

TWO NORTH AMERICAN SONG POPULATIONS OF THE MARSH WREN REACH DISTRIBUTIONAL LIMITS IN THE CENTRAL GREAT PLAINS¹

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Abstract. The Marsh Wren (*Cistothorus palustris*), like several other North American avian taxa, consists of eastern and western counterparts with distributional limits in the Great Plains. One style of Marsh Wren singer occurs to the east of a northwest-southeast, 100-km-wide "no-wren" corridor centered on O'Neill, Nebraska. These eastern males have relatively simple songs that usually begin with a characteristic nasal buzz followed by a song that consists largely of a series of brief tonal notes. The diversity of sounds is low, both in the number of different songs in a repertoire and in the contrast between different songs within that repertoire. Males to the west of the corridor have much larger repertoires of song types that contain both tonal sounds and harsh, broad-band sounds; the overall variety of sounds is exceptionally high. Some behavioral differences, such as song repertoire size, are genetically based, but others, such as the song structure and tonal quality, are culturally based. Two males singing the eastern style, with no evidence of hybrid singing behaviors, were found among the easternmost western populations, suggesting that little if any interbreeding occurs in the central Great Plains of the United States.

Key words: Marsh Wren; song; populations; species; Great Plains; distribution.

INTRODUCTION

Over 100 avian taxa reach distributional limits in the central Great Plains. Eleven pairs of these taxa involve eastern and western counterparts that were probably isolated from each other during the Pleistocene, and hybrids for nine of the 11 pairs have been found at the present zones of presumed secondary contact (Rising 1983a). Whether or not to give species status to many of these pairs remains a dilemma. The AOU (1983), for example, has recently lumped the taxon pairs in the genera *Colaptes* and *Icterus*, retained as separate species each pair in the genera *Pheucticus* and *Passerina*, and maintained the two *Pipilo* taxa as one species.

Striking morphological or behavioral differences often facilitate study of these groups at the zones of secondary contact. Hybrid flickers, orioles, towhees, buntings, and grosbeaks are readily detected by plumage, and the degree of interbreeding at the contact zone can be determined relatively easily (Short 1965, Rising 1983b, Sibley and West 1959, Emlen et al. 1975, Kroodsma 1974, respectively). With other species, however, such as the sibling *Sturnella* meadowlarks and *Contopus* pewees, morphological differences are minor, and differences in behavior have been

important in identifying the respective taxa in the field (Lanyon 1957, Rising and Schueler 1980). Among some groups, genetic evolution sufficient to warrant species status may not be obvious from external morphology, though behavioral differences may be striking and may play a key role in maintaining reproductive isolation.

The Marsh Wren (*Cistothorus palustris*), presently listed as a single species by the AOU (1983), is another taxon with eastern and western counterparts that meet in the Great Plains. Morphological differences among Marsh Wren populations are slight (Oberholser 1897), though sufficient for delineating a number of subspecies in both the eastern and western halves of the continent (AOU 1957). The most easily recognized difference between the two Marsh Wren groups is the singing behavior of the male. Here I document a number of behavioral differences in singing, some of which are genetically based but others of which are acquired and maintained through imitation. These two "song populations" in the central United States are largely disjunct, with about a 100-km gap between the two forms, but some overlap occurs with no observed behavioral hybridization.

METHODS

During 5-13 June 1986 I tape-recorded Marsh Wrens at 11 localities in Nebraska, South Da-

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kota, and Iowa (Fig. 1). In addition, I used recordings of Marsh Wrens from eight other locations in western and eastern North America (locations listed in Fig. 4).

The recording system varied by location. At the 11 localities in the Great Plains I recorded birds with a Nagra IS-DT (19 cm/sec) and Sennheiser 816 ultradirectional microphone. For some birds I used Scotch 209 (22.5 min at 19 cm/sec), but for 45-min recording times I used Scotch 179 or 214. Birds at other locations were recorded with the Nagra or with Uher reel-to-reel recorders, and with either a Sennheiser shotgun microphone or a parabolic microphone. The minor differences in specifications of the recording systems do not affect the gross measures of behaviors used in this study.

The duration of the tape recordings from different birds varied. For some birds, I wanted to determine their approximate repertoire of different song types, and I therefore attempted to record at least 200 songs. For other birds, however, I wanted only to assess several important song characteristics, and from them I recorded only 30–50 songs (the number of males used for these two purposes are provided in Figs. 4 and 5).

In the laboratory, I analyzed songs of the wrens from all locations with a Kay Elemetrics 8160 Digital Spectrum Analyzer. The output on a Tektronix oscilloscope (model 5110) was filmed with a Grass camera (model C4R). The film clippings for each bird were then measured, sorted, and categorized by song type as described in Kroodsmma and Canady (1985).

To index the degree of contrast within and among songs, I measured the period (i.e., seconds/syllable) of the repeated syllables in the trills from each different song type that I recorded from each bird (see Verner [1975], Kroodsmma and Canady [1985], and Kroodsmma and Verner [1987] for methods of identifying song types). For the sample of syllable periods from each bird, I then determined the syllable period of briefest and greatest duration, the difference between those two measures, and the coefficient of variation of the syllable period for each male.

To indicate how males used their song types during a singing performance, I used a "repetition index." Marsh Wrens usually sang with "immediate variety," i.e., ABCDEFGHI . . . (typically western) or ABACDCDEFG . . . (typically eastern), with each letter representing a song type.

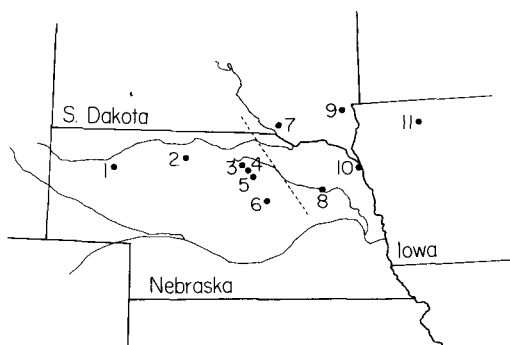


FIGURE 1. Localities in the Great Plains where Marsh Wrens were recorded. (1) Smith Lake, about 36 km south of Rushville, Sheridan County, (2) Watts Lake and Hackberry Lake, Valentine National Wildlife Refuge, about 35 km south-southwest of Valentine, Cherry County, (3) Pony Lake, 23 km directly south of Newport, Holt County, (4) Doolittle Lake, about 15 km southeast of Pony Lake, and 34 km south and 8 km east of Stuart, Holt County, (5) Swan Lake, in south-western Holt County, (6) Ericson Lake, about 1 km southeast of Ericson, Wheeler County, (7) Owens Bay, Lake Andes National Wildlife Refuge, about 8 km east of Lake Andes, Charles Mix County, (8) unnamed, privately owned marshes on old oxbow of the Elkhorn River, about 7 km west-southwest of Stanton, Stanton County, (9) two small unnamed marshes, one about 2 km northwest and the other 7 km north-northeast of Tea, Lincoln County, (10) Crystal Cove State Park, in an old oxbow of the Missouri River at South Sioux City, Dakota County, and (11) Deweys Pasture and Smiths Slough State Game Management Areas, about 18 km east-northeast of Spencer, Clay County. The dashed line through O'Neill, Nebraska, is at the approximate center of a 100-km-wide gap between the distributions of the western and eastern song populations of the Marsh Wren.

Western wrens were less likely than eastern wrens to alternate renditions of a given song type with other song types before abandoning that particular type for some time. The repetition index is thus the number of renditions of a given song type that occurred in a brief series of songs, where a "series" is a sequence of songs in which a particular song type is not separated from other renditions of that type by more than 10 songs of other song types. Each series for a particular song type was considered to be one independent occurrence of that type.

I also determined the predictability of song type sequences that males used. For each male with about 200 songs in a recorded sample, I selected 10 song types at random. I then selected for each of those 10 song types two renditions that were separated by at least 30 other songs,

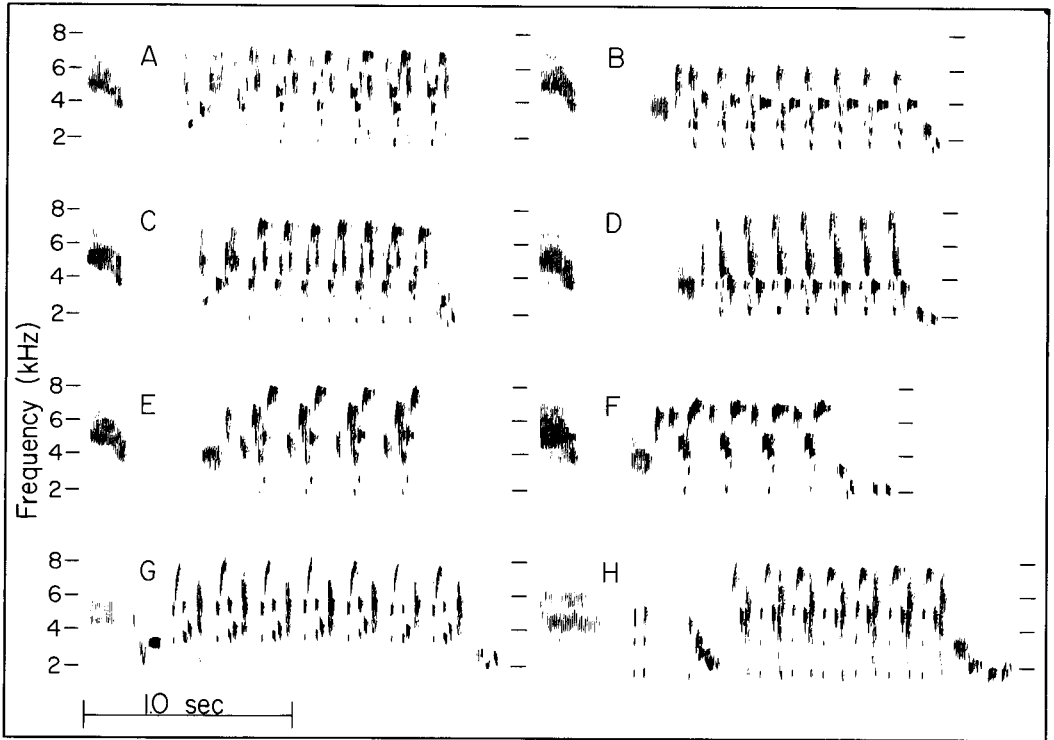


FIGURE 2. Characteristic songs of eastern wrens. Eastern songs typically began with a nasal buzz, followed by a few brief introductory notes and a trill of repeated syllables, each of which consisted largely of a series of brief tonal notes. Songs often ended with a few brief notes of relatively low frequency (B–D, F–H). Songs A–F are from a male at Stanton, Nebraska (location 8 in Fig. 1) and G and H are from the Illinois sample. (Songs were graphed with a 150 Hz filter, with tape played at half speed, on a Kay Elemetrics 7029A Sona-Graph.)

and determined whether the next song type in the series was the same or different on those two occasions. Predictability could thus range from 0.0 (no pairs of sequences identical) to 1.0 (all 10 pairs of sequences identical).

Nonrandom sequences of song types made it difficult to document the exact sizes of song repertoires among the Marsh Wrens, but my goal was to determine whether repertoire size changed abruptly at the distributional limits in Nebraska, and a rough index of repertoire size was adequate for that purpose. I therefore used as an index the number of different song types in a recorded sample of about 200 songs divided by an index of sample coverage. This sample coverage was an estimate of the degree to which a recorded sample included the entire repertoire, and increased as fewer and fewer new song types were found in additional recorded songs. Sample coverage was estimated using the formula $1 - S/N$, where S is the number of song types that occurred in only one series in the sample and N is the number

of series for all song types totaled (see Canady et al. 1984 for discussion of this index).

RESULTS

In this study, each Marsh Wren could be readily identified as either an eastern- or western-style singer. Even two eastern-style singers on the western side of the Great Plains distributional gap (one at Pony Lake and one at Doolittle Lake, locations 3 and 4 in Fig. 1) that were singing within dense populations of western wrens showed no evidence of having acquired any western behaviors. I therefore first describe several general differences in singing behavior between the two Marsh Wren groups, and then I demonstrate how those behaviors changed abruptly in Nebraska.

Many of the differences between the songs of the eastern and western Marsh Wrens were evident in the field. The birds singing with the eastern style, for example, often introduced each song with a unique nasal note (Figs. 2A–H). The 10

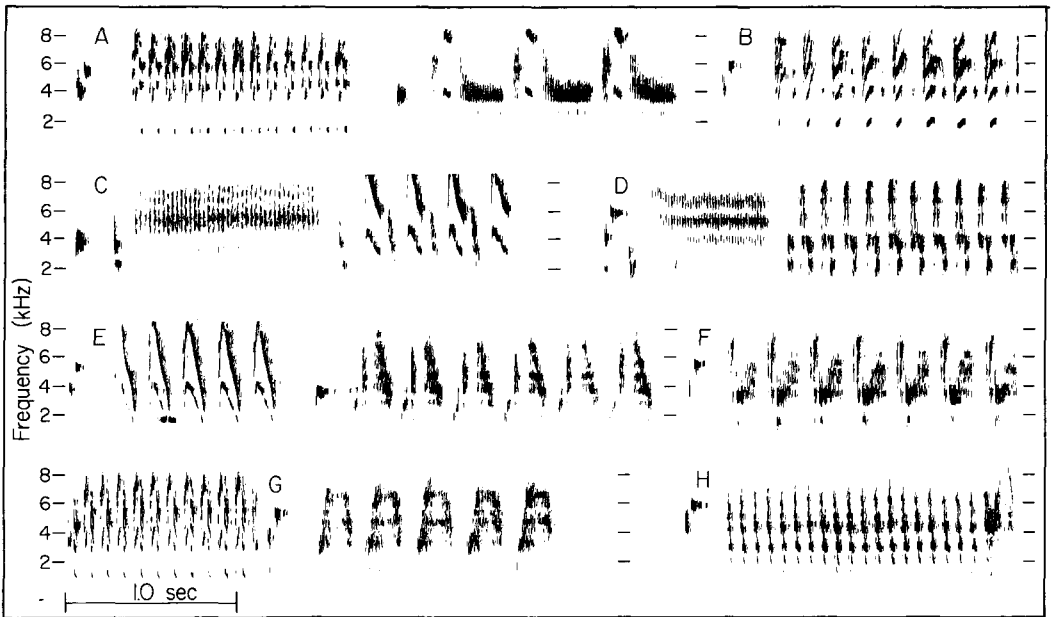


FIGURE 3. Characteristic songs of western wrens. Many songs were delivered as "multiple songs" (A, C, E, G), two or more songs delivered back-to-back in rapid succession. Western songs often contained loud tonal sounds (C, E), broad-band, harsh sounds (A, C-G), or both (C, E). Songs E and G are from a male at Ericson, and the others are from a male at Valentine refuge (locations 6 and 2 in Fig. 1, respectively).

males at Sioux Falls, South Dakota, from which I analyzed a total of 807 songs, used this nasal note before 98% of their songs (range for 10 birds = 97–100%). The frequency of use of this note varied among birds and locations, however; in my Texas sample only 33% of all songs were introduced by this note ($n = 595$ songs from four males, range = 1–68%). This same note was often repeated without the song by males that were nest building. It was used by all eastern songsters and by no western songsters.

One of the greatest differences between songs of the eastern and western birds was that of tonal quality. Songs of western birds contained tonal sounds of greater duration and intensity (e.g., Fig. 3, second half of C and first half of E) and they contained more harsh, grating, broad-band noise (Fig. 3, second half of A, E, G, first half of C, D) than did the songs of the eastern birds (Fig. 2). The contrast between tonal sounds and harsh sounds in the same songs, as in Figures 3C and E, was often striking.

Songs of eastern birds, on the other hand, contained none of these broad-band, grating sounds so typical of western birds. Instead, as could be heard by slowing the tapes to one-quarter and

especially one-eighth of normal speed, the entire song consisted largely of a series of brief tonal sounds. Each syllable, whether in the introduction, the main trill, or the conclusion to the song, consisted of these brief and consistently identifiable tonal sounds (see especially Fig. 2G).

Western males seemed to enhance the contrast within songs by uttering tonal and harsh sounds back-to-back with no "punctuating notes" between them (also see Verner 1975). At Pony Lake, Nebraska, for example, 22 of 202 songs (11%) recorded from seven western-style singers contained these "double trills," but at Tea, South Dakota, none of 807 songs from 10 eastern-style singers contained a double trill.

The incidence of multiple songs, in which two or more songs (each with customary introductory notes) were sung in rapid succession, also varied geographically. Western males most frequently sang these multiple songs (Figs. 3A, C, E, G; see also Verner 1975), but this behavior seemed to vary with the motivation of the male. Among seven western singers at Pony Lake, Nebraska, the percentage of the total songs involved in these multiple songs ranged from 0% to 57% (median = 47%). Among 10 eastern-style singers at Tea,

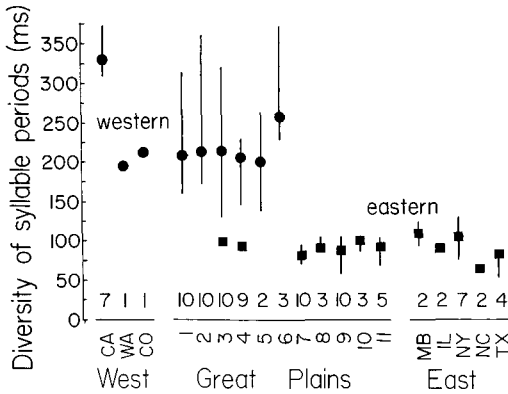


FIGURE 4. Differences in the diversity of song syllables produced by western and eastern wrens from 19 locations in North America. Locations in the Great Plains as in Figure 1. Western sites were (CA) Grizzly Island Wildlife Area, about 15 km southeast of Fairfield, Solano County, (WA) Hilltop Lake, 10 km southwest of George, Grant County, and (CO) Lower Latham Reservoir, 4 km east of LaSalle, Weld County. Eastern sites were (MB) Delta Marsh, southern end of Lake Manitoba, (IL) Goose Lake Prairie State Park, about 10 km east of Morris, Grundy County, (NY) North Bay, on the Hudson River, just south of Tivoli, Dutchess County, (NC) North River, Morehead City, Carteret County, and (TX) Anahuac National Wildlife Refuge, on the Gulf coast, Chambers County. The temporal diversity of syllable periods is the difference in milliseconds (ms) between the maximum and minimum syllable period produced in a record sample from a given bird. The number of birds (*n*) from each location is provided just above the abscissa. The median for all birds of a given singing style at each location is indicated by a solid disc (western wren) or square (eastern wren). Range is indicated by the vertical line. Diversity values for individual western males with about 200 recorded songs were all >194, well outside the range of eastern males.

South Dakota, the percentage was lower, ranging from 6% to 33% (median = 14%). The percentage of songs in multiple-song patterns declined in more eastern and southern populations, reaching a low of 0% of 595 songs in the Texas population.

Several east-west differences in temporal aspects of song delivery were due to the remarkable variety of sounds that the western birds made. The western-style singers, for example, consistently sang syllables at the extremes of syllable duration. For locations 1–6 in Nebraska with predominantly western-style singers, the median briefest syllable periods for all recorded males were 0.047 sec, 0.039 sec, 0.041 sec, 0.039 sec, 0.045 sec, and 0.037 sec, respectively (*n* in Fig. 4). For locations 7–11 with eastern singers, the median briefest syllable periods were 0.064 sec,

0.067 sec, 0.063 sec, 0.062 sec, and 0.059 sec, respectively. The briefest syllables for the eastern-style singers at Doolittle Lake and Pony Lake were 0.064 sec and 0.060 sec, respectively, indicating that this feature of their singing was typical of eastern songsters.

The western birds also sang the syllables with the greatest duration. The median greatest duration of syllable periods for western locations 1–6 was 0.26 sec, 0.25 sec, 0.25 sec, 0.25 sec, 0.25 sec, and 0.30 sec, respectively, and for eastern locations 7–11 was 0.15 sec, 0.16 sec, 0.15 sec, 0.16 sec, and 0.15 sec, respectively. The syllables of greatest duration for the two eastern-style singers at Doolittle Lake and Pony Lake were both 0.16 sec, again indicating that those two males were typical eastern-style singers.

The difference in syllable periods clearly revealed two classes of songsters, each largely confined to one side of the distributional gap in the Great Plains (Fig. 4). Birds on the eastern half of the continent, from Nebraska to Manitoba to New York to North Carolina to Texas, were remarkably similar to one another. The western males, from Nebraska to Colorado to Washington to California, were also a relatively homogeneous group. In the divergent California sample, males sang songs with both briefer (median = 0.017 sec for seven males) and greater (0.35 sec) syllable periods than in the other western samples. The extremely brief “syllable periods” for these males were to some extent an artifact of the classification scheme, because these California birds used frequency- and amplitude-modulated “buzzes” for songs, and the brief syllable periods reflected the high rates of modulation in those songs.

The differences between maximum and minimum syllable periods could merely have reflected the differences in repertoire size (see below), but the coefficient of variation (CV) demonstrated clearly that the distribution of syllable periods was flatter for western than for eastern birds. The median CV for western populations ranged from 40% to 52%, and for eastern populations, excluding New York, from 20% to 26%. The two eastern birds at Doolittle and Pony lakes, each with a CV of 22%, were again clearly eastern. The median CV for New York birds (33%) was relatively high for eastern birds, and was in part the consequence of a bimodal distribution of the syllable period (see Kroodsma and Verner 1987).

Western and eastern birds also differed in how

TABLE 1. In a brief series of songs, western Marsh Wren males are less likely to repeat a given song type than are eastern males.

	Repetition index ^a										
	1.00-1.09	1.10-1.19	1.20-1.29	1.30-1.39	1.40-1.49	1.50-1.59	1.60-1.69	1.70-1.79	1.80-1.89	1.90-1.99	>2.00
Number of males sampled											
Western	15 (5) ^b	15 (7)	13 (6)	4 (1)	0	1	0	0	1 (1) ^c	0	0
Eastern	0	3 (1)	3	6 (1) ^d	9 (8) ^e	6	4 (2)	3 (1)	4 (1)	1	8 (1) ^f

^a The difference between western and eastern songsters is significant (two-tailed Mann-Whitney *U*-test, $P < 0.05$).

^b Values in parentheses are the subset from locations 3-8 that border the distributional gap of the two Marsh Wrens.

^c The amount of song playback to this male was unusually large and probably produced this extreme value.

^d Includes the eastern male from Pony Lake.

^e Includes the eastern male from Doolittle Lake.

^f Four of six samples from North Carolina and Texas had repetition indices that were >2.0 , revealing the divergent singing behavior of these coastal wrens.

rapidly they progressed through their song repertoire during a given performance (Table 1). Western wrens typically sang one rendition of a song type and then one rendition of each of many other types before eventually returning to the first type (see also Verner 1975). The median song-type repetition index (i.e., number of renditions of a given song type occurring in a brief series of songs) for these western birds was 1.1. Thus, for only one song in 10 did these western wrens typically sing a second rendition. The median repetition index for eastern Marsh Wrens was 1.5, indicating that, on average, for five out of 10 songs a male sang two renditions. Two eastern populations, the coastal wrens from North Carolina and Texas, were especially divergent from other populations in this behavior; repetition indices for six males at these two locations averaged 2.4 (range = 1.6-4.1).

Associated with the more rapid delivery of different song types among western wrens was a more predictable transition from one song type to the next (Table 2). For western males, given one song type in a sequence, one could on average predict the next song in the sequence with a probability of 0.3 (range = 0.1-0.7 for samples from 17 males). For 30 eastern males the probability of correctly predicting the next song type in a sequence was only 0.1 (range = 0.0-0.4).

Repertoire size also changed abruptly at the

disjunction in Nebraska (Fig. 5). For the eight western Marsh Wrens from the Great Plains samples (locations 1-6), the index of repertoire size ranged from 134 to 919 (median 211 song types). Estimates of sample coverage ranged from 0.17 (for the male with an estimated 919 song types) to 0.70 (median 0.59). In contrast, for the 12 eastern Marsh Wrens from locations 7 to 11, the index of repertoire size ranged from 30 to 58 (median 48 song types). Sample coverage was much higher for eastern songsters, ranging from 0.89 to 0.99 (median 0.96). Thus, within the sample of 200 songs, most eastern males had cycled through their repertoire two or three times, and for the 12 eastern males a median of only 12.8% (range = 6.2%-28.3%) of the recorded song types had occurred only once (i.e., in one series) in the sample. In spite of singing fewer repetitions of each song type during each pass through their repertoire, the eight western males clearly had just managed to present most of their repertoire in the first 200 songs, with a median of 61.6% (range = 51.1%-91.1%) of the recorded song types occurring only once in the sample.

The differences between eastern and western males that were singing side-by-side at Doolittle Lake and Pony Lake, Nebraska, were especially evident. During a 1-hr session at Doolittle Lake, I recorded 200 songs from both the eastern songster and his immediate western neighbor.

TABLE 2. Predictability of song sequences is higher for western Marsh Wrens than for eastern Marsh Wrens.

	Predictability of song sequence ^a							
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7
Number of males sampled								
Western	0	3 (2) ^b	5	3	0	3 (1)	2 (1)	1
Eastern	11 (2)	9 (4)	6 (1)	3	1	0	0	0

^a The difference between western and eastern singers is significant (two-tailed Mann-Whitney *U*-test, $P < 0.05$).

^b Data in parentheses are the subset from locations 3-8 that border the distributional gap of the two Marsh Wrens.

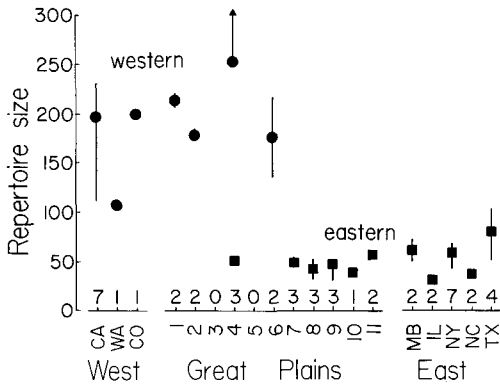


FIGURE 5. Differences in repertoire size for wrens from 17 locations in North America. The index of repertoire size is the number of different song types recorded in a sample of 200 recorded songs divided by an estimator of sample coverage, i.e., an estimate of the extent to which the entire repertoire has been sampled. Format is largely the same as in Figure 4. One repertoire estimate (919, see text) for location 4 was exceptionally high (solid triangle pointed up), and I therefore used the lower of the two values to indicate the median value for that location.

Descriptive parameters for the eastern and western songster, respectively, were as follows: number of song types, 43 vs. 139; sample coverage, 0.94 vs. 0.59; estimated repertoire size, 46 vs. 254; repetition index, 1.42 vs. 1.03; and percentage of song types occurring only once in the sample, 20.9% vs. 64.7%. Data from the eastern male and his immediate western neighbors from Pony Lake were comparable, but I recorded only 50 songs from that eastern male and therefore could not calculate the same statistics for him. The Doolittle Lake male and the Pony Lake male appeared to be pure eastern songsters in all aspects of their singing behaviors.

DISCUSSION

The behavioral differences between these two Marsh Wren song populations are both genetically and culturally based, as determined in a laboratory study of song development by hand-reared individuals from New York and California populations (Kroodsma and Canady 1985). The difference in song repertoire size appears to have a genetic component. In spite of being reared in identical acoustical environments, the eastern males from New York learned only 40% as many song types as did the western males from California. One might argue that eastern songsters in nature could overcome this relative inability to learn, because social interactions among free-liv-

ing wrens might enable the learning of larger repertoires. Social interactions can certainly facilitate song learning (Payne 1981, Petrinovich and Baptista 1987), yet in nature the social environment of males from both song populations would be enhanced in comparison to the laboratory. Another genetically based difference is reflected in the repetition index: as in nature (Table 1), the western laboratory-reared males sped through their repertoires at a faster rate than did the eastern laboratory-reared birds.

In contrast, the striking difference in song structure (as illustrated in Figs. 2, 3), which are the most noticeable differences in the field, are apparently culturally based: New York and California laboratory-reared wrens are fully capable of learning songs from the home population of the other songster (Kroodsma and Canady 1985). The diversity of sounds, as indexed in Figure 4, is therefore only a cultural difference. The six New York laboratory-reared wrens, when exposed to both California and New York songs, developed a median "diversity of syllable periods" of 0.302 (range of individual medians = 0.185–0.436), well above that for any eastern population illustrated in Figure 4. The six California laboratory-reared wrens, hearing the same songs, developed a median diversity index of 0.356 (range = 0.259–0.577; difference between the two hand-reared groups not significant with two-tailed Mann-Whitney *U*-test, *P* = 0.24).

In the central Great Plains of the United States, there appears to be minimal contact between these two Marsh Wren song populations. The distributional gap in northeastern Nebraska contains little suitable habitat, and this lack of habitat may be an effective isolating barrier between the two populations. The two eastern birds that I found on the western side of this corridor may be a result of immigration from eastern populations, or they could be part of a small eastern population breeding among predominantly western birds.

Like the Marsh Wren, three other Great Plains taxon pairs discussed by Rising (1983a) lack striking plumage differences but have noticeable vocal differences: the *Contopus* pewees, the *Parus* Black-capped/Carolina Chickadee complex, and the *Sturnella* meadowlarks. Data for the two meadowlark species are perhaps most similar to those for the Marsh Wrens. Eastern and western meadowlarks also learn each others' songs in the laboratory (Lanyon 1957, 1960), and both the tonal quality of the songs and the song repertoire

size differ markedly between the eastern and western forms (Falls and d'Agincourt 1982). Additional surveys of Marsh Wrens will be needed to determine if one can occasionally find, as among meadowlarks (Szijj 1963, Lanyon 1966, Rohwer 1972), mixed pairings, morphologically intermediate individuals, and mixed songsters.

The two discrete singing behaviors in the Great Plains and throughout the continent suggest the existence of two independent evolutionary units of the Marsh Wren. These two Marsh Wrens also differ in some fundamental aspects of their breeding biology, such as degree of polygyny and population density (reviewed in Canady et al. 1984, Kroodsma and Verner 1987). Additional data from a second zone of contact in the northern Great Plains may provide crucial information. Harper (1926), apparently unaware of differences in singing behaviors, believed that two described subspecies met and intergraded in southcentral Saskatchewan, with the approximate boundary between the plains of the west and the prairies on the east. Careful study of both culturally and genetically based differences in behavior, as well as study of morphology (Oberholser 1897, James and Rising 1985, Robbins et al. 1986) and population genetics (Braun and Robbins 1986, Mack et al. 1986, Grudzien et al. 1987), will be required in this potential overlap zone to assess the extent of hybridization, if any, and its consequences for these two Marsh Wren song populations.

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