992) is an intriguing possibility, as it provides not only a mechanistic explanation for the persistence of stereotyped song forms, but also a potential means by which aspects of signal form could be inherited and, therefore, subject to modification by natural selection.

Coexistence of two distinct patterns of variation.—If the breeding biology and cultural evolutionary history of Chestnut-sided Warblers led to repertoires partitioned into stereotyped and variable components, what other species' song systems show a similar outcome? Other paruline warblers with two-category repertoires also seem to have geographically conserved first category songs (sensu Spector 1992; AE songs are in this category). Both Blue-winged Warblers (Kroodma 1981) and Golden-winged Warblers (*Vermivora chrysoptera*, Highsmith 1989) use the same first category song type across their ranges (unlike Chestnut-sided Warblers, these two *Vermivora* species have only a single first-category song type), but have geographically variable second category songs. Outside of the Parulinae, Black-capped Chickadee repertoires contain both geographically stereotyped whistle songs and geographically variable "gargle" vocalizations (Ficken et al. 1987). In both the chickadees and the *Vermivora* warblers, the stereotyped form is more associated with intersexual behavior, while the variable form is associated with aggression (Otter and Ratcliffe

1993, Ficken et al. 1987, Highsmith 1989). Scarlet Rosefinches (*Carpodacus erythrinus*) also sing two kinds of songs, one of which varies microgeographically and one of which is "similar among all males" (Björklund 1989). The use and functions of the two types have not been systematically investigated, but Björklund reported that the variable form is "a loud, advertising song" and the stereotyped form is "used only in . . . aggressive encounters between two males, [or] at the first approach of a female." If these observational impressions of song use in the Scarlet Rosefinch are accurate, the relationship between stereotypy and song use seems to be somewhat different than that found in the wood-warblers and the Black-capped Chickadee.

Viewed separately, AE and UE songs behave so differently that they might have been recorded from two different species. The evidence indicates that the two song categories have distinct communication functions (Kroodsma et al. 1989) and modes of ontogeny (Byers and Kroodsma 1992). It is clear that the divergence in the patterns of geographic variation of AE and UE songs is related to the distinctions in communicative function and ontogeny between the two song categories. In particular, the stereotype of AE songs must be related to their role in male-female interactions, and the variability of UE songs to their role in male-male interactions. For example, if female Chestnut-sided Warblers assess sustained bouts of AE singing as part of their process of mate choice, a male whose signal deviated from the established standard might be at a disadvantage. Conversely, in interactions between socially familiar neighboring males, the important comparison is not between the signaler and other members of the species, but between the signaler's current motivational state and his past motivational states. This kind of communication might not require a stereotyped signal, and UE songs, freed from the need for stereotypy, might proceed towards a more plastic and variable song that can encode finer gradations of meaning.

ACKNOWLEDGMENTS

I thank Donald Kroodsma, James D. Rising, and an anonymous reviewer for advice and critical review of the manuscript, and am grateful to J. Wells, M. Kroodsma, and D. Spector, who classified sonagrams. Field recordists D. Albrecht, S. Hopp, and D. Kroodsma provided tapes from Minnesota and Virginia. S.

Gaunt and the Borrer Laboratory of Bioacoustics kindly copied archived recordings and allowed their use. The Library of Natural Sounds at the Cornell Laboratory of Ornithology also supplied recordings. The Western Massachusetts Electric Company and the state of Massachusetts granted access to the main study site. This research was supported by the National Science Foundation (Graduate Fellowship and BNS-8812084, BNS-9111666 to D. Kroodsma).

LITERATURE CITED

- BEEMAN, K. 1993. Signal user's guide, version 2.2. Engineering Design, Belmont, Massachusetts.
- BJÖRKLUND, M. 1989. Microgeographic variation in the song of the Scarlet Rosefinch, *Carpodacus erythrinus*. *Ornis Scand.* 20:255-264.
- BRYAN, K., R. MODENHAUER, AND D. E. KROODSMA. 1987. Geographic uniformity in the songs of the Prothonotary Warbler. *Wilson Bull.* 99:369-376.
- BYERS, B. E. 1995. Song types, repertoires, and song variability in a population of Chestnut-sided Warblers. *Condor* 97:390-401.
- BYERS, B. E., AND D. E. KROODSMA. 1992. Development of two song categories by Chestnut-sided Warblers. *Anim. Behav.* 44:799-810.
- CLIFF, A. D., AND J. K. ORD. 1981. Spatial processes: Models and applications. Pion, London.
- CUNNINGHAM, M. A., M. C. BAKER, AND T. J. BOARDMAN. 1987. Microgeographic song variation in the Nuttall's White-crowned Sparrow. *Condor* 89:261-275.
- FALLS, J. B. 1985. Song matching in Western Meadowlarks, *Sturnella neglecta*. *Can. J. Zool.* 63:2520-2524.
- FICKEN, M. S., C. M. WEISE, AND J. A. REINARTZ. 1987. A complex vocalization of the Black-capped Chickadee. II. Repertoires, dominance, and dialects. *Auk* 89:500-509.
- GOULD, S. J., AND R. F. JOHNSTON. 1972. Geographic variation. *Annu. Rev. Syst. Ecol.* 3:457-498.
- GRANT, B. R. 1984. The significance of song variation in a population of Darwin's finches. *Behaviour* 89:90-116.
- GÜTTINGER, H. R. 1976. Variable and constant structures in Greenfinch (*Chloris chloris*) songs in different locations. *Behaviour* 60:304-318.
- HAILMAN, J. P. 1989. The organization of major vocalizations in the Paridae. *Wilson Bull.* 101:305-343.
- HIGHSMITH, R. T. 1989. Function, form, and recognition of the songs of the Golden-winged (*Vermivora chrysoptera*) and Blue-winged (*Vermivora pinus*) warblers. Ph.D. dissertation, Univ. Massachusetts, Amherst.
- KREBS, J. R., AND D. E. KROODSMA. 1980. Repertoires and geographical variation in bird song. Pages 143-177 in *Advances in the study of behavior* (J. Rosenblatt, R. Hinde, C. Beer, and M. C. Busnel, Eds.). Academic Press, New York.

- KROODSMA, D. E. 1981. Geographical variation and functions of song types in warblers (Parulidae). *Auk* 98:743-751.
- KROODSMA, D. E., R. C. BERESON, B. E. BYERS, AND E. MINEAR. 1989. Use of song types by the Chestnut-sided Warbler: Evidence for both intra- and inter-sexual functions. *Can. J. Zool.* 67:447-456.
- LYNCH, A., AND A. J. BAKER. 1993. A population memetics approach to cultural evolution in Chaffinch song: Meme diversity within populations. *Am. Nat.* 141:597-620.
- MANLY, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.
- MARLER, P. 1990. Innate learning preferences: Signals for communication. *Dev. Psychobiol.* 23:557-568.
- MARLER, P., AND D. N. NELSON. 1992. Neuroselection and song learning in birds: Species universals in a culturally transmitted behavior. *Semin. Neurosci.* 4:415-423.
- MARLER, P., AND R. PICKERT. 1984. Species-universal microstructure in the learned song of the Swamp Sparrow (*Melospiza georgiana*). *Anim. Behav.* 32:673-689.
- MCGREGOR, P. K., AND J. R. KREBS. 1982. Song types in a population of Great Tits (*Parus major*): Their distribution, abundance, and acquisition by individuals. *Behaviour* 79:126-152.
- MCGREGOR, P. K., AND J. R. KREBS. 1989. Song learning in adult Great Tits (*Parus major*): Effects of neighbours. *Behaviour* 108:139-159.
- MILLINGTON, S. J., AND T. D. PRICE. 1985. Song inheritance and mating patterns in Darwin's finches. *Auk* 102:342-346.
- MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in acquired vocalizations of birds. Pages 147-208 in *Acoustic communication in birds* (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.
- O'LOGHLEN, A. J., AND S. I. ROTHSTEIN. 1993. An extreme example of delayed vocal development: Song learning in a population of wild Brown-headed Cowbirds. *Anim. Behav.* 46:293-304.
- OTTER, K., AND L. RATCLIFFE. 1993. Changes in singing behavior of male Black-capped Chickadees (*Parus atricapillus*) following mate removal. *Behav. Ecol. Sociobiol.* 33:409-414.
- PAYNE, R. B. 1982. Ecological consequences of song matching: Breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63:401-411.
- ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987. Vocal dialects and their possible relationship to honest signaling in the Brown-headed Cowbird. *Condor* 89:1-23.
- SLATER, P. J. B., AND S. A. INCE. 1982. Song development in Chaffinches: What is learnt and when? *Ibis* 124:21-26.
- SOKAL, R. R. 1979. Testing statistical significance of geographic variation patterns. *Syst. Zool.* 28:227-232.
- SOKAL, R. R., AND N. L. ODEN. 1978. Spatial autocorrelation in biology. 1. Methodology. *Biol. J. Linn. Soc.* 10:199-228.
- SPECTOR, D. A. 1992. Wood-warbler song systems: A review of paruline singing behaviors. *Curr. Ornithol.* 9:199-238.
- THIELCKE, G. 1973. On the origin of divergence of learned signals in isolated populations. *Ibis* 115:511-516.
- THIELCKE, G. 1987. Long-time consistency of Short-toed Treecreeper dialect. *J. Ornithol.* 128:389-390.
- THOMPSON, W. L. 1970. Song variation in a population of Indigo Buntings. *Auk* 87:58-71.
- VERNER, J. 1976. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. *Living Bird* 14:263-300.
- WHITNEY, C. L. 1989. Geographical variation in Wood Thrush song: A comparison of samples recorded in New York and South Carolina, USA. *Behaviour* 111:49-60.
- WHITNEY, C. L., AND J. MILLER. 1987. Distribution and variability of song types in the Wood Thrush. *Behaviour* 103:49-67.