

GEOGRAPHIC UNIFORMITY IN SONGS OF THE PROTHONOTARY WARBLER

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ABSTRACT.—Oscine songs, which are typically imitated from adult conspecifics, usually vary geographically, but here we document a surprising lack of geographic variation in the songs of the Prothonotary Warbler (*Protonotaria citrea*). A typical song of this species consists of 4 to 14 repeated syllables of one type. Using cluster analysis, we showed that the geographic origins of the similar songs within the state of Texas were closer together than were the locations of song pairs chosen at random. But this statistical demonstration of geographic patterning within Texas was overshadowed by the lack of broad geographic variation: a given Texas song was no more likely to be more similar to another Texas song than to a song from distant portions of eastern North America. How a songbird species can maintain such geographic uniformity in a presumably learned song raises questions about our understanding of the flexibility provided by imitation during song ontogeny. *Received 24 Sept. 1986, accepted 22 Jan. 1987.*

Songbirds typically develop their songs through imitation of conspecifics (e.g., Kroodsma 1982), and because dispersal from the site of learning is usually limited, neighborhoods (or larger regions) of males with similar song types occur. Documenting and understanding these patterns of local geographic song variation in different species, which are a consequence of this vocal imitation, has been a major focus of research in avian bioacoustics (e.g., see reviews of Baker 1982, Mundinger 1982, Slater 1983).

Although most workers have concentrated on *differences* in song structure among populations of a given species, others have revealed constant features of songs that occur throughout the geographic range of a species (cf. Becker 1982). Even the casual bird watcher in his travels realizes that general features of songs such as duration, frequency, or tonal quality usually enable unambiguous identification of most species. An increasing number of studies, however, are demonstrating that the repertoire of different sounds (figures, notes, syllables; i.e., the basic building blocks of songs) that are used to construct songs of a given species is quite limited (Shiovitz and Thompson 1970, James 1984, Marler and Pickert 1984). Vocal learning seems to be required for proper development of this fine structure within oscine song (Rice and Thompson 1968, Güttinger 1979, Marler and Sherman 1985); in our preoccupation with identifying song

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dialects, however, we had come to expect that this learned microstructure would be the first feature of songs to vary geographically. Additional study of the geographic uniformity of learned songs could tell us much about the role of genetic and environmental (i.e., learned) factors in song ontogeny (Güttinger 1979, Marler et al. 1981).

Here we present a striking example of how presumably learned songs (see Kroodsma 1982) recur throughout the geographic range of a songbird, the Prothonotary Warbler (*Protonotaria citrea*). The limited evidence that we have for some geographic structuring within our Texas samples is overshadowed by the broad geographic uniformity of the songs over the eastern half of North America.

METHODS

Between 22 April and 13 June 1978, songs of 150 Prothonotary Warblers were recorded at 10 locations in eastern Texas. Of those 150 songs, three were highly unusual for Prothonotary Warblers (Fig. 1, sonograms 1–3) and were therefore excluded from our study of geographic variation. Six males, however, sang “double songs” that included two different syllable types (see RESULTS for additional description of songs). For our geographic analyses, then, we used a total of 153 syllables from songs of 147 Prothonotary Warblers. The 10 recording locations, together with the sample size of the number of different syllable types used in our analyses from each location ($N = 153$), were as follows: Brazos Bend State Park, Fort Bend County ($N = 7$); Upper Lake Conroe, Walker County ($N = 8$); McCardell Lake, Polk County ($N = 14$); Engeling Wildlife Management Area, Anderson County ($N = 17$); Ft. Worth Nature Center, Tarrant County ($N = 8$); Beaumont Unit, Big Thicket National Preserve, Hardin, Jefferson, Orange, and Jasper counties ($N = 13$); B. A. Steinhagen Reservoir, Tyler and Jasper counties ($N = 21$); Upper Toledo Bend Reservoir, Shelby and Panola counties ($N = 22$); Caddo Lake, Marion and Harrison counties ($N = 21$); and Wright Patman Reservoir, Bowie and Cass counties ($N = 22$). We recorded songs on Ampex 641 tape at 19 cm-sec^{-1} with a Uher 4000 Report IC and used a Dan Gibson P650 parabolic microphone. The original recordings have been deposited in the Texas Bird Sound Library, Division of Life Sciences, Geology, and Geography, Sam Houston State University.

We obtained an additional 39 recordings of Prothonotary Warblers from the Cornell Library of Natural Sounds, the Borror Laboratory of Bioacoustics of the Ohio State University, and the Florida State Museum at Gainesville. These recordings contained 42 different syllable types; three males sang double songs, but one-half of one double song was unusual (Fig. 1, sonogram 4) and was not included in our cluster analysis. We divided these samples into two geographic regions: the Great Lakes Region (Illinois, Ohio, Ontario) and the southeastern United States (Florida, Georgia, North Carolina, South Carolina).

We graphed a total of 2380 songs on a Kay Elemetrics 6061B Sound Spectrograph with the “wideband” (300 Hz) filter, but chose for analysis only the highest quality sonogram from each male. For each of the 194 syllables analyzed in this study we measured six temporal and six frequency parameters on the second or third from the last repeated syllable in the song (Fig. 2) (see also RESULTS for a more detailed description of the song). These syllables were typically the loudest, and therefore made the clearest print on the sonogram. For the cluster analysis we used the NTSYS program (Euclidean distance) developed by Rohlf and Kishpaugh (1972).

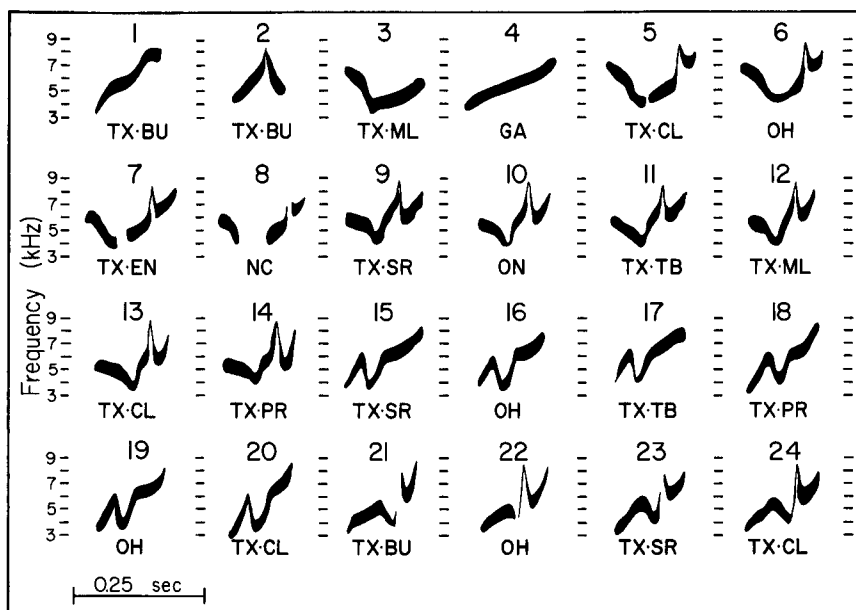


FIG. 1. Examples of atypical syllables omitted from the geographic analyses (1–4) and of syllable patterns that recur throughout the geographic range of the species (5–24). Songs 5–14 are of pattern A, and songs 15–24 are of pattern B (see Fig. 1 and text). State or province locations are provided on the figure; additional information on location and individual is provided for the Texas samples. Exact locations are as follows: (1) Texas, Beaumont Unit Bird 12; (2) Texas, Beaumont Unit Bird 3; (3) Texas, McCardell Lake Bird 3; (4) Georgia, Camp Stephen Foster (Cornell LNS Cut 12); (5) Texas, Caddo Lake Bird 4; (6) Ohio, Winous Pt. (OSU Borrer Cut 1444); (7) Texas, Engling WMA Bird 6; (8) N. Carolina, Oconeechee (Univ. Fla. Cut 3); (9) Texas, Steinhagen Reservoir Bird 14; (10) Ontario, Rondeau Park (Cornell LNS Cut 1); (11) Texas, Toledo Bend Bird 9; (12) Texas, McCardell Lake Bird 14; (13) Texas, Caddo Lake Bird 14; (14) Texas, Patman Reservoir Bird 3; (15) Texas, Steinhagen Reservoir Bird 5; (16) Ohio, Winous Pt. (Borrer Cut 1068); (17) Texas, Toledo Bend Bird 7; (18) Texas, Patman Reservoir Bird 9; (19) Ohio, Winous Pt. (Borrer Cuts 7581, 7593); (20) Texas, Caddo Lake Bird 3; (21) Texas, Beaumont Unit Bird 8; (22) Ohio, Shreve (Borrer Cut 6941); (23) Texas, Steinhagen Reservoir Bird 2; (24) Texas, Caddo Lake Bird 1. In our cluster analysis, for example, syllable 5 (from a Texas song) was more similar to syllable 6 (from Ohio) than to any other syllable in our sample. A list of illustrated syllable pairs in which the first listed (e.g., 5) is more similar to the second listed (e.g., 6) than to any other syllable in the sample follows: 5, 6; 7, 8; 9, 10; 11, 10; 12, 10; 13, 14; 14, 13; 15, 16; 17, 15; 18, 19; 20, 18; 21, 22; 23, 24; 24, 23.

RESULTS

Songs of the Prothonotary Warbler. — The song of a Prothonotary Warbler usually consisted of a series of 4 to 14 repeated syllables of a single type, which generally increased in amplitude from the beginning to the

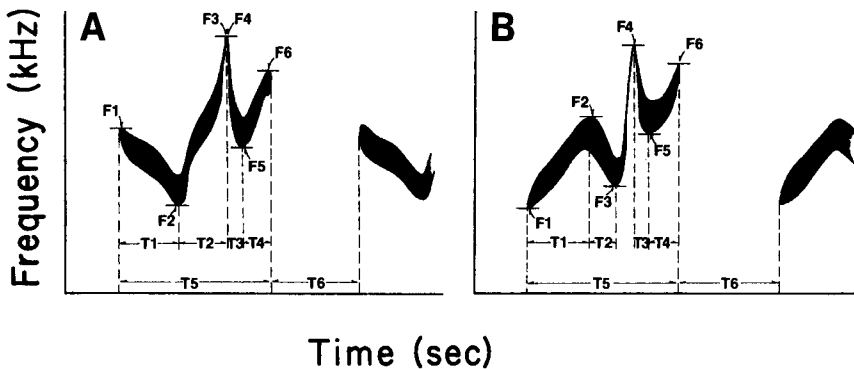


Fig. 2. An illustration of the 12 morphometric measurements on two representative syllable patterns (A and B) found in songs of the Prothonotary Warbler. F1–F6 are frequency measurements, T1–T6 temporal measurements.

end of the song (see sonograms of entire songs in Borror and Gunn 1985). Songs of a given male were stable over time; we recorded three color-banded males during two consecutive months of the same breeding season and one of these banded males in successive years. We could detect no change in the songs of these males.

Nine of 189 males in this study sang a more complicated “double” song that consisted of two series of distinctly different syllable types. Most of the time (60% of all songs), however, even these males sang a simpler song with only one, and usually only the first (8 of 9 males), syllable pattern.

Careful inspection of the sonograms revealed that there were two basic forms of syllables in use by the males (Figs. 1, 2). Both forms were modulated in frequency, but one form (A) initially decreased in frequency while the other (B) initially increased in frequency. In Texas both syllable forms occurred at all locations (frequency of occurrence of “A” syllables ranged from 29% to 68% of the sample, with a median of 55%), and overall there was nearly a 1:1 (actually A:B, 99:95) ratio of these two syllable forms in our analyzed sample of 194 syllables.

Geographic variation in songs.—We found recurrences of particular syllable types of the Prothonotary Warbler throughout the geographic range of the species (Fig. 1) (see also Borror and Gunn 1985). These recurrences, moreover, were so frequent that we could find no patterns of geographic variation in syllable types of this warbler in eastern North America. We used the matrix of phenetic distances provided by the cluster analysis program to determine the most similar syllable type to each of the 194 syllable types in our sample. We found that 29 of 153 Texas syllables were actually more similar to syllables from the Great Lakes or

Southeastern regions than they were to other syllables from Texas; this value was clearly not different from the 32.5 that we would have expected by chance, based only on sample sizes. When we analyzed syllables from the Great Lakes and Southeastern region separately, we found the same result: there was no tendency for syllable types that were most similar to each other to occur in the same geographic region.

When we restricted our analyses to Texas samples, we did find some evidence that the syllables most similar to each other also tended to occur closer together geographically. Thus, in Texas there was a tendency for syllable types that were most similar to each other to occur at the same geographic location ($\chi^2 = 2.73$, $df = 1$, $P = 0.1$). The most similar pairs of syllables were actually recorded from locations separated by a median distance of 178 km, but syllable pairs chosen at random were from locations that were 202 km apart (difference was statistically significant; 2-tailed Mann-Whitney U -test, $n_1 = n_2 = 153$, $P = 0.002$). Because this warbler lives in floodplain habitats that are relatively isolated, we also tested to see if the most similar songs were likely to occur in the same floodplain; we found no evidence, however, of song type distributions by floodplain ($\chi^2 = 0.20$, $df = 1$, $P > 0.5$). Thus, neighboring males or males from the same location in Texas did not necessarily have the most similar songs, but the most similar pairs of songs came from locations that were slightly closer together than expected by chance.

DISCUSSION

There is some evidence of local geographic variation within our samples of Prothonotary Warbler songs. Within our Texas samples we found that the geographic locations of the most similar pairs of songs were closer together than were the locations of song type pairs chosen at random. In addition, some preliminary multivariate analyses (χ^2 , MANOVA, and canonical analysis; see Bryan 1979 for those analyses and for overall phenograms of data presented in this paper) suggest that some overall variation in temporal or frequency parameters of the songs of this warbler may be explained by geographic location.

What remains most striking about our data, however, are the recurrences of the relatively simple Prothonotary Warbler songs, which consist of a single repeated syllable, throughout the bird's geographic range. A given song from our Texas sample, for example, is equally likely to be most similar to another Texas song, as it is likely to be most similar to a song from Ohio, Ontario, North Carolina, or another distant portion of the geographic range.

Such geographic uniformity of the basic building blocks from which songs are constructed has also been demonstrated in other species. Shio-vitz and Thompson (1970) and Emlen (1971) first demonstrated that a

limited number of song elements comprised the songs of the Indigo Bunting (*Passerina cyanea*). Neighboring males learn from each other nearly identical sequences of selected subsets of those song elements (Thompson 1970, Payne 1982), but the basic elements from which the songs are constructed are essentially the same in Michigan, New York, and Kentucky. The congeneric Lazuli Bunting (*P. amoena*) likewise has a limited set of song elements, about 20% of which match elements in the Indigo Bunting (Thompson 1976). Limited repertoires of song elements or reduced geographic variation in at least some song forms also occurs in the Greenfinch (*Chloris chloris*; Güttinger 1977), Yellow Warbler (*Dendroica petechia*; Bankwitz and Thompson 1979), Cirl Bunting (*Emberiza cirlus*; Kreutzer 1979), Chestnut-sided Warbler and Blue-winged Warbler (*Dendroica pensylvanica*, *Vermivora pinus*; Kroodsma 1981), Yellow-throated Vireo (*Vireo flavifrons*; James 1984), Swamp Sparrow (*Melospiza georgiana*; Marler and Pickert 1984), and Summer and Scarlet tanagers (*Piranga rubra*, *P. olivacea*; Shy 1984, 1985).

The relative stereotypy of oscine song over broad geographic regions is difficult to explain. Such geographic constancy would be expected in subsoscine flycatchers, in which highly stereotyped songs appear to be under strong genetic control (e.g., Kroodsma 1984). But vocal imitation among oscines (including warblers—Kroodsma, unpubl. data) has led to striking examples of song dialects (e.g., Baker 1982) as well as to mimicry of an extraordinary diversity of conspecific, heterospecific, or even non-animal sounds (see Kroodsma and Baylis 1982 for lists of species). This tremendous potential among some oscines for producing such a diversity of sounds must be limited somehow in other species by forces that preserve a remarkable uniformity of songs, often over thousands of kilometers.

The exact means by which some songbirds are held to a limited set of sounds remains unclear. Marler et al. (1981) argue eloquently that in some way the perceptual development of these birds may be “canalized” (sensu Waddington 1957), just as morphological systems in the body are canalized in their development. The limited set of elements from which Swamp Sparrow songs are constructed is certainly consistent with the idea of “an innate repertoire of note types, with a species-specific morphology that is genetically controlled” (Marler and Pickert 1984:686).

A number of questions remain unanswered. Are sound repertoires of most species really far more restricted than we had formerly appreciated? Is each male singer equipped with some mechanism that identifies rather precisely the appropriate sounds in the environment that must be imitated (cf. Marler 1976)? Is it possible that nonsinging females of many species may actually limit the variability in male songs by responding only to selected sounds that males are capable of producing (King and West 1983)? Clearly, we must reassess how we view song learning in oscines and must

attempt a better understanding of the developmental guidelines and the interplay between genetic and environmental (i.e., learned) factors that control vocal ontogeny (Güttinger 1979, Marler et al. 1981).

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