

# USE OF SONG REPERTOIRES AMONG MARSH WREN POPULATIONS

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**ABSTRACT.**—To survey singing behaviors among populations of Marsh Wrens (*Cistothorus palustris*), we tape-recorded and analyzed songs of 18 individuals from 5 states. Median repertoires of song types were 33 for Illinois ( $n = 2$  birds), 40 for North Carolina (2), 53 for New York (7), 141 for central Washington (1), and 162 for California (6) birds. North Carolina males ranked the lowest or second lowest in most measures of singing complexity, including recurrence numbers, rates, three measures of singing versatility, repertoire size, and percentage performance time. Western birds, in contrast, sang with the greatest complexity in these measures. Among the 5 populations, repertoire size correlated positively with the percentage performance time, the predictability of the next song type in a sequence, and the variability (as measured by coefficient of variation) of the syllable period in the trill of repeated song units. By comparing syllable periods within songs, we found that successive songs in frequently used transitions were more different from one another than expected by chance. Received 7 February 1986, accepted 20 July 1986.

THE evolution of song repertoires persists as one of the most fascinating puzzles of vocal communication among birds. Many descriptive studies have added significantly to our understanding of these repertoires. Documenting the existence and use of repertoires among interacting birds has been an important preliminary approach (e.g. Lemon 1965, 1968; Wildenthal 1965; Lein 1978; Payne 1979; Slater 1981). Comparative surveys that relate social systems or ecology to the use of repertoires have yielded intriguing correlations among North American wrens, European *Acrocephalus* warblers, and European *Emberiza* sparrows (Kroodsma 1977, Catchpole 1980, Catchpole and McGregor 1985).

Complementing these observational approaches is an increasingly elegant series of experimental studies. Removal of males and their replacement with speakers that broadcast repertoires of different sizes has revealed that repertoires may function as effective "keep-out" signals for territorial males (Krebs et al. 1978, Yasukawa 1981). Song playbacks to territorial or captive birds have revealed some of the complex rules that appear to be used during countersinging (e.g. Verner 1975, Todt 1981, Falls and D'Agincourt 1982, Falls et al. 1982, Wolffgramm and Todt 1982, Kramer et al. 1985, Whitney 1985). In addition, use of female displays as a bioassay for the potency of male song has provided a new technique with potential

for determining the intersexual functions of these male song repertoires (Searcy and Marler 1981, 1984; King and West 1983; Catchpole et al. 1984).

In our study we chose an approach that we believe has much promise but that has been largely neglected: a comparative, descriptive survey among populations of the same species (see Hunter and Krebs 1979, Kroodsma 1982 for sample surveys, Clutton-Brock and Harvey 1984 for rationale). We used the Marsh Wren (*Cistothorus palustris*) because previous studies had shown that repertoire size, singing behaviors, and mating systems varied among populations (Welter 1935; Kale 1965; Verner 1965, 1975; Kroodsma and Canady 1985). A thorough understanding of how songs were used in each population then became the first step in attempting to establish a correlation between vocal behaviors and the social systems among the different populations of this species.

## METHODS

We recorded and analyzed songs of Marsh Wrens at five locations: North Bay, Tivoli on the Hudson River, New York ( $n = 7$  males; hereafter designated NY-1, NY-2, etc.); Grizzly Island Wildlife Area, Fairfield, California ( $n = 6$ ; CA-1 to CA-6); Goose Lake Prairie State Park, Grundy Co., Illinois ( $n = 2$ ; IL-1, IL-2); North River, Morehead City, North Carolina ( $n = 2$ ; NC-1, NC-2); and Hilltop Lake, Grant Co.,

TABLE 1. Song and "trill" duration for Marsh Wrens at the five locations. The sample size for each location was 30 songs, divided equally among the males recorded at that location. Durations are given in seconds, with the standard errors in parentheses.

Location <sup>a</sup>	Song	Trill
Illinois (IL)	1.41 (0.02)	0.76 (0.02)
North Carolina (NC)	1.79 (0.04)	0.70 (0.02)
New York (NY)	1.56 (0.04)	0.78 (0.02)
Washington (WA)	1.29 (0.03)	0.87 (0.03)
California (CA)	1.60 (0.08)	1.00 (0.06)

<sup>a</sup> Exact location in each state given in Methods.

Washington ( $n = 1$ ; WA-1). Our samples for three of the populations were from one or two males, yet from other work (e.g. Verner 1975, Kroodsma and Canady 1985, Kroodsma unpubl. data) we believe that the data presented here are representative of each location.

For each male except NC-1, we obtained a long, continuous recording of songs during the first hour(s) of morning activity when males were in full song during the breeding season. NC-1 was recorded during the evening hours (just before sunset), and was the only bird with which playback of Marsh Wren song was used to initiate and maintain singing. We are confident that each of our recordings contained songs from only one male: our recording sessions were brief (1–2 h), territories were stable, and careful inspection of each recorded sample revealed that a single songster was involved.

We used either a Uher 4000, Uher 4200, Uher 4400, or a Nagra IS-DT tape recorder at 7½ ips (19 cm/s). A 60-cm parabolic reflector was used with the NC and WA males, and a Sennheiser 816 "shotgun" microphone was used with all other males.

We graphed all songs with a PAR model 4512 FFT spectrum analyzer and a Grass oscilloscope camera loaded with Kodak 1930 35-mm photographic paper. For all but three males (CA-1, CA-2, and CA-6), we measured song duration and intersong intervals to the nearest millimeter ( $\frac{1}{40}$  s) on the Kodak photographic paper.

In this study, any series of repeated syllables separated from other such series by characteristic "punctuation" (notes of an introduction or conclusion—see Verner 1975: figs. 2–5, 7–9; Kroodsma 1978: fig. 1) was used to identify a "song." Eastern males typically sang single songs, each song isolated from another by one to several seconds; western birds, however, often sang two or more different songs in rapid succession. A few western songs also consisted of two consecutive series of different syllables with no punctuation between them; by our definition, these were considered single songs. Identifying songs by the repeated trills separated by the characteristic "punctuation" was consistent with the approach used by Verner

(1975), Canady et al. (1984), and Kroodsma and Canady (1985).

## RESULTS

### SONG DESCRIPTION

At all locations the song of the Marsh Wren consisted of several introductory notes, a trill of repeated syllables, and usually one to several concluding notes (see figures in Verner 1975, Kroodsma 1978). The overall duration of these components varied among locations (Table 1). The trills from North Carolina were the briefest, yet the songs from this location had the greatest duration; the long introductory portion made these North Carolina songs sound unique. We could not distinguish by ear the songs of New York and Illinois birds. They were similar in overall duration and proportion of trill syllables. Songs of the males from the two western populations usually could be identified by the relatively brief introductory and concluding notes, but the greater range of syllable periods (see Singing Behavior) was most distinctive.

Males among locations also differed in the tendency to sing "double" songs. Of 300 songs sampled from Washington (1 male) and 300 from California (3 males), for example, 20.0 and 26.7% of all songs, respectively, were sung as part of double songs, in which a pause of less than 0.1 s separated the two songs. Only 7.4% of Illinois songs (1,191 songs sampled from 2 birds), 1.3% of New York songs (300 songs, 3 birds), and 0% of North Carolina songs (300 songs, 2 birds) were sung as part of double songs.

The variable rate of singing among males at the same location masked any consistent among-location effects of singing rates (Table 2). The number of songs per minute ranged from 10.7 to 15.3 in New York males, for example, and from 12.4 to 20.4 in California males. The median "percentage performance times," the percentages of time the birds actually were singing (sum of all song durations  $\times$  100/total duration of singing session), were 29.2, 31.8, 33.0, 34.3, and 34.6, respectively, for Illinois, North Carolina, New York, Washington, and California birds. Although these differences in the percentages were not striking, these five locations ranked in the same order when arranged from the smallest to the largest song repertoires (see next section).

TABLE 2. Sample sizes and indexes of singing behavior for 18 individual Marsh Wrens by location. "Songs sampled" is the total number of recorded songs in the sample, with the number of independent occurrences ( $N$ ) of song types in parentheses. If successive renditions of the same song type were separated by 10 or more songs of other song types (recurrence number  $\geq 10$ ), we considered those renditions to have occurred independently of one another [see Canady et al. (1984) and Kroodsmas and Canady (1985) for rationale]. "Song types" is the number of song types in the recorded sample ( $n$ ), with the number of song types occurring only once ( $S$ ) given in parentheses. For each song type that occurred 5 or more times in our sample from a given bird, we determined which other song types most frequently followed. We then calculated the transition probability for that sequence (e.g. if song type A occurred 20 times in a sample, and type B followed type A on 15 of those occasions, the transition probability would be  $15/20 = 0.75$ ). Values reported here are the median of all "qualifying" (i.e. occurred  $\geq 5$  times) types for each bird (sample sizes are given in parentheses). We did not determine song rates per minute or percentage performance time for the 3 California birds with the poorest quality recordings.

Male	Songs sampled	Song types	Estimated repertoire size [ $n/(1 - S/N)$ ]	Transition probability	Songs/min	Percentage performance time <sup>a</sup>
IL-1	482 (287)	36 (0)	36.0	0.25 (33)	13.3	30.3
IL-2	709 (592)	30 (0)	30.0	0.17 (29)	14.1	28.2
NC-1	278 (116)	36 (3)	37.0	0.20 (26)	10.7	31.5
NC-2	358 (222)	41 (10)	42.9	0.20 (27)	11.5	32.1
NY-1	300 (239)	42 (1)	42.2	0.27 (27)	12.2	33.0
NY-2	298 (153)	42 (6)	43.7	0.25 (30)	15.3	35.5
NY-3	294 (237)	45 (3)	45.6	0.22 (31)	14.0	34.2
NY-4	300 (122)	50 (6)	52.6	0.37 (27)	10.7	36.4
NY-5	292 (184)	59 (4)	60.3	0.40 (35)	13.0	32.0
NY-6	300 (207)	59 (4)	60.2	0.27 (31)	12.1	29.2
NY-7	300 (207)	58 (10)	60.9	0.23 (29)	11.4	27.9
WA-1	363 (311)	121 (44)	140.9	0.42 (25)	17.1	34.3
CA-1	593 (478)	192 (58)	219.0	0.40 (39)	—	—
CA-2	661 (479)	156 (34)	167.9	0.37 (57)	—	—
CA-3	646 (536)	150 (17)	154.9	0.40 (60)	12.4	32.5
CA-4	602 (549)	119 (13)	121.9	0.60 (65)	13.8	34.6
CA-5	844 (820)	181 (21)	185.8	0.67 (81)	20.4	47.4
CA-6	594 (485)	144 (26)	152.2	0.60 (55)	—	—

<sup>a</sup> (Total duration of songs in sample)  $\times$  100/(total duration of recorded sample).

#### SONG REPERTOIRE SIZE

The disparity in song repertoire sizes between western (California, Washington) and eastern (New York, North Carolina, Illinois) populations was clearly shown by cumulative curves of the number of new song types in a sample (Fig. 1): western males sang at least twice as many song types as their eastern counterparts. Among the eastern populations, males from New York had repertoires that appeared to be about 50% larger than those of males from either North Carolina or Illinois.

To obtain estimates of song repertoires that attempted to compensate for unequal samples, we used an index of sample coverage, which is an estimate of the probability that the next sampled song will be of a type already encountered (Good 1953, Fagan and Goldman 1977). This method uses the number of song types that occur only once in the sample to estimate

the number of songs that the male was capable of singing but that did not actually occur in the sample (see Table 2 for the formula, and Canady et al. 1984 and Kroodsmas and Canady 1985 for additional details).

The estimated repertoires for most males were only slightly larger than the sample repertoires and did not alter the impressions gained from Fig. 1. In the Illinois birds, for example, all song types occurred two or more times in our large samples, and the estimate of sample coverage was therefore 100%; the estimated repertoire size was thus identical to the recorded sample size. The sample coverage for New York birds (median of 97.8%) and North Carolina birds (96.4%) was also high, resulting in only small adjustments to the sample repertoire. Sample coverage for California males ranged from 87.9% (CA-1) to 97.6% (CA-4), with a median of 95.7%. The sample coverage for the Washing-

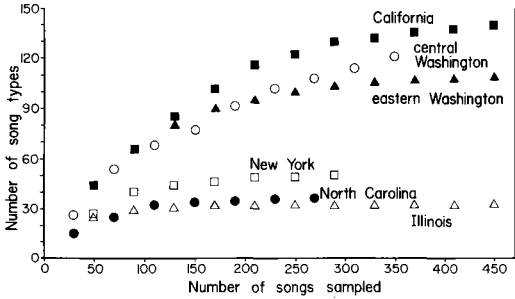


Fig. 1. Population differences in song repertoire size illustrated as a plot of the cumulative number of song types that occur in a sample. The abscissa is the total number of songs in the sample, the ordinate the number of types encountered. Median song repertoires are plotted for California ( $n = 6$ ), New York ( $n = 7$ ), North Carolina ( $n = 2$ ), and Illinois ( $n = 2$ ) males. The data for central Washington are from a single male. For comparison we include the data from eastern Washington (means for 5 birds from Verner 1975: fig. 6). Data points are staggered on the abscissa so that the graphs may be read more easily; data for eastern Washington are indistinguishable from the California data below 100 songs sampled.

ton male was the lowest (85.9%), leading to a 16.4% adjustment to the sample repertoire size. Overall, the repertoires of the California and Washington males were about 3 times larger than those of the New York males, which in turn were about 30% larger than the North Carolina and 60% larger than the Illinois repertoires.

#### SINGING BEHAVIOR

We found several interrelated approaches useful to describe how these Marsh Wrens used their songs. These approaches included an examination of how a given song type reoccurs in the sample (recurrence numbers), the predictability of the next different song type in the sample (transition probabilities), an examination of the degree of contrast in successive songs, and an overall examination of the "versatility" of the singing performance.

*Recurrence numbers.*—The recurrence number (RN), the number of other songs that occur between successive renditions of the same song type, was a good index of how males used particular song types (Table 3). Males with the largest song repertoires, those from the two western populations, tended to sing with the least repetition of their song types. The per-

TABLE 3. Recurrence numbers (RN) for song types among Marsh Wren males at the five locations. Values are the probabilities that the second song in a sequence will be of the same type as the first (RN = 0), that the third (but not the second) will be the same as the first (RN = 1), and so on. All values are medians of probabilities for the males at each location. Sample sizes for the number of males and number of songs/male are given in Table 2.

Loca- tion	Recurrence number				
	0	1	2	3	≤3
IL	0.026	0.136	0.070	0.034	0.266
NC	0.334	0.110	0.023	0.011	0.478
NY	0.031	0.181	0.053	0.032	0.297
WA	0.011	0.069	0.047	0.008	0.135
CA	0.050	0.074	0.044	0.014	0.182

centages of all recurrence numbers that were ≤3 from each location were 13.5 and 18.2 in the Washington and California populations, but 26.6, 29.7, and 47.8 in the Illinois, New York, and North Carolina populations.

North Carolina males sang their relatively small song repertoires with a different style. They frequently sang with "eventual variety," repeating one song type several times in succession (RN = 0) before introducing another song type. Brief samples from other males in this population indicated that they, too, were singing with this same style. Overall, the second song type in a sequence was the same as the first 33.4% of the time, and the first song type occurred at either the second or the third position in the song sequence 44.4% of the time.

Males at the other four locations sang with greater "variety," with probabilities of only 1 in 100 (Washington) to 1 in 20 (California) that successive songs would be the same. If a given song type were to recur in a brief sequence of songs, there was for these four locations a higher probability that the recurrence would be at the third (RN = 1), or even the fourth (RN = 2), than at the second (RN = 0) song in the sequence.

*Transition probabilities.*—Recurrence numbers provided an index of whether successive songs in a sequence were the same or different, but transition probabilities provided an index of the predictability of which particular new song type would be next in the sequence. The median transition probabilities for each location indicated that western birds, with their larger song repertoires, sang with the greatest pre-

dictability (0.42 for both Washington and California birds). Thus, given any song from one of the western birds, one could predict the next song type 42% of the time. Illinois and North Carolina birds, with the smallest repertoires, sang with the least predictability (0.22 and 0.20, respectively). The New York birds were intermediate in both song repertoire size and predictability (0.27) of the next song type.

*Contrast in successive songs.*—Each Marsh Wren that we studied had a large repertoire of song types, all of which were distinctly different from one another. Syllables of one song type differed from those of other types in the distribution of sound energy over time and frequency, and we were continually impressed with both the variety of syllables and the ability of the Marsh Wrens to recall and sing the precise details of each particular song type. It appeared as if the Marsh Wren, perhaps like other birds with large repertoires, had evolved not just a large repertoire, but a large repertoire of distinctly different, highly contrasting discrete song types. Effective use of these different song types during a singing performance could exploit the diversity of syllables by using especially different song types in succession, or perhaps by pausing longer between successive renditions of the same or similar song types. We used the syllable period, i.e. the duration from the beginning of one to the beginning of the next syllable in the repeated trill of each song type, to characterize each song, and we then inspected the sequential and temporal organization of singing behaviors to see if males exploited the potential contrast available in this feature.

The clear relationship between the distribution of syllable periods (Table 4) and the median song repertoire size (calculated from data in Table 2) at the five locations suggested that this measure of contrast was of significance to the birds. The Marsh Wrens appeared to develop larger song-type repertoires to a large extent by using a far greater diversity of syllable periods. This diversity was indicated by the range and especially by the coefficient of variation of the syllable periods. North Carolina and Illinois birds with small repertoires had small coefficients of variation (21–22%), while the California birds with the largest repertoires had by far the greatest variability in syllable periods (54%). There was a highly significant, positive correlation between the median rep-

TABLE 4. Syllable periods in Marsh Wren songs.

Means are the duration (in seconds) from the beginning of one to the beginning of the next repeated syllable in the trill. Mean and coefficient of variation (CV) values are the average of two birds from each location (except Washington, where we recorded only one bird). The NY and CA males were chosen at random from the available males.

Location	Syllable period		
	Mean	Range	CV <sup>a</sup>
IL	0.096	0.058–0.159	21.2
NC	0.087	0.053–0.119	21.8
NY	0.092	0.043–0.188	32.8
WA	0.096	0.027–0.223	44.8
CA	0.131	0.018–0.363	54.3

<sup>a</sup> Males from each location tended to share song types, and hence there was little variability among males in the distribution (and CV) of syllable periods. The two NC, NY, and CA males differed from the average CV by less than 1%, and the two IL birds differed by only 1.8%.

ertoire size and the coefficient of variation of syllable periods among the five locations ( $n = 5$ ,  $r = 0.97$ ,  $P < 0.01$ ).

One way in which male Marsh Wrens could have used the syllable diversity in their performances was to sing successive songs that were especially different from one another. To test this possibility, we examined the use of each song type by each bird. If a particular song type occurred 5 or more times in the sample and if the transition probability to the next song type was  $\geq 0.25$ , we called that sequence a "favored transition." We then compared the difference in syllable periods between song types involved in these favored transitions with the differences in syllable periods of an equal sample size of song-type pairs chosen at random from the same male's repertoire.

These frequently used, i.e. favored, pairs of song types were more different from one another than expected by chance alone. Of 16 birds with a difference between the median of the observed and random distributions, 12 birds sang favored pairs of song types that were more different than expected. In 4 of these birds the difference was statistically significant (one-tailed Mann-Whitney  $U$ -test; NY-1,  $P = 0.001$ ,  $n_1 = n_2 = 20$ ; NY-3,  $P = 0.041$ ,  $n = 15$ ; NY-5,  $P = 0.017$ ,  $n = 39$ ; IL-1,  $P = 0.042$ ,  $n = 19$ ). In only 4 birds (1 from California, 2 from New York, and 1 from Illinois), randomly chosen song pairs were more different, but not significantly so, than favored song pairs. Overall,

these trends supported the idea that song types used in favored transitions were more different from one another than would be expected by a random pairing of song types (one-tailed Wilcoxon matched-pairs signed-ranks test,  $P < 0.005$ ).

One feature of the distribution of syllable periods for the New York birds seemed especially suited for choosing highly contrasting pairs of songs: the distribution for all seven birds was clearly bimodal. We had no evidence that the song types of these two parts of the distribution served different functions, but song types were more likely to be paired in favored transitions with types in the other peak of this bimodal distribution than with different song types in the same peak of the distribution ( $\chi^2 = 8.99$ ,  $P < 0.005$ ).

Still another way in which Marsh Wrens could effectively use contrast in successive songs was by adjusting the temporal rather than the sequential organization of a singing performance. Especially different songs delivered in quick succession would offer more of a contrast than would either the same song type or two similar song types delivered as quickly. We therefore searched for a negative correlation between the degree of contrast between two successive songs and the intersong interval between them.

We first compared the intersong intervals between the same and different song types. All 13 male Marsh Wrens that sang successive renditions of at least 5 song types had longer intersong intervals between successive renditions of the same song type than they did between successive songs of different song types (see Verner 1975 for similar data on eastern Washington birds). Furthermore, a clear relationship existed between the overall singing style of the population and the relative timing between like and unlike songs. For North Carolina males, song patterning often involved immediate repetition of song types (Table 3), and the interval between identical songs was only 4% greater than the interval between different songs ( $n = 50$  song types for the 2 males combined; median durations between like and unlike songs were determined for each bird separately, and the median of those medians was then compared here). In New York and Illinois, males were more likely to sing with immediate variety, but renditions of the same song type were likely to occur at every second

or third song during a burst of singing. At each location the intervals between successive renditions of the same song type were 48% longer than intervals between different songs (7 New York birds, 65 song types; 2 Illinois birds, 18 song types). Finally, in California, where the repertoires were the largest and where the overall tendency to repeat song types was the lowest, time between successive renditions of the same song type was much higher than it was for unlike songs (101%; 3 birds, 20 song types).

In a second approach to examining song contrast and temporal organization, we searched for a more general relationship between relative similarity of successive songs and the time between them. We omitted all transitions with recurrence numbers of 0 (successive renditions of the same song type), and then for each male's song type that occurred 10 or more times in our samples we calculated the correlation coefficient for the intersong interval and the difference in syllable periods between the successive songs. Of 161 correlations, 82 were negative and 79 were positive; there clearly was no difference. The Marsh Wrens apparently were not making fine adjustments in temporal patterning, for our measure of contrast in more rapidly delivered pairs of song types was no greater than the contrast in those song-type pairs delivered at a more leisurely pace.

*Singing versatility.*—Three final measures provided a good index of how a male presented his diversity of song types during a relatively brief sequence of songs. Song-type versatility is the number of different song types that occur in a sequence of 10 songs, and transition versatility is the number of transitions between unlike songs in that same sequence (the eleventh song is included to obtain the tenth transition). The product of these two measures was designated total versatility (see Kroodsma and Verner 1978).

Among our Marsh Wrens, the males from North Carolina sang with the least versatility (Table 5). Neither of the 2 birds in 29 samples used 10 different consecutive song types, and immediate repetitions of a song type (recurrence number of 0) were used in 25 of the 29 samples (86.2%). Both transition and song-type versatility contributed to the very low total versatility.

As was also evident from the recurrence numbers, males from the other four locations

were more like each other in their singing versatility than they were like the North Carolina males. Males from these four locations rarely repeated a given song type (median transition versatility was at the maximum of 10 for all four populations). In song-type versatility, however, the two western populations ranked higher, giving them the highest total versatility (Table 5).

#### DISCUSSION

*Repertoire size.*—The observed variation in repertoire size, correlated with differences in repertoire organization (see next section), suggests two major styles of singing behavior in Marsh Wren populations separated by the Great Plains. Repertoire size does not decline gradually from west to east: Illinois repertoires are small, and a preliminary analysis gives an estimate of 140 song types in the repertoire of a male recorded by M. C. Baker near Fort Collins, Colorado (Kroodsma unpubl. data). Additional samples from both sides of this gap, together with samples from south-central Saskatchewan, where eastern and western subspecies meet (Bent 1948, A.O.U. 1957), may reveal a distribution of behaviors comparable to the distribution of morphological characters in other groups with semispecies isolated by the Great Plains (see Rising 1983).

We found no consistent latitudinal variation in repertoire size. The central Washington bird and those described earlier by Verner (1975) had smaller repertoires than did the California birds, but repertoires of the New York males were larger than those of the North Carolina males. Similarly, we did not find a consistent difference between migrant and resident populations: males from a migrant population in eastern Washington (Verner 1975) had smaller repertoires than the resident males we sampled from central Washington and from California, but migrant birds from New York had larger repertoires than the more resident birds in North Carolina.

*Repertoire organization.*—The western birds had the largest repertoires, the fastest singing rates, the highest percentage performance times, the lowest recurrence numbers, and the highest measures of song-type and transition versatility. A style of singing that indicates high motivational states in many other species—rapid switching among song types (references

TABLE 5. Median versatility of singing behaviors among Marsh Wrens. We used 15 samples of 10-song sequences from each bird at each location, except for NC, where only 14 samples were available for 1 bird (thus,  $2 \times 15 = 30$ ,  $15 + 14 = 29$ , etc.). The measures of versatility are the median number of different song types/10 songs, the number of transitions in an 11-song sequence in which successive songs were of a different type, and the product of song-type and transition versatility, respectively. Maximum possible versatility for song-type, transition, and total versatility is 10, 10, and 100, respectively. In parentheses is the percentage of the sample that was at maximum versatility. For example, of the 30 IL samples, 23.3%, or 7, consisted of 10-song sequences in which 10 different song types occurred.

Loca- tion	n	Versatility		
		Song-type	Transition	Total
IL	30	8 (23.3)	10 (86.7)	80 (9.5)
NC	29	6 (0.0)	7 (13.8)	42 (0.0)
NY	105	7 (9.5)	10 (71.4)	70 (23.3)
WA	15	9 (40.0)	10 (93.3)	90 (40.0)
CA	90	9 (38.9)	10 (86.7)	90 (40.0)

below)—appears to have been stylized in these western Marsh Wrens. Higher densities and levels of polygyny may have played a key role in the evolution of these more complex behaviors (Verner 1975, Kroodsma 1977). Additional sampling of other populations throughout the continent might settle this question.

The singing behavior of North Carolina males was the most distinctive among the populations we sampled. The North Carolina birds ranked last in most measures of singing complexity—lowest recurrence numbers, slowest singing rates, and lowest in all three measures of singing versatility. Only in the North Carolina sample was the pause between successive renditions of the same song type not significantly longer than the pause between unlike songs. These birds ranked next to last in song repertoire size and percentage performance time. But the North Carolina males had the greatest variability within songs. Their songs were longest, and the trill portion was the shortest and constituted the lowest percentage of the total song. The long and relatively complex introductory patterns of their different song types provided considerable contrast within each song. [Verner (1975) also found measurable contrast within songs of Marsh Wrens in eastern Washington.]

Further support for an inverse relationship between song complexity and sequencing variety is seen among other North American wren species. The Winter Wren (*Troglodytes troglodytes*), for example, sings with the highest percentage performance time (about 50%) and repeats a song type several times in succession, but this wren also has by far the most complex songs among the wrens (Kroodsma 1977, 1980).

The positive correlation between repertoire size and the predictability of successive song types in a sequence might be explained in one of at least three ways. (1) Countersinging with neighboring males can influence the predictability of a sequence (e.g. see Thimm 1980, Wolffgramm 1980, Todt 1981, Wolffgramm and Todt 1982, Slater 1983, Whitney 1985). Although countersinging decreases predictability in most species, neighboring male western Marsh Wrens, as demonstrated by Verner (1975) in eastern Washington, tend to countersing together through matching sequences of song types. Eastern males, perhaps because of their larger territories, do not engage in such countersinging duels as frequently or intensely. Ritualized countersinging among western birds may train them to more stereotyped sequences. (2) The increased predictability in song sequences of western birds could be a consequence of their higher singing rates. In the Mistle Thrush (*Turdus viscivorus*; Isaac and Marler 1963) and the Red-eyed Vireo (*Vireo olivaceus*; Lemon 1971), for example, shorter pauses between songs or song elements increase the predictability of the next unit. (3) Selection may favor less predictable sequences among eastern birds. Reducing the predictability of the next song type in the sequence in a smaller repertoire may be one way to increase the variety of the display.

A singing performance may be most effective if it consists of sequences of carefully chosen, highly contrasting song types (see Verner 1975, Krebs 1976, Whitney 1981, Yasukawa 1981, and Kroodsma 1982 for discussion). Such a display, especially by a bird that sings different song types in succession, would be more stimulating and less likely to induce habituation in listeners (or even in the singer). The increased contrast we found between successive songs in sequences by Marsh Wrens supports this "contrast hypothesis" for the organization of their repertoires. These larger repertoires are generated partly by increasing the range of syllable

periods, and the significant, positive correlation ( $r = 0.97$ ) between repertoire size and the coefficient of variation of the syllable period suggests that syllable periods are crucial for maintaining the recognizability of discrete, highly contrasting song types used in these sequences.

It is intriguing that support for the contrast hypothesis is strongest among birds from New York and Illinois, where repertoires are relatively small. Perhaps with smaller repertoires extra contrast in frequently used song transitions has a greater impact on a listener. Among males in eastern Washington, where repertoires ranged from 105 to 114 song types, Verner (1975) found that only the presence or absence of "musical notes" or "terminal buzzes," not syllable periods or any of 12 other variables, were more different in successive songs than expected by chance. By focusing on favored pairs of song types in frequently used transitions, we have used a slightly different approach here. But perhaps such fine adjustments in the song delivery by western males would be superfluous, because those birds with their great diversity of song types and high singing rates already have a highly stimulating song performance.

There is additional and more general support for the contrast hypothesis. In the Varied Thrush (*Ixoreus naevius*; Whitney 1981), the most dissimilar songs in an individual's repertoire are sung in succession more often than predicted by chance. Also, in the Rock Wren (*Salpinctes obsoletus*; Kroodsma 1975), the frequency range of syllables and, to a lesser extent, the number of syllables per second are more different in favored sequences of song types than expected by chance.

Like Marsh Wrens, Varied Thrushes and Rock Wrens typically sing with immediate variety (successive song types different), but support for the contrast hypothesis is also found among species that usually sing with eventual variety (successive song types the same). During periods of heightened motivation, when interacting with either females or other males, individuals switch their song types more rapidly. This behavior is documented in groups as diverse as wrens (Kroodsma 1977, Kroodsma and Verner 1978), blackbirds and meadowlarks (Smith and Reid 1979, D'Agincourt 1981, Falls and D'Agincourt 1982), and sparrows (Kramer and Lemon 1983, Kramer et al. 1985).



## ACKNOWLEDGMENTS

We thank Roberta Pickert for help with initial studies in New York, Richard Canady for help with recording New York and California wrens, Dennis Forsythe for help with initial efforts in the Carolinas, Cynthia Staicer for her programming skills, Tony Masuk and Rachel Bereson for statistical analyses, Beatrice Van Horn and an anonymous reviewer for comments, Joyce Britt for "processing" this manuscript, and numerous work-study students who toiled over the data. DEK thanks the National Science Foundation for a series of grants that have helped fund this project since 1974 (especially BNS 82-01085 and BNS 85-06996). We also thank the Illinois State Department of Conservation for cooperation in use of Goose Lake Prairie State Park and personnel of the Grizzly Island Wildlife Area for assistance there.

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