

The Auk

A Quarterly Journal
of Ornithology

Vol. 109 No. 2 April 1992

The Auk 109(2):215-222, 1992

TWO SONG POPULATIONS OF THE NORTHERN PARULA

RALPH R. MOLDENHAUER

Department of Biological Sciences, Sam Houston State University, Huntsville, Texas 77341, USA

ABSTRACT.—Two distinctly different Type A songs characterize eastern and western populations within the breeding range of the Northern Parula (*Parula americana*). These two song variants differ mainly in the last note, but also have other significantly different frequency and temporal characters. The eastern-style singers terminate their song with two glissando-figures forming an inverted "V" on a sonagram. The western Type A song ends with a less intense buzzy note or vibrato-figure with an up slur. The song length of eastern birds averages 0.12 s shorter than western singers. Other significant differences include trill duration, trill rate, period between the first two syllables and the maximum frequencies of the first and last syllables. The two song populations are nearly allopatric, overlapping in southwestern Alabama and eastern Kentucky, where the two song forms can be heard in adjacent areas but where no intermediate songs are found. Morphological differences coupled with the differences in the Type A song suggest that the two populations are recognizable and may be in the early stages of allopatric divergence. I suggest that the eastern populations be recognized as *P. americana americana* and the western populations as *P. americana ludoviciana*. Received 30 August 1990, accepted 10 January 1992.

SONG is an important aspect of avian breeding biology that often is used as a guide for species relatedness (Payne 1986). Studies dealing with geographic song variation have led to the discovery of distinct song or call differences between populations that are morphologically indistinct. Such populations are judged to be either geographical races or sibling species when sufficient behavioral and genetic information exists to indicate reproductive isolation. Examples of such populations include flycatchers (*Empidonax traillii* and *alnorum*; Stein 1958, 1963), Pine Grosbeaks (*Pinicola enucleator*; Adkisson 1981), and Marsh Wrens (*Cistothorus palustris*; Kroodsma 1989).

The Northern Parula (*Parula americana*) breeds from southeastern Manitoba to Nova Scotia, and south to central Texas and central Florida. The winter range is mainly in east-central Mexico and on the islands of the Greater and Lesser Antilles (AOU 1983). Early investigators rec-

ognized as many as three races of *P. americana*: the northeastern *P. a. pusilla* (= *usneae*); the southeastern *P. a. americana*; and the western *P. a. ludoviciana* (= *ramalinae*) (Brewster 1896, Ridgway 1902, Oberholser 1938, 1974). Parkes (1954), however, argued against recognition of these populations because of the difficulty in separating specimens by color characters and measurements. The species is now treated as being monotypic (AOU 1957). Some authors (Mayr and Short 1970) have considered *P. americana* to be conspecific with *P. pitiauyumi*.

The Northern Parula has two primary song types (see Borror and Gunn 1985). The Type A song (Type 1 of Borror and Gunn) is a simple and more commonly sung buzzy trill ending in a short, separated note. The less frequent, Type B song (Type 2 of Borror and Gunn) consists of a series of buzzy notes. The Type A song has been described as the Accented Ending Song and the Type B as the Unaccented Ending Song

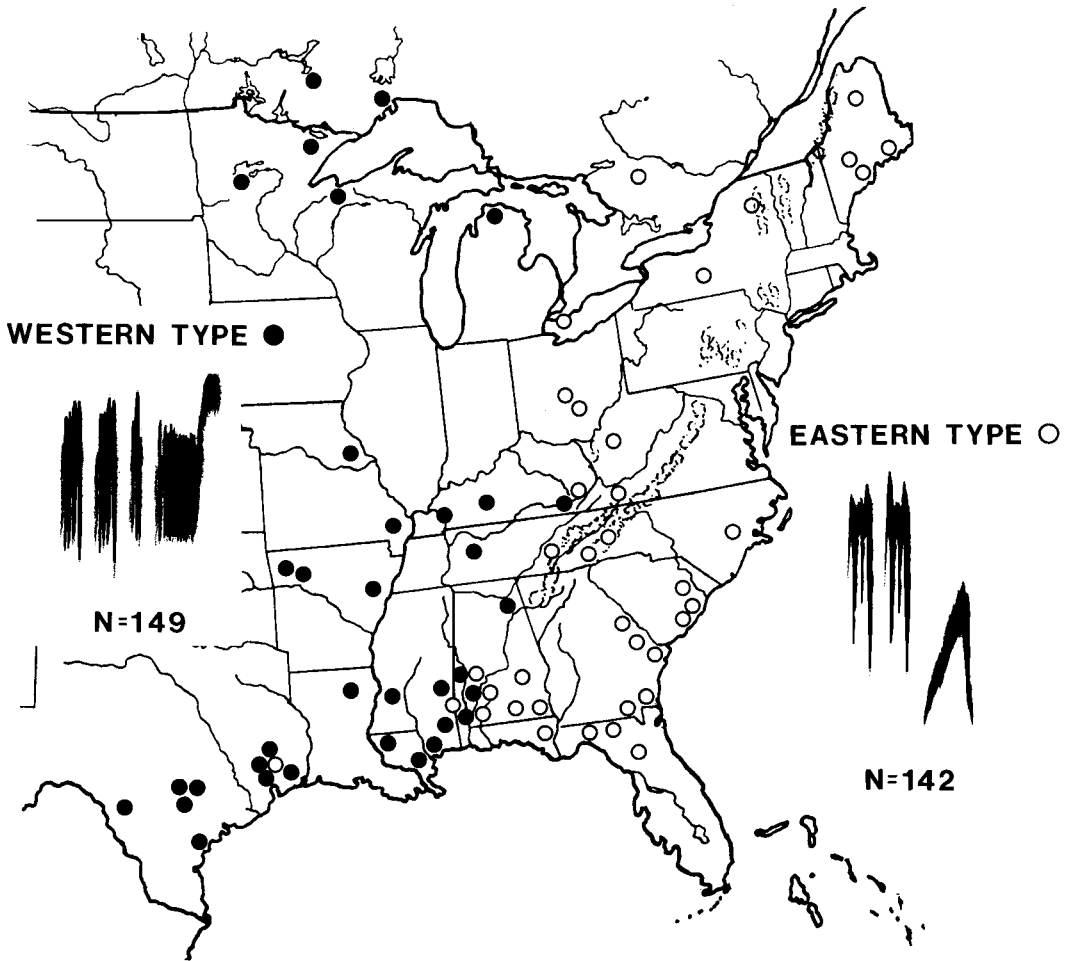


Fig. 1. Distribution of recorded eastern and western Type A songs of *Parula americana*. See Appendix for sample sizes at each location.

(Morse 1989). There have been no published reports of song variation in this species in which recorded songs were analyzed spectrographically.

Using audiospectrographic analysis, I discovered two distinct Type A songs that characterize eastern and western populations within the species breeding range. The ranges of these two variants are sympatric in southwestern Alabama and eastern Kentucky. The existence of these two song forms suggests that the Northern *Parula* consists of at least two geographic races or, perhaps, even two sibling species.

METHODS

Type A song recordings of 291 Northern *Parulas* were analyzed in this study. The locations of the re-

cording sites are listed in the Appendix and are mapped in Figure 1. The recordings were made between 1953 and 1989, but most (74%) were recorded after 1981. A Uher reel-to-reel tape recorder (19 cm/s) with a Dan Gibson P650 parabolic microphone was used for 215 recordings. These recordings have been deposited in the Texas Bird Sound Library (Department of Biological Sciences, Sam Houston State University). Copies of 76 additional recordings were obtained from: Borror Bioacoustic Laboratory (47 recordings); Library of Natural Sounds (23); Florida State Museum (2); Greg Lasley (2); John Arvin (1); and W. M. Meriweather (1). A Nagra III recorder (38 cm/s) was used for 35 of these recordings, and 31 were made with a Magnemite (38 cm/s). An AKG microphone (or an unspecified one) with a parabola was used when making these recordings. The make of recording equipment for the remaining 10 birds is unknown; however, 4 recordings were made on cassette recorders.

Songs for each bird were graphed using the 80–8,000 Hz frequency range on a Kay Elemetrics 6061B Sona-Graph with a wideband filter. I chose the most representative sonagraph for each bird to analyze geographic variation in the structure of the Type A song. The Northern Parula Type A song consists of an initial series of rapidly repeated syllables, termed a “trill” or “buzzy-trill,” and a terminal note (Fig. 2). Visual examination of the sonagrams indicated that the terminal note consists of two distinctive types and can be used to easily separate birds into eastern and western song populations. To determine if other song differences existed between the two populations, I measured the following nine song variables for 277 of the 291 song audiospectrographs (Fig. 2): (1) song duration; (2) trill duration; (3) duration from end of trill to end of song; (4) period between first two syllables; (5) period between last two syllables; (6) maximum frequency of first syllable; (7) maximum frequency of last syllable; (8) number of trill syllables; and (9) trill rate (no. syllables/s). Measurements were made to the nearest 0.5 mm on the spectrographs and then converted to the appropriate temporal or frequency value. Fourteen spectrographs were unusable for these measurements, but still had identifiable terminal notes so that the songs could be classified as eastern or western song types.

Using ANOVA and MANOVA statistical computer programs of SAS (version 6.06, 1989; SAS Institute 1985), I made univariate and multivariate comparisons of all song variables between and within eastern and western song populations. A discriminant-function analysis (DISCRIM program of SAS) was used to predict the percentage of songs that could be correctly identified as eastern or western song types based on eight song variables. Song duration was not used in the MANOVA or DISCRIM analysis, because it is the sum of trill duration and duration from the end of the trill to the end of the song (variables 2 and 3 in Fig. 2).

RESULTS

Two distinctively different Type A songs characterize eastern and western populations of *P. americana* within its breeding range. As indicated earlier, the two song forms are distinguished mainly by the terminal note. The terminal note of eastern birds appears as two fused glissando-figures forming an inverted “V”, or chevron, on a sonagram (Fig. 3). Western birds terminate the song with a less intense “buzzy” note or vibrato-figure with an up slur (Fig. 3). With training, an observer can audibly detect the differences in the two song endings. The eastern song ending sounds more intense and accentuated than that in the western song. No bird sang both types of endings, and three birds

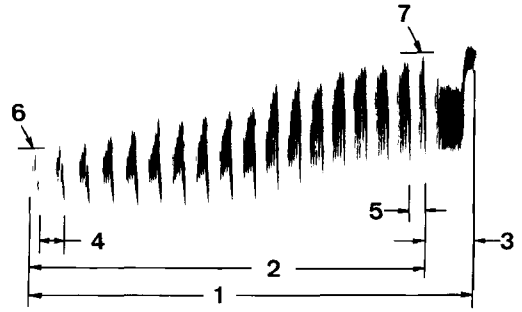


Fig. 2. Illustration of seven of nine song variables measured and compared statistically for eastern and western song types. Variables 1–5 are duration measures and 6–7 are frequency measures. See text for explanation of numbers. Type A is the western-type ending, while type B is eastern-type ending.

did not have one of these terminal notes in their song. Figure 4 illustrates some of the variation in the two song endings. From a series of spectrographs, I could not visibly detect intra-individual variation in the structure of the total song pattern. However, some birds occasionally would lengthen the trill by adding one or two syllables.

Based on the mapped recording localities, the distributions of the two forms of Type A songs are nearly allopatric (Fig. 1). Except for two eastern type songs recorded in eastern Texas, I found only two areas where the two song populations overlap—southwestern Alabama and eastern Kentucky. In suitable habitat, other areas of overlap probably exist in eastern Tennessee, central Ohio, Michigan and Ontario; these regions were not sampled extensively in this study. The area of overlap in Alabama (Fig. 5) is north of Mobile and extends about 140 km from the Mississippi–Alabama border to Selma, Alabama. Although both eastern and western song forms were recorded in adjacent areas, none of the recordings made within this area of sympatry indicated intergradation of song types.

A statistical comparison of nine morphometric song measurements revealed several significant differences between the eastern and western populations (Table 1). The overall song duration of eastern singers averaged 0.12 s shorter than western singers. Both the trill duration and the duration from the end of the trill to the end of terminal note contributed to the shorter duration of the song. Although there was no significant difference between the number of trill syllables, the trill rate was significantly higher in eastern singers (23.0/s) than in

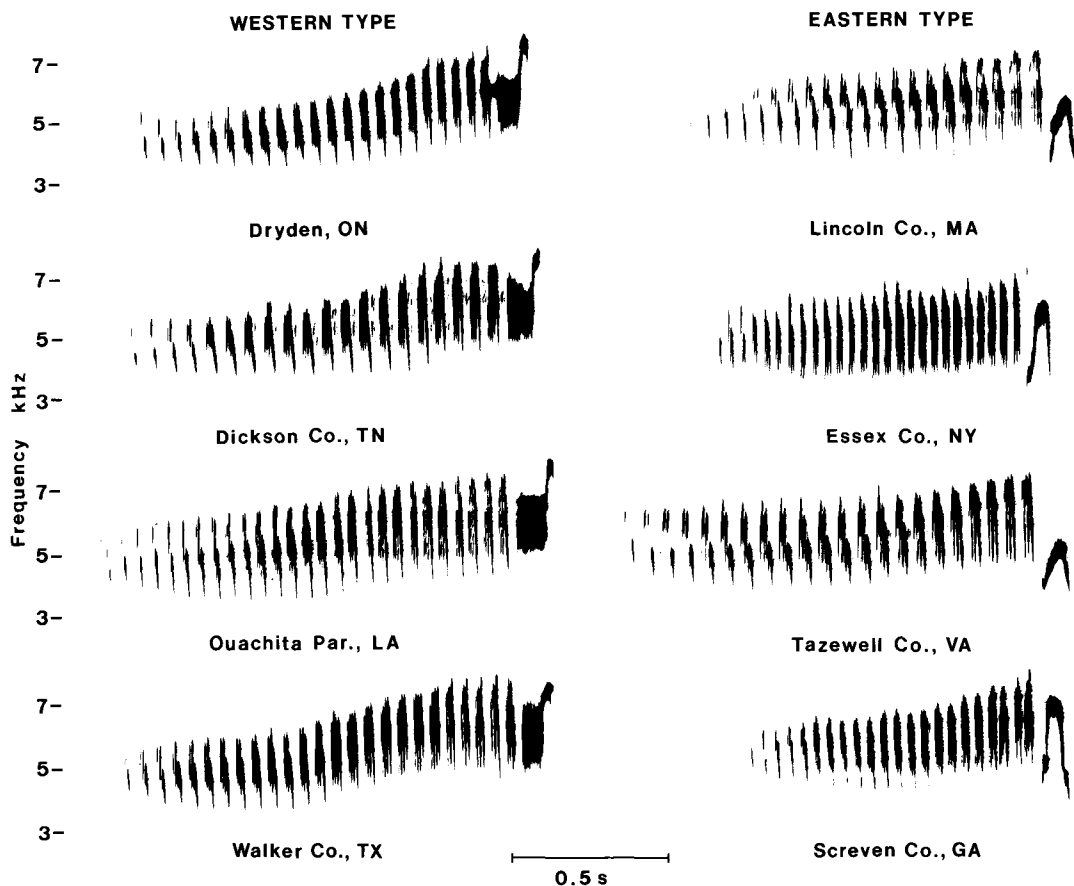


Fig. 3. Examples of eastern and western Type A songs of Northern Parulas.

western singers (21.4/s). The higher trill rate was reflected also in the significant difference in the time between the first two trill syllables. Eastern singers had a shorter interval between the first two syllables than western singers; the eastern singers tended to maintain this interval to the end of the trill. Western singers began the trill slower (i.e. they had a longer period between the first two syllables) and then gradually increased the rate. There was no significant difference between eastern and western singers for the period between the last two syllables. Eastern singers sang at significantly higher frequencies both at the start and end of the trill. Discriminant-function analysis of the nine variables indicated that no single measurement can predict correctly the song type greater than 80% of the time. When eight variables were considered together, 88.7% of the eastern songs and 83.7% of the western songs were accurately identified. Multivariate analy-

sis (MANOVA) of eight variables indicated a highly significant difference between the two song populations ($P < 0.0001$).

The situation at the time the songs were recorded was not always indicated by the observer. Songs were recorded normally (without playback stimulus), after song playback (the bird's own song or that of another parula), or both. The sonagram used for analysis was chosen for its clarity and could represent a song recorded before or after playback. To evaluate whether there was any change in the song characteristics from before to after playback, I analyzed nine Type A song variables of 11 birds (six eastern and five western) with the General Linear Model MANOVA (SAS Institute 1985). There was a small but significant difference between songs recorded before and after playback ($F = 5.2$, $df = 8$ and 44 , $P < 0.001$). The basic change in the song after playback was the addition of trill syllables within the same time

WESTERN-TYPE ENDING



EASTERN-TYPE ENDING

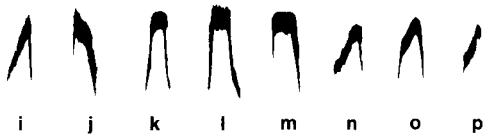


Fig. 4. Variation in terminal note of eastern and western Northern Parula songs. Western-type endings: (a-c) Texas, Montgomery and Walker counties, respectively; (d) Louisiana, St. Tammany Parish; (e-f) Tennessee, Cheatham Co.; (g) Mississippi, Hinds Co.; (h) Kentucky, Whitley Co. Eastern-type endings: (i-j) Georgia, Screven and Camden counties, respectively; (k) Alabama, Wilcox Co.; (l) Florida, Calhoun Co.; (m-n) North Carolina, Wayne Co.; (o-p) Maine, Lincoln Co.

frame, resulting in a higher trill rate (syllables/s). There also was a slightly higher maximum frequency (kHz) of the last syllable. However, there was no visible change in the basic structure of the song pattern. From the same analysis, a highly significant difference was obtained between eastern and western song types ($F = 179.6$, $df = 8$ and 44 , $P < 0.0001$). There was no interaction between the before/after and eastern/western factors ($F = 1.46$, $df = 8$ and 44 , $P = 0.2$), indicating that the small playback effects on song variables were comparable in eastern and western birds. Assuming a more or less random choice of songs (with respect to playback situations) for analysis, the small playback effects would cancel out in comparisons of the nine song variables for eastern and western birds.

I also tested northern and southern song populations within each song type. I found no significant differences between the seven western songs recorded in Michigan, Wisconsin, Minnesota and Ontario and the remaining western type songs recorded in the south (MANOVA $F = 0.88$, $P = 0.54$). When I compared eastern-type singers north and south of the Virginia-North Carolina border, which approximates the dividing line between the two eastern subspecies of Oberholser (1974), I found a small but

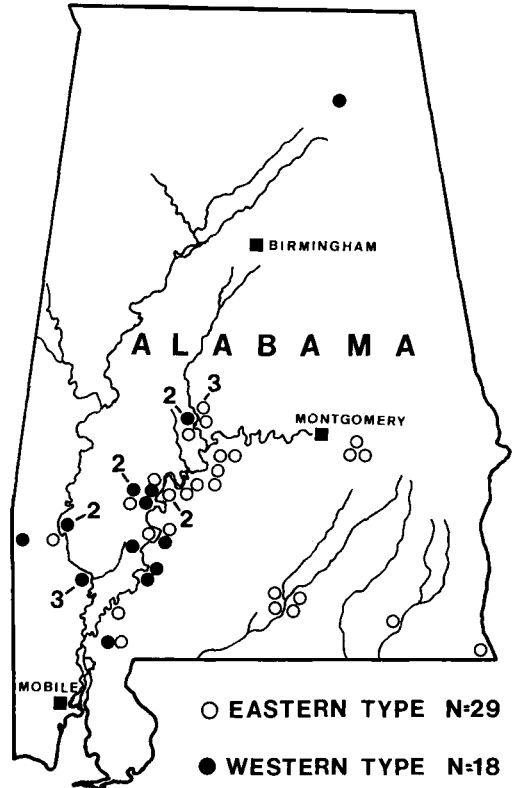


Fig. 5. Distribution of recorded Northern Parula eastern and western Type A songs in overlap area of Alabama. Symbols represent recording sites. Number indicates multiple bird samples for particular location.

significant difference (MANOVA $F = 3.12$, $P = 0.003$) between the two groups. Northern birds had a shorter trill duration and a shorter duration from the end of the trill to the end of the song, resulting in an overall shorter song duration. The maximum frequencies at the start and end of the trill were lower in the northern songs. Results of discriminant-function analysis of the three populations are shown in Table 2. Based on eight variables, 78.3% of the north/eastern-type songs and 61.2% of the south/eastern-type songs were correctly identified. Only 10 of the 131 eastern-type songs were incorrectly identified as western songs. The two eastern-type singers recorded in Texas were correctly identified as having eastern-type songs.

DISCUSSION

Two Type A songs characterize eastern and western populations of *P. americana* within its

TABLE 1. Means (\pm SD) and univariate *F*-values of nine variables comparing eastern and western Type A songs of Northern Parulas.^a

Variable	Type		ANOVA ^b <i>F</i> -value
	Eastern (<i>n</i> = 133)	Western (<i>n</i> = 144)	
Song duration (s)	1.19 \pm 0.20	1.31 \pm 0.16	28.87**
Trill duration (s)	1.09 \pm 0.20	1.18 \pm 0.15	18.07**
No. trill syllables	24.9 \pm 7.6	25.1 \pm 6.7	0.05
Trill rate (syllables/s)	23.0 \pm 5.7	21.4 \pm 5.1	6.33*
Song duration - trill duration (s)	0.11 \pm 0.02	0.14 \pm 0.03	79.40**
Period between first two syllables (msec)	47.9 \pm 13.4	56.1 \pm 14.8	23.02**
Period between last two syllables (msec)	51.3 \pm 13.6	50.2 \pm 8.6	0.62
Maximum frequency, first syllable (kHz)	5.68 \pm 0.63	5.10 \pm 0.57	84.60**
Maximum frequency, last syllable (kHz)	7.47 \pm 0.47	7.36 \pm 0.45	6.14*

^a MANOVA *F*-value = 32.04, *P* < 0.0001.

^b * *P* = 0.01; ** *P* < 0.001.

breeding range. The distribution of these eastern- and western-style singers corresponds very closely to the ranges of three unrecognized *P. americana* subspecies described by Oberholser (1974). The eastern Type A singers range from central Ontario east to Maine, and south to southwestern Alabama and northern Florida (Fig. 1). This distribution encompasses precisely the described ranges of the northeastern race (*P. a. pusilla*) and the southeastern race (*P. a. americana*). The distribution of the western race (*P. a. ludoviciana*) matches the western Type A singers ranging from Manitoba through western Ontario, and south to southeastern Texas and southwestern Alabama. Thus, the western race and southeastern race overlap in southwestern Alabama, as do the eastern and western song populations. The two eastern-style singers recorded in Walker County, Texas, during May were probably migrants. Oberholser (1974) reported specimen records for *P. a. americana* and *P. a. pusilla* from eastern and southern Texas during migration.

Parkes (1954) argued against subspecific recognition of the three *P. americana* populations, because of the extensive overlap in measurements and the difficulty in distinguishing specimens by coloration. He admitted that there are certain trends in color and size, but recommended against subspecific recognition. Oberholser (1974) argued in favor of the three races based on color characters and measurements. He stated that the western race is smaller than both eastern races and that *pusilla* is larger than the southeastern race *americana*. I made wing, tail, bill and tarsal measurements of 269 male and 94 female adult skins taken from various

locations throughout the species' breeding range and obtained similar results (unpubl. data) to those of Oberholser. Separation of the *pusilla* and *americana* races also is supported by differences in the Type A song. Multivariate statistics and discriminant-function analysis (Table 2) indicate significant differences between the songs of northern and southern populations of eastern singers, but the differences were in the trill characters and are not readily identifiable by ear or sonagram. I believe that *pusilla* and *americana* show some divergence based on skin characters and song measurements, but these differences are subtle and, as such, are impractical for individual recognition (as was argued by Parkes 1954). The terminal note of the Type A song is distinctive and can be detected audibly or visually by sonagram. It is the only reliable indicator (essentially 100% accurate) for recognition of individuals from the two allopatric populations. Thus, based on the characteristic chevron ending of the Type A song and its distribution within the breeding range, I consider

TABLE 2. Percentages of eastern- and western-style singers correctly identified by discriminant-function criteria for eight Type A song variables.

Song type	Sample size	Correctly predicted	
		Number	Percent
Eastern-type ending			
Northern population	46	36	78.3
Southern population	85	52	61.2
Western-type ending			
	141	114	82.3

the eastern-style singers as constituting a single population equivalent to the two races *pusilla* and *americana*. The western-style singers I consider equivalent to *ludoviciana* based on the characteristic ending and range of the western Type A song. I recommend that the two song populations be given subspecific recognition with the eastern-style singers designated as *P. a. americana* and the western-style singers as *P. a. ludoviciana*. The Tropical Parula (*P. pitaiayumi*) has a Type A song similar to the western Type A of *P. americana*. The initial trill is followed by a terminal note that is a vibrato-figure ending with a downward inflection (Borrer and Gunn 1985). The breeding ranges of *P. pitaiayumi* and the western style singers of *P. americana* meet in the Rio Grande Valley of southern Texas.

Song differences have been used as an indicator of evolutionary divergence in bird populations that appear to be nearly morphologically monomorphic throughout their range (Payne 1986). The distinctive terminal notes of the Type A song are a recognizable difference that suggests divergence within *P. americana*. However, no genetic difference between the two populations has yet been detected (i.e. mtDNA restriction fragment; Moldenhauer and F. Gill, unpubl. data). Song need not have a genetic basis (Kroodsma 1989) and evidence for vocal learning has been documented for many passerine species, including members of the subfamily Parulinae (Kroodsma 1982). Nothing is known about parula song development and its timing, or whether the Type A song with its distinctive endings has a genetic or cultural basis.

In the Alabama overlap region, males of the two song types were heard and recorded in adjacent areas (across the road from one another), but no intermediate song types were identified. Female song preferences are not known. If song is learned in the Northern Parula, why are there no intermediate songs in the area of sympatry (Fig. 5)? This may be due to sample size, or to early imprinting of the young before they have a chance to hear males other than their fathers. Males have been observed singing while the young were being fed. Spector et al. (1989) suggested that the Yellow Warbler (*Dendroica petechia*) may learn certain songs as nestlings.

The wintering distribution of the Northern Parula is disjunct. Limited evidence indicates that males sing on the wintering grounds, and sonagrams of Northern Parula recordings from

Puerto Rico show a plastic song with a typical eastern chevron ending, but with an unrefined trill (C. Staicer, pers. comm.). The eastern Type A singers may migrate through Florida to the Greater and Lesser Antilles, while the western-style singers migrate to east central Mexico. This could have a reinforcing or modifying effect upon song learning. Additional studies in reproductive behavior, song development, migration and genetics are needed to determine the degree of divergence between the two song populations of *Parula americana* and to learn the role, if any, that the song endings might have on the reproductive biology and evolution of the species.

ACKNOWLEDGMENTS

I am indebted to the following for their generous help during the course of the study: Michael Bay, Bill Lovejoy, Melissa Rhodes, Michael Kelly, Janet Stowell and Janet Peterson for their help in collecting data; Andrew Dewees for his statistical and computer advice; Cindy Staicer for sharing her personal observations on singing behavior and her constructive comments on the manuscript; Frank Gill, Don Kroodsma, and Bill Abbott for their comments and help on the manuscript; an anonymous reviewer; and the personnel at various sound libraries and museums for kindly loaning their specimens and song recordings. Support was provided in part by grants from San Houston State University and the National Science Foundation (ROA Grant with F. B. Gill).

LITERATURE CITED

- ADKISSON, C. S. 1981. Geographic variation in vocalizations and evolution of North American Pine Grosbeaks. *Condor* 83:277-288.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, 5th ed. Am. Ornithol. Union, Washington, D.C.
- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. Am. Ornithol. Union, Washington, D.C.
- BORROR, D. J., AND W. H. GUNN. 1985. Songs of the warblers of North America. Cornell Laboratory of Ornithology, Ithaca, New York.
- BREWSTER, W. 1896. Descriptions of a new warbler and a new Song Sparrow. *Auk* 13:44-47.
- KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals in birds. Pages 1-23 in *Acoustic communication in birds*, vol. 2. (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.
- KROODSMA, D. E. 1989. Two North American song populations of the Marsh Wren reach distributional limits in the central Great Plains. *Condor* 91:332-340.

- MAYR, E., AND L. L. SHORT. 1970. Species taxa of North American birds: A contribution to comparative systematics. Nuttall Ornithological Club, Cambridge, Massachusetts. No. 9.
- MORSE, D. H. 1989. Song patterns of warblers at dawn and dusk. *Wilson Bull.* 101:26-35.
- OBERHOLSER, H. C. 1938. The bird life of Louisiana. Louisiana State Dep. Conserv. Bull. 28.
- OBERHOLSER, H. C. 1974. The bird life of Texas, 2 vols. (E. D. Kincaid, Jr., Ed.). Univ. Texas Press, Austin.
- PARKES, K. C. 1954. Notes on some birds of the Adirondack and Catskill mountains, New York. *Ann. Carnegie Mus.* 33:149-178.
- PAYNE, R. B. 1986. Bird songs and avian systematics. *Curr. Ornithol.* 3:87-126.
- RIDGWAY, R. 1902. The birds of North and Middle America. *Bull. U.S. Natl. Mus.* 50, part 1.
- SAS INSTITUTE. 1985. User's guide: Statistics. SAS Institute, Inc., Cary, North Carolina.
- SPECTOR, D. A., L. K. MCKIM, AND D. E. KROODSMA. 1989. Yellow Warblers are able to learn songs and situations in which to use them. *Anim. Behav.* 38:723-725.
- STEIN, R. C. 1958. The behavioral, ecological and morphological characteristics of two populations of the Alder Flycatcher *Empidonax traillii* (Audubon). *N.Y. State Mus. Bull.* 371:1-63.
- STEIN, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatchers. *Proc. Am. Philos. Soc.* 107:1-50.
- APPENDIX. Recording localities for Northern Parula eastern and western Type A songs mapped in Figure 1. Localities listed by state and county or parish. Number of eastern- and western-style singers (E and W) found per locale given in parentheses.
-
- Alabama:** Baldwin (2E, 1W), Choctaw (1E, 3W), Clarke (1W), Covington (4E), Dale (1E), Dallas (8E, 2W), DeKalb (1W), Houston (1E), Macon (3E), Monroe (2E, 3W), Washington (3W), Wilcox (7E, 4W). **Arkansas:** Madison (2W), Newton (2W), St. Francis-Cross (3W). **Florida:** Alachua (1E), Calhoun (3E), Hamilton (3E), Jackson (1E), Leon (1E), Wakulla (3E). **Georgia:** Bulloch (2E), Camden (2E), Charlton (1E), Chatham (1E), Jenkins (3E), Richmond (1E), Screven (8E). **Kentucky:** Edmonson (1W), Lyon (4W), Whitley (1E, 4W). **Louisiana:** E. Baton Rouge (1W), Ouachita (1W), St. Tammany (6W). **Maine:** Franklin (1E), Hancock (1E), Lincoln (28E), Piscataquis (1E). **Michigan:** Cheboygan (2W). **Minnesota:** Mahanomen (1W), St. Louis (1W). **Mississippi:** Clarke (3W), George (12W), Hancock (4W), Hinds (4W), Wayne (1E, 1W). **Missouri:** Butler (1W), Lincoln (2W). **New York:** Essex (3E), Tompkins (1E). **North Carolina:** Avery (2E), Buncombe (1E), Swain (1E), Wayne (4E). **Ohio:** Franklin (2E), Hocking (6E). **South Carolina:** Berkeley (1E), Charleston (11E), Clarendon (4E). **Tennessee:** Benton (2W), Blount (2E), Cheatham (4W), Dickson (1W), Sevier (2E). **Texas:** Bastrop (1W), Gonzales (2W), Hardin (6W), Houston (2W), Montgomery (2W), San Jacinto (2W), San Patriciole (1W), Trinity (4W), Uvalde (1W), Walker (2E, 45W). **Virginia:** Smyth (4E). **West Virginia:** Kanawha (2E). **Wisconsin:** Bayfield (1W). **Ontario:** Essex (1E), Kenora (1W), Nipissing (1E), Thunder Bay (1W).
-