

COMPLEX SINGING BEHAVIORS AMONG *CISTOTHORUS* WRENS

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ABSTRACT.—The song of the Sedge Wren in North America consists of several introductory notes and a trill of repeated syllables. All males studied had nearly identical song introductions of four different note types, but the trill types were extremely variable: two males studied most intensively used 84 and 148 song types, but only about 5% of trill types in the repertoire of neighboring males were similar to one another. Three hand-reared males learned no songs from a tutor tape that was presented between 15 and 90 days of age; however, shared components in their repertoires indicated that the males did, to a limited extent, imitate one another.

Neighboring male Sedge Wrens tended to avoid singing simultaneously and changed song types together; furthermore, when other males were singing, song rates increased and a greater variety of song types was used. Overall, as song rates increased, successive songs were more likely to be different and new song types were introduced after fewer songs (i.e. versatility increased). Faster song rates, together with correlated changes in singing behaviors, bombard listeners with a greater diversity of song stimuli per unit time and presumably play a role in capturing and maintaining attention of recipients.

Breeding biologies of the Sedge and Marsh wrens (*Cistothorus* spp.) are similar, yet these two species differ in 1) the degree of similarity in song repertoires among neighboring males, which directly affects the ability to countersing with like songs; 2) the extent of geographical variation in song; and 3) the ability to learn songs from a tutor tape between 15 and 90 days of age. Species differences in habitat stability, site fidelity, and dispersal may contribute to this divergence in patterns of vocal behavior. *Received 17 January 1978, accepted 4 April 1978.*

THE singing behaviors of different oscine species are remarkably diverse. Some appear extremely simple, such as the hiccupping “tsi-lick” of the Henslow’s Sparrow (*Passerherbulus henslowii*); others are extremely complex, as in the Marsh Wren³ (*Cistothorus palustris*) of eastern Washington, where neighboring males have nearly identical song repertoires of over 100 song types, sing their many songs in the same highly stereotyped sequences, and tend to synchronize their sequences with one another during singing performances (Verner 1975). Selective forces involved in the evolution and/or maintenance of these different behaviors can best be clarified by comparing the biologies of different populations within a species or of different species within a genus. Such a comparative approach has been successful in many areas of biology.

In an attempt to contribute toward our understanding of the evolution of complex avian singing behaviors, we began a geographical survey of Marsh Wren singing behaviors (Verner and Kroodsma in prep.) as well as the present study of the singing behavior of the only North American congener, the Sedge Wren³ (*Cistothorus pla-*

³ The genus *Telmatodytes* has been merged with *Cistothorus* (American Ornithologists’ Union 1976), and we encourage a further change in common names. In this paper we refer to the Long-billed Marsh Wren as the Marsh Wren, and the Short-billed Marsh Wren as the Sedge Wren; others have also suggested this change (see Eisenmann 1955, Peterson 1973), and the recommended names better reflect the habitats of the two species.

tensis). These two *Cistothorus* species are sympatric throughout much of the mid-west; territories of the two species may be adjacent or even overlap one another, but preferred habitats do differ, as the Sedge Wren prefers moist upland meadows rather than the cattail and bulrush marshes frequented by the Marsh Wren. Breeding biologies are similar yet, as shall be seen, the singing behaviors of the two species differ markedly in several respects.

Specifically, the focus of this paper is on the Sedge Wren: 1) the variability of the song within and among individual males in nature, 2) the ontogeny of song as studied in three hand-reared males, 3) the patterns and correlates of different singing behaviors, and 4) interactions between males during song duels. Where possible comparisons are made with data available for Marsh Wrens.

COMPLEX SINGING BEHAVIORS—DEFINING VERSATILITY

Individuals of a few species utter a single song type throughout the day, season, and from year to year. The Chipping Sparrow (*Spizella passerina*) and Hutton's Vireo (*Vireo huttoni*) are good examples; Hartshorne (1973) classified such songsters as monotonous and lacking variety, since successive songs are essentially identical.

On the other hand, males of most bird species have more than one song type in their repertoire; 33 of 39 species listed by Dobson and Lemon (1975) had repertoires of 2 or more song types. Males of these species sing with "variety," and Hartshorne recognized two different classes of such songsters. Males may repeat a song type many times before introducing another type; this is "eventual variety," and if each letter represents the rendition of a given song type, such behavior may be denoted AAAAA . . . BBBBB . . . Males of other species may sing with "immediate variety," where successive songs are different from one another (e.g. ABCDEFGHIJ . . .).

Close study of oscine singing behaviors reveals that species do not fit nicely into the discrete categories established by Hartshorne (1973); rather, many different sequencing behaviors occur among species, among different populations of the same species, and even within the behavior of an individual male. Categorization becomes less interesting than attempting to clarify the selective forces involved in molding these different sequencing behaviors, but understanding the variety of sequencing and establishing a useful terminology are prerequisites for further discussion.

Let us consider six different singing behaviors (see Fig. 1), and examine in detail the sequencing behavior over 10 song utterances. Two measures that contribute most to our perception of complexity or versatility in oscine singing behaviors are (a) the number of different song types in a sequence and (b) the number of transitions that are between unlike songs (in our calculations, the transition between the 10th and 11th song is included as the 10th transition). Either (a) *song type versatility* or (b) *transition versatility* could be used as an index of overall versatility, but neither by itself adequately reflects the complexity of different behaviors. For example, behaviors 2 and 6 in Fig. 1 have equal song type versatility, but transition versatility differs markedly; likewise, transition versatility for behaviors 4, 5, and 6 remains constant at 10, but song type versatility ranges from 10 down to 2. Unfortunately, (a) and (b) are not independent variables; over a sequence of 10 songs, if $a = 1$, $0 \leq b \leq 1$, but with $a > 1$, $a - 1 \leq b \leq 10$. While neither (a) nor (b) alone is a suitable measure of versatility, the product (a)(b) does give (c) a *total versatility* measure ranging from 0 to 100 (over a 10-song sequence) and which matches our intuition

| SINGING BEHAVIOR TYPE | SONG NUMBER IN SEQUENCE | | | | | | | | | | | | | | | (a) | (b) | (c) | (d) | (e) |
|--------------------------|-------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|--------------------------|---------------------------|----------------------|-----------------------|--------------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | SONG TYPE VERSATILITY | TRANSITION VERSATILITY | TOTAL VERSATILITY | RECURRENCE NUMBERS | RENDITIONS/ SONG TYPE |
| | 1 | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | 1 | 0 | 0 | 0.0 |
| 2 | A | A | A | A | A | B | B | B | B | B | C | C | C | C | C | 2 | 2 | 4 | 0.0 | 5.0 |
| 3 | A | A | B | B | C | C | D | D | E | E | F | F | G | G | H | 5 | 5 | 25 | 0.0 | 2.0 |
| 4 | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | 10 | 10 | 100 | — | 1.0 |
| 5 | A | B | A | B | C | D | C | D | E | F | E | F | G | H | G | 6 | 10 | 60 | 1.0 | 2.0 |
| 6 | A | B | A | B | A | B | A | B | A | B | C | D | C | D | C | 2 | 10 | 20 | 1.0 | 5.0 |

Fig. 1. Six hypothetical examples of different singing behaviors. (a) is the number of different song types occurring in 10 songs; (b) is the number of transitions between songs of different song types of the 10 transitions from 1-2 through 10-11; (c) = (a)×(b); (d) is the average number of songs occurring between successive renditions of a song type—recurrence numbers of ≤5 are considered here (see text for fuller explanation), undefined if recurrence numbers all >5; (e) is the number of renditions of a song type occurring within a series of songs where recurrence numbers do not exceed 5 (undefined if repertoire consists of only one song type).

of versatility ranks for the six behaviors in Fig. 1. [A third factor, the predictability of the next song type, could be included as a further refinement in indexing total versatility. If (a) = 2, a random sequence with b < 10 might be less monotonous than behavior type 6 in Fig. 1. Other factors, such as (d) through (h) below might also be considered, but the ultimate answer must come, of course, from the birds themselves—at present we have little evidence as to how the avian brain actually perceives “versatility.”]

The (d) *recurrence number* is the number of songs between successive renditions of a given song type. In this study, recurrence numbers of 0 and 1 were most common; overall, recurrence numbers of 0, 1, 2, 3, 4, 5 occurred 2,498, 1,916, 147, 39, 4, and 3 times, respectively, in our sample of 4,607. No recurrence numbers of 6 through 10 were found throughout this study and usually several hundred songs would intervene before a given song type was reintroduced. The number of (e) *renditions/song type* that occurs within the relatively brief time interval where

TABLE 1. Composition of tutor tape presented to Sedge Wrens

| Song Format ^a | Number of Songs |
|--------------------------|-----------------|
| S S - ^b | 9 |
| M S - | 5 |
| M S M | 5 |
| M M M ^b | 9 |
| S M - | 5 |
| S M M | 5 |
| S B - | 2 |
| S B M | 2 |
| M B - | 2 |
| M B M | 2 |
| B B - ^b | 4 |
| S P - | 3 |
| S P M | 3 |
| M P - | 3 |
| M P M | 3 |
| - P - ^b | 5 |
| | 67 |

^a Normal Sedge Wren songs consist of an introduction and a trill (see Fig. 2A); Marsh Wren songs are similar but usually add several brief notes after the trill as a conclusion. As part of a larger experiment on selective learning among *Cistothorus* wrens, a tutor tape of 67 songs with components from normal songs of the two wrens (S = Sedge Wren, M = Marsh Wren), the Swamp Sparrow (P; *Melospiza georgiana*), and the Bewick's Wren (B; *Thryomanes bewickii*) was prepared. The song formats listed in the table give the source of the introduction, the trill, and the conclusion from which each song model was derived. A dash indicates that one song component was not included in that particular format

^b Normal song for this species

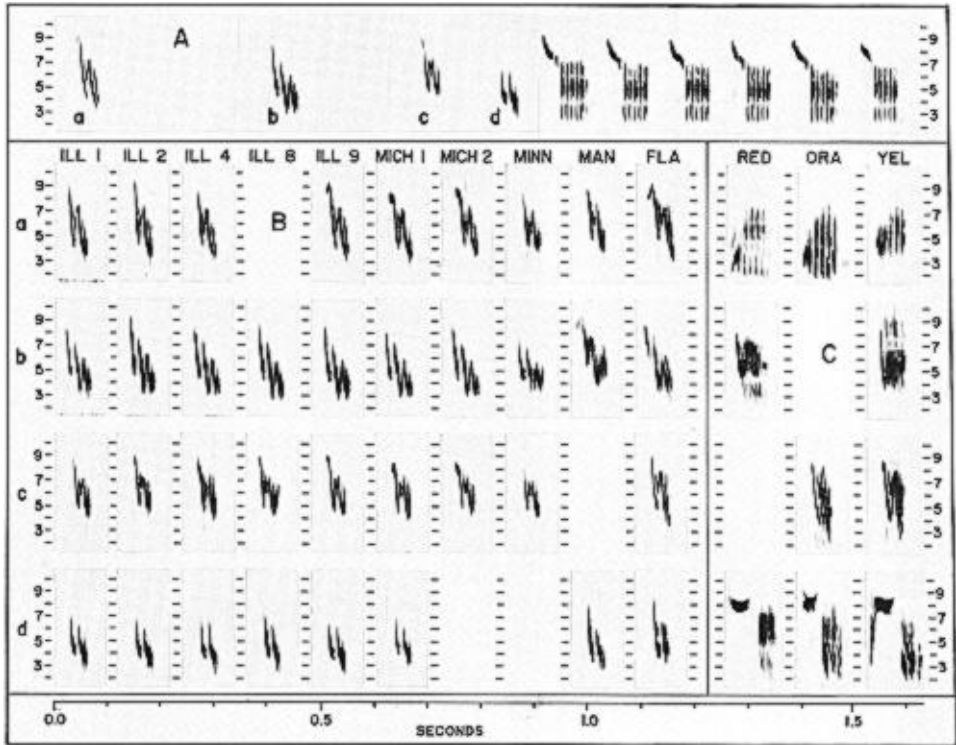


Fig. 2. Examples of songs and song components from Sedge Wren songs. The abscissa is in seconds, while the ordinate is kHz. **A.** A typical song recorded on the Illinois study site, with each of four different introductory notes labelled. **B.** Examples of song introductory notes from 10 males throughout the range of the Sedge Wren; columns are different males, while rows are the different notes as labelled in **A.** **C.** Examples of introductory notes from three hand-reared males.

successive renditions of the song type are not separated by more than five other songs is another descriptive measure of a bird's singing behavior. The descriptive terms (a) through (e) are all, in a sense, measures of versatility, for all five reflect the variety of song types and song sequences during a song performance.

Three other measures have proven useful in this study. The (f) *songs/minute* and (g) *song length* are used in calculating the overall (h) *percentage performance time*, i.e. $100fg/60$.

METHODS

The bulk of the tape recordings used in this study were made 17–20 June 1974 at Goose Lake Prairie State Park, Grundy County, Illinois. Additional recordings were made in Michigan near Vriesland (Ottawa County) and at the Bernard W. Baker Sanctuary (Calhoun County) between 28 June and 3 July 1975. Uher 4000 Report-L tape recorders, Uher M514 microphones, and parabolic reflectors were used in all cases. Neighboring territorial males in Illinois were recorded simultaneously with separate recorders and parabolas, and tapes were synchronized by walkie-talkie and/or by recording the neighboring male in the background of the primary tape. All recordings were analyzed on a real time analyzer (Hopkins et al. 1974), displaying frequency vs. time.

Ten Sedge Wren nestlings were collected in Calhoun County, Michigan and reared by hand in New York. The diet, used extensively on Marsh Wrens as well, consisted of 4 lb raw ground beef, 4 lb raw beef liver, 18 hard boiled eggs (without shells for nestlings), 1 lb cottage cheese, 3 lb baked carrots, 4½ lb turkey starter crumbles (about 30% crude protein), 1 lb dried mosquito larvae, 2 cups Brewer's yeast,

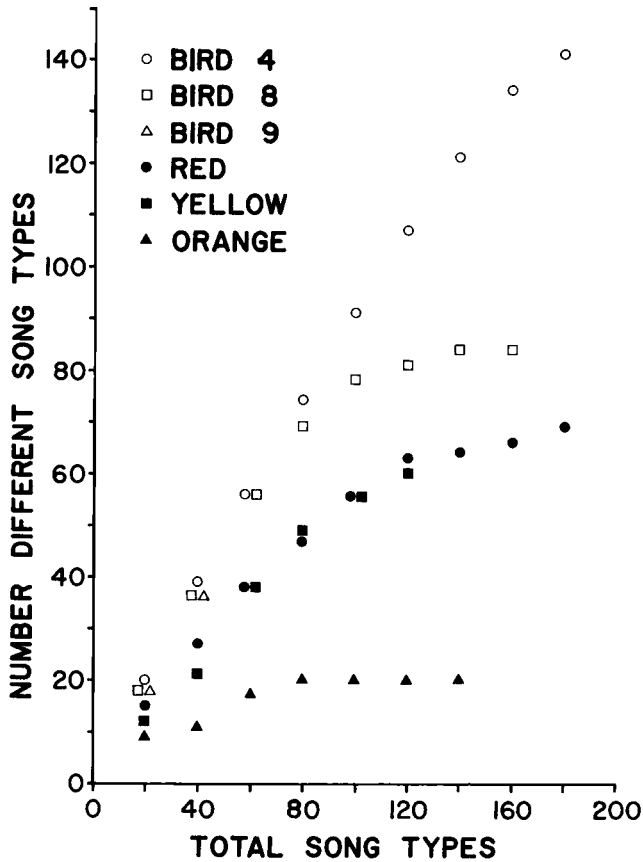


Fig. 3. Song repertoire sizes studied in three wild males (Birds 4, 8, and 9 of Illinois) and three hand-reared males (Red, Orange, Yellow). "Total song types" is the cumulative total of the number of times song types were introduced (first occurrence of a particular song type) or reintroduced (considered a "repeat," since that particular song type had not occurred in at least the 10 and usually $\gg 10$ previous songs; see text, "Defining versatility"), while "Number different song types" is the cumulative total of new song types introduced to the repertoire. Repertoire sizes differed among wild and among hand-reared males; further sampling would have produced few if any new song types for Orange and Bird 8, but sampling was incomplete for the other four males.

1 cup wheat germ, and 1 cup calcium gluconate (or ground oyster shells). Ingredients were ground up, mixed thoroughly, and frozen in bulk. This diet was fortified with mealworms, a vitamin-amino acid supplement, and, during the nestling and fledgling stages, with moths captured at an ultraviolet light.

These 10 nestlings, of which 3 proved to be males, were tutored with a variety of songs between the ages of 15 and 90 days (see Table 1 for composition of tutor tape). Sedge Wrens were housed with 11-13 Marsh Wrens until day 120, and after that with the Marsh Wrens and a variety of other birds in a birdroom at the Rockefeller University Field Research Center.

RESULTS

DESCRIPTION OF SONG

The song of the Sedge Wren consisted of several introductory notes of brief duration and broad frequency spectrum followed by any one of a variety of trills (a serial repetition of a given syllable type; see Fig. 2). The introductory notes were highly stereotyped and similar both within and between populations, with most

males using four different notes; the Michigan and Illinois introductions were especially similar, but samples from Manitoba and the wintering grounds in Florida were little different. Illinois Male 8 and Michigan Male 2 used only three note types in the several hundred ($n > 400$ for each male) songs sampled (see Fig. 2), so not all birds used the four note types. Common note sequences were ABC, ABCD, and BCD, with a few infrequent variations on those sequences (e.g. AABC).

In stark contrast to the stereotypy of introductory notes, the males in Illinois and Michigan had large repertoires of trill types. For example, 1,112 songs were recorded from Bird 8. For a given song type, syllable rates varied less than 3% from one rendition to the next and the detailed morphology of the syllables (as measured on sonograms) remained constant; the number of trill types leveled off in the mid-80's (see Fig. 3). On the other hand, Bird 4 had a larger repertoire, for in 755 songs, 148 different song types were used. A limited sample from Bird 9 revealed a repertoire size comparable to that of Birds 4 and 8.

The variability of trill types between males was equally great. For example, Birds 8 and 9 were immediate neighbors, but of the 36 trill types recorded from Bird 9, only 2 (5.6%) were similar to trills in the repertoire of Bird 8. And of 40 song types from the repertoire of Bird 8, only 2 (5.0%) were similar to song types of Bird 4. Other males in the population also had relatively unique repertoires of song types, though exact degrees of similarity with neighboring males were not quantified. "Similar" is, of course, a relative term; here songs of two different males had to have 1) indistinguishable syllable morphologies, and 2) syllable rates within 10% of each other in order to be called similar. Sedge Wren males sing with great individual variation in trill types, and inter-male similarity is at a minimum; this contrasts sharply with Marsh Wrens, where neighboring males have nearly identical song type repertoires (Verner 1975).

SONG DEVELOPMENT

The hand-reared males developed sizeable repertoires of song types that consisted of an introductory portion together with a concluding trill. However, only portions of those introductions (see Fig. 2C) and none of the trill types ($n = 70 + 60 + 20 = 150$, see Fig. 3) developed by the three males were good copies of the training songs.

On the other hand, the hand-reared males developed introductory notes similar to one another (see labelled notes in Fig. 2C), suggesting that, while introductions were not learned extensively from the training songs, the males did learn and develop them from one another. The trill types also revealed evidence of learning, not from the training tapes, but among the hand-reared subjects: two of Orange's 20 songs (10.0%) were similar to songs in the repertoires of Red and Yellow, while Red and Yellow had 16 song types in common (20.0% and 22.9% of their respective repertoires). This degree of sharing is high compared to the 5% level observed among neighboring males in nature.

Even though trill types were not learned from the training tapes, the great majority of them would fall within the variability of temporal and frequency patterns found in wild-type songs recorded in the Illinois and Michigan populations.

PATTERNS OF SINGING BEHAVIOR

Bird 4 of Illinois sang during most of the daylight hours, and about 8 h of recordings were obtained from this male alone. The data in Table 2 summarize 17

TABLE 2. Singing behaviors of five Sedge Wren males during half-hour periods of the day.

| Bird | Time of day | Number of songs | Song type versatility | Transition versatility | Total versatility | Renditions | | Songs/minute | Song length | Percentage performance time | Recurrence numbers |
|------|-------------|-----------------|-----------------------|------------------------|-------------------|---------------|------|--------------|-------------|-----------------------------|--------------------|
| | | | | | | per song type | type | | | | |
| 4 | 0430-0500 | 332 | 4.57 | 9.94 | 45.4 | 3.32 | 1.44 | 15.8 | 1.44 | 37.9 | 1.16 |
| 4 | 0500-0530 | 389 | 4.32 | 9.56 | 41.3 | 3.89 | 1.42 | 17.0 | 1.42 | 40.2 | 1.16 |
| 4 | 0500-0530 | 230 | 4.62 | 9.57 | 44.2 | 3.19 | 1.42 | 17.3 | 1.42 | 40.9 | 1.15 |
| 4 | 0530-0600 | 264 | 3.90 | 9.66 | 37.7 | 4.26 | 1.45 | 15.9 | 1.45 | 38.4 | 1.10 |
| 4 | 0530-0600 | 282 | 4.62 | 9.86 | 45.6 | 3.36 | 1.45 | 16.4 | 1.45 | 39.6 | 1.05 |
| 4 | 0600-0630 | 389 | 3.38 | 9.36 | 31.6 | 4.86 | 1.39 | 15.7 | 1.39 | 36.4 | 0.96 |
| 4 | 0600-0630 | 302 | 3.85 | 8.84 | 34.0 | 4.08 | 1.44 | 14.4 | 1.44 | 34.6 | 0.85 |
| 4 | 0630-0700 | 169 | 3.57 | 5.86 | 20.9 | 5.63 | 1.38 | 13.9 | 1.38 | 32.0 | 0.91 |
| 4 | 0630-0700 | 258 | 3.62 | 8.60 | 31.1 | 4.96 | 1.33 | 14.6 | 1.33 | 32.4 | 0.96 |
| 4 | 0630-0700 | 220 | 2.95 | 8.86 | 26.1 | 4.78 | 1.45 | 14.8 | 1.45 | 35.8 | 0.40 |
| 4 | 0700-0730 | 154 | 2.89 | 5.84 | 16.9 | 6.42 | 1.38 | 12.8 | 1.38 | 29.4 | 0.24 |
| 4 | 0700-0730 | 157 | 2.67 | 7.96 | 21.2 | 6.04 | 1.41 | 15.2 | 1.41 | 35.7 | 0.75 |
| 4 | 0730-0800 | 288 | 3.44 | 7.95 | 27.3 | 5.33 | 1.39 | 15.4 | 1.39 | 35.7 | 0.86 |
| 4 | 0800-0830 | 301 | 3.45 | 8.70 | 30.0 | 4.70 | 1.38 | 14.6 | 1.38 | 33.6 | 0.81 |
| 4 | 1300-1330 | 116 | 2.47 | 3.97 | 9.8 | 7.25 | 1.41 | 14.8 | 1.41 | 34.8 | 0.14 |
| 4 | 1330-1400 | 124 | 2.33 | 4.27 | 9.9 | 6.89 | 1.38 | 15.4 | 1.38 | 35.4 | 0.30 |
| 4 | 1400-1430 | 95 | 2.33 | 4.74 | 11.0 | 7.92 | 1.44 | 14.6 | 1.44 | 35.0 | 0.33 |
| 1 | 0430-0500 | 163 | 3.47 | 7.98 | 27.7 | 4.79 | 1.46 | 16.8 | 1.46 | 40.9 | 0.69 |
| 1 | 0500-0530 | 376 | 2.19 | 1.60 | 3.5 | 8.17 | 1.31 | 14.5 | 1.31 | 31.7 | 0.04 |
| 1 | 0530-0600 | 91 | 2.00 | 1.10 | 2.2 | 9.10 | 1.42 | 15.0 | 1.42 | 35.5 | 0.00 |
| 1 | 0700-0730 | 31 | 3.00 | 6.77 | 20.3 | 5.17 | 1.42 | 15.0 | 1.42 | 35.5 | 0.53 |
| 2 | 0500-0530 | 242 | 3.92 | 9.01 | 35.3 | 4.48 | 1.52 | 15.2 | 1.52 | 38.5 | 0.93 |
| 2 | 0700-0730 | 102 | 3.24 | 5.78 | 18.7 | 5.10 | 1.47 | 13.2 | 1.47 | 33.4 | 0.66 |
| 2 | 0730-0800 | 188 | 2.43 | 4.04 | 9.8 | 6.27 | 1.71 | 13.8 | 1.71 | 33.8 | 0.33 |
| 8 | 0600-0630 | 191 | 1.89 | 1.30 | 2.5 | 8.68 | 1.69 | 11.2 | 1.69 | 31.9 | 0.00 |
| 8 | 1530-1600 | 72 | 2.00 | 1.11 | 2.2 | 9.00 | 1.68 | 10.8 | 1.68 | 30.4 | 0.00 |
| 8 | 1600-1630 | 240 | 2.00 | 1.50 | 3.0 | 6.67 | 1.68 | 13.8 | 1.68 | 38.0 | 0.00 |
| 8 | 1630-1700 | 242 | 2.06 | 1.49 | 3.1 | 7.56 | 1.68 | 13.2 | 1.68 | 37.0 | 0.02 |
| 8 | 1700-1730 | 121 | 1.93 | 0.99 | 1.9 | 10.08 | 1.66 | 11.7 | 1.66 | 32.4 | 0.00 |
| 8 | 1730-1800 | 184 | 2.08 | 1.09 | 2.3 | 9.20 | 1.66 | 12.1 | 1.66 | 33.5 | 0.00 |
| 9 | 1600-1630 | 188 | 1.67 | 0.53 | 0.9 | 18.80 | 1.72 | 13.7 | 1.72 | 39.3 | 0.00 |

TABLE 3. Statistical significance of correlation coefficients between different measures of singing behaviors for Sedge Wrens 1, 2, and 4 of Illinois.

| | Male | Percentage performance time | Song length | Recurrence numbers | Renditions/song type | Transition versatility | Song type versatility | Total versatility |
|-----------------------------|------|-----------------------------|-------------|--------------------|----------------------|------------------------|-----------------------|-------------------|
| Song rate | 1 | ** | * | ** | ** | ** | ** | ** |
| | 2 | ** | — | ** | — | ** | ** | ** |
| | 4 | ** | — | ** | * | * | * | ** |
| Percentage performance time | 1 | | ** | ** | * | ** | ** | ** |
| | 2 | | — | ** | — | ** | — | ** |
| | 4 | | * | * | * | * | * | ** |
| Song length | 1 | | — | — | — | — | — | — |
| | 2 | | — | — | — | — | — | — |
| | 4 | | — | — | — | — | — | — |
| Recurrence numbers | 1 | | | — | ** | ** | ** | ** |
| | 2 | | | — | ** | ** | ** | ** |
| | 4 | | | — | ** | ** | ** | ** |
| Renditions/song type | 1 | | | — | ** | ** | ** | ** |
| | 2 | | | — | ** | ** | ** | ** |
| | 4 | | | — | ** | ** | ** | ** |
| Transition versatility | 1 | | | — | ** | ** | ** | ** |
| | 2 | | | — | ** | ** | ** | ** |
| | 4 | | | — | ** | ** | ** | ** |
| Song type versatility | 1 | | | — | ** | ** | ** | ** |
| | 2 | | | — | ** | ** | ** | ** |
| | 4 | | | — | ** | ** | ** | ** |

* $P < 0.05$; ** $P < 0.01$; — No significant correlation

half-hour sampling periods for this male. Other males sang less than Bird 4, and this is reflected in fewer sampling periods for Males 1, 2, 8, and 9. Data for Birds 1 and 2 were further broken down into 27 10-song sequences, and, together with the tabulated data of Bird 4, examined for correlations among the different descriptive statistics described above (see Table 3). Summary statements on patterns of singing behaviors are based on these correlations as well as examination of the data in Table 2.

(1) *Individual variation* in song patterning among the males is striking. Birds 8 and 9, for example, sang almost exclusively in an AAA . . . BBB . . . format; of 1,184 measured recurrence intervals for these two males, 99.7% were 0 and only 0.3% were 1. On the other hand, Birds 1, 2, and 4 often alternated song types; of 3,423 intervals, 38.5% were 0, 55.9% were 1, and 5.6% ranged from 2 to 5. This difference in song patterning is indicated in a number of other descriptive measures as well (Table 2 and below).

(2) *Diurnal variation* is evident in the behaviors of Males 1, 2, and 4. All five versatility measures (d through k in Table 2) reveal that Bird 4 sang with greater versatility during the morning than during the afternoon sampling periods ($P < 0.02$ in each of the five measures, two-tailed Mann-Whitney U -test). Singing versatility generally decreased throughout the morning (Birds 1, 2, 4), but during brief periods and perhaps in specific contexts versatility could increase again (Bird 1, 0700–0730). Singing versatility of Bird 8, on the other hand, remained very low by all measures during an early morning and several afternoon sampling periods.

(3) *Song rates and versatility* measures are highly correlated. Song rates are positively correlated with recurrence numbers, transition versatility, song type versatility, and total versatility, and negatively correlated with the number of renditions/song type ($P < 0.05$ in all cases—see Table 3). The five versatility measures are not independent of one another, but rather represent slightly different approaches of measuring the same overall behavior, namely, the degree of “variety” in a singing performance. Thus, the relationship between song rates and versatility appears very robust.

(4) *Percentage performance time and versatility* are also highly correlated. In general, an individual male did not adjust its song length to different song rates, and therefore song rates and percentage performance time were highly correlated in all three males (Table 3). Hartshorne (1973) predicted a correlation between percentage performance time and whether a bird species sang with immediate or eventual variety (see above). In our data, the time interval between like songs was greater than the time interval between unlike songs ($n_1 = n_2 = 10$, $P < 0.001$ for Bird 4, Mann-Whitney U -test), and transition versatility (a continuous variable representing Hartshorne's two categories of variety) was highly correlated with the percentage performance time. This relationship did not hold for Birds 8 and 9, however, as in our samples they sang with consistently low versatility regardless of the percentage performance time.

INTERACTIONS BETWEEN MALES

Neighboring male Sedge Wrens did not have identical song type repertoires and hence did not interact in countersinging as did Marsh Wrens in eastern Washington, where males matched song types during song duels (Verner 1975). Close study of synchronized tape recordings of neighboring Sedge Wrens revealed no matching of

TABLE 4. Singing interactions between two male Sedge Wrens.

| | Bird 8 | | Bird 9 | |
|-----------------------------------|---------------|-----|----------------|----------------|
| | Bird 9 silent | | Bird 9 singing | Bird 8 singing |
| Renditions/song type ^a | 9.0 (71) | ** | 7.0 (33) | 13.0 (17) |
| Songs/minute | 12.1 (15) | *** | 14.7 (15) | 13.4 (15) |
| Percentage performance time | 32.9 | | 39.9 | 35.7 |

^a Median value with sample size in parentheses. **, *** are $P < 0.01$ and $P < 0.001$, respectively; 2-tailed Mann-Whitney U -test

song types during song duels, but the males definitely did react to one another, as could be detected in a number of measures.

Two birds (8 and 9) with adjacent territories but well removed from other males at Goose Lake Prairie provided our best evidence for these interactions (see Table 4). Data were collected between 1530 and 1800 on 19 June when Bird 8 sang almost continuously and Bird 9 sang perhaps half the time. Both males sang in AAA . . . BBB . . . fashion almost exclusively, and overall, Bird 8 sang fewer renditions/song type than did Bird 9 ($P < 0.001$, two-tail Mann-Whitney U -test). However, the behavior of Bird 8 was highly dependent on whether or not Bird 9 was singing: Bird 8 sang fewer renditions/song type, at a faster rate, and a greater percentage of total time when Bird 9 was singing than when Bird 9 was silent.

The two males also avoided singing simultaneously (see also Ficken et al. 1974). Bird 8 sang 40% of the total time while Bird 9 was singing; thus, if no avoidance occurred, 40% of Bird 9's songs should have begun while Bird 8 was singing. In 20 independent samples chosen from different singing sessions, only one song was initiated by Bird 9 when Bird 8 was singing (observed vs. expected is different, $P < 0.002$, χ^2 test). Heated countersinging between other males where singing rates were higher and repetition indices were lower led to overlap of the introductory notes of one male with the end of the trill of the second bird, but rarely did the trill portions overlap.

The singing of Bird 9 influenced Bird 8 in still another way: Bird 8 tended to change song types just after Bird 9 changed. We counted the number of songs and measured the elapsed time from the introduction of one song type to the introduction of another. By examining these series of consecutive like songs from Bird 8, we found that 6 of 20 series by elapsed time (30.0%) and 7 of 22 series by elapsed songs (31.8%) were at least 90% completed at the time Bird 9 changed song types. If Bird 8 had not reacted to the changes of Bird 9, only 10% of the series would have been 90% complete at that time; differences between observed and expected elapsed songs and elapsed time were significant ($P < 0.005$, χ^2 test).

DISCUSSION

SONG DEVELOPMENT

Failure of the Sedge Wrens to learn tutor songs between 15 and 90 days of age could be interpreted in at least two ways. First, the sensitive period may occur before or after this age period. It is unlikely that it occurs entirely before 15 days, as such a sensitive period would be far earlier than those found in other songbirds. Most songbirds have a sensitive period within the first 3 months of life when most or all of the songs are learned. Examples include the Chaffinch (*Fringilla coelebs*,

Thorpe 1958), White-crowned Sparrow (*Zonotrichia leucophrys*, Marler 1970), Zebra Finch (*Poephila guttata*, Immelmann 1969), and Marsh Wren (Kroodsma unpubl. data). Other species do, however, continue to learn later in life. Indigo Buntings (*Passerina cyanea*) in some laboratory conditions learn songs or portions of songs up to 18 months of age (Rice and Thompson 1968); this species also demonstrates a remarkable uniformity of syllable types over the entire geographical range of the species. It is possible that an extended sensitive period for song learning, together with appreciable dispersal, contributes to this general lack of geographical variation in syllable types of the Indigo Bunting as well as in the introductory notes of the Sedge Wren. In many instances, Sedge Wrens are hatched so late in the season that active singing by males on territory has all but ceased. These wrens do, however, sing on the wintering grounds in Florida (see Fig. 2), and the young could learn songs either there or on their first breeding territory the next spring.

Second, the fact that the hand-reared male Sedge Wrens learned both introductory notes and trill types from one another may be an indication that social interaction is a prerequisite for song learning. Among Marsh Wrens, social interactions seem to enhance song learning (Kroodsma unpubl. data). Zebra Finches will learn little to nothing during the first few months if exposed only to songs over a loudspeaker—the juvenile seems also to require the visual stimulus of a live tutor male (Price pers. comm.). European Creepers (*Certhia* spp.) may also require live tutor males for song imitation (Thielcke 1970).

Whether Sedge and Marsh Wrens differ in the timing of their sensitive period, the degree of social interaction required for song learning, the extent of song learning itself, or the extent of dispersal and subsequent fidelity to breeding sites, the resulting adult singing behaviors are strikingly different. Clarification of the selective forces involved in two such divergent behavior patterns among congeners, otherwise remarkably similar in their biologies, must await further study of the population ecologies of the two species, but especially the Sedge Wren.

PATTERNS OF SINGING BEHAVIOR

During countersinging duels male Sedge Wrens do interact: they avoid singing simultaneously, tend to change song types together, and when other males are singing they sing faster and repeat songs of a given type less frequently. And, in general, as the male sings faster and a greater percentage of the total time, the “versatility” of his performance increases, until the male is barraging his listeners (be it male, mate, or potential mate) with a seemingly endless variety of stimuli. To the human listener, the faster singing rates (together with the other correlated behaviors) are the most exhilarating, and quite a contrast to the relatively monotonous singing performance where a song type may be repeated as many as 31 times in succession over a 3-min period (Bird 9). One interpretation is that the males, during heated countersinging and high motivational states, use a sequencing behavior that minimizes habituation and maximizes stimulation of listeners (see Petrinovich et al. 1976).

Hartshorne (1956, 1973) has championed the idea of a correlation between the continuity of singing and the probability of successive songs being different, but Dobson and Lemon (1975), after compiling data from 39 species, state that “these data do not support Hartshorne’s hypothesis.” However, Dobson and Lemon did not actually test Hartshorne’s hypothesis, for they used repertoire size as a measure

of versatility. Hartshorne (1973) focused on *song patterning* of different species, i.e. whether successive songs were likely to be the same (either eventual or no variety) or different (immediate variety). A Carolina Wren (*Thryothorus ludovicianus*), for example, has a large repertoire size (high Dobson and Lemon versatility), but a male may sing a song type 100 times in succession before changing to another (*non-versatile* according to Hartshorne). If the compiled data of Dobson and Lemon (1975) are reorganized according to Hartshorne's versatility measure, the 39 species as a whole still do not support Hartshorne. However, the nine vireo species differ from the remaining 30 species in having a very short song length and intersong interval ($P < 0.001$, two-tailed Mann-Whitney U -test). Data for the non-vireo species do support Hartshorne's notion of a direct relationship between percentage performance time and versatility (Kroodsma 1978). Our data on Sedge Wrens also reveal, within the behavior of an individual, a direct relationship between percentage performance time and versatility indices (the probability that successive songs will be different). Data from Rock Wrens (*Salpinctes obsoletus*, Kroodsma 1975) and Marsh Wrens (Verner 1975) are similar, for time intervals between songs of the same song type are two to three times longer than are time intervals between songs of different song types.

As in Marsh Wrens (Verner 1963), the breeding status of the male undoubtedly affects his singing behavior. The Sedge Wren males studied near Vriesland, Michigan were unmated, and during the early morning hours (0030–0900) they sang rapidly and with a high versatility. Birds 2–9 in Table 2 were mated, and the mate of Bird 9, who sang with low versatility, began laying a day or two following the conclusion of our recording period. Our data are not extensive enough to attempt correlating the different behaviors with different aspects of the breeding cycle, but we suspect that a thorough song budget analysis of the Sedge Wren would reveal song patterning behaviors highly dependent upon breeding status.

CORRELATES OF VOCAL BEHAVIOR AMONG *CISTOTHORUS* WRENS

The Marsh and Sedge Wrens are congeneric species with similar breeding biologies: 1) males of each species are polygynous (Verner 1965, Welter 1935, Kale 1965, Crawford 1977, Burns 1977); 2) the density of breeding pairs is high; 3) preferred habitats are marshes or wet meadows, essentially monolayers without an appreciable vertical dimension, where overall avifaunal diversity is low, usually making the wren the most abundant species present (Kroodsma 1977); 4) males sing a relatively high percentage of the time (30–40% singing, 60–70% in silence during an actual singing performance); 5) they use large song type repertoires, which may number well over 100 in some populations; and 6) they continue to sing (presumably for additional mates), often day and night, throughout much of the breeding season. The details of their singing behaviors, however, differ. First, Marsh Wren males in a given population share high percentages of their song type repertoires (Verner 1975, Verner and Kroodsma in prep.); Sedge Wren males in the same population have dissimilar song types and unequal repertoire sizes. Second, when countersinging, neighboring male Marsh Wrens in some populations answer each other with like song types (Verner 1975, Verner and Kroodsma in prep.); Sedge Wrens cannot countersing with like songs, though they definitely do influence one another while singing. And third, in the laboratory, Marsh Wrens between the ages of 20 and 80 days readily learn the precise details of songs presented to them over loudspeakers

(Kroodsma in prep.); male Sedge Wrens in the laboratory between 15 and 90 days of age demonstrate little to no ability to learn tutor songs presented over loudspeakers.

Perhaps a key element in these different vocal behaviors lies in the relative habitat stability of the two species. In North Dakota, for example, yearly fluctuations in surface water levels of wetland habitats are pronounced. The Sedge Wrens occur in wetlands with shallower water than do Marsh Wrens. Sedge Wren habitat thus dries up more frequently, leading to greater fluctuations in Sedge Wren populations (R. E. Stewart pers. comm.).

Others have found that arrival dates and population levels of Sedge Wrens are unpredictable from year to year. In Iowa, Sherman (1952) found them arriving in July (18 yr), August (3 yr), or September (2 yr), with arrival dates suggesting that the birds had first nested elsewhere. Sedge Wrens arrived in Arkansas rice fields in July, just when the season's crop matured; eggs and young were found into September (Meanly 1952). Burns (pers. comm.) banded 10 breeding males, none of which returned to his Minnesota study site the following year, and Walkinshaw (1935) characterized the breeding behavior of the Sedge Wrens as opportunistic.

Our meagre data from Illinois suggest the same sort of shifting about by Sedge Wrens. Observations of territorial birds at Goose Lake Prairie were made on a weekly or biweekly basis from late May through mid-September 1975. Sedge Wrens arrived in late May, and 4 of 5 territorial males were color banded by 20 June. Between 17 and 23 July at least 3 (maybe 4) of those males disappeared from the prairie and at least 4 (maybe 5) new males took their places. During the same week, Sedge Wrens appeared for the first time in a grassy section of Parklands Nature Preserve, about 20 km north of Bloomington, Illinois (D. E. Birkenholz pers. comm.). Thus it appears that Sedge Wrens have evolved a mobility quite uncharacteristic of most North American passerines (compare the Dickcissel, *Spiza americana*, which occupies rather similar habitats; Fretwell 1977). They certainly contrast with the Marsh Wren, in which site fidelity from year to year is pronounced and males tend to remain on the same territory for the duration of a breeding season (Verner 1971).

Local song dialects are often maintained in sedentary populations (Baptista 1975, Kroodsma 1974); however, with the mobility demonstrated by the Sedge Wren, local song variants would soon be swamped. The song of the Sedge Wren, with its stereotyped (but probably learned) introduction and highly variable trill, may be a compromise that enables population mixing; the species-typical introduction is a good species identification signal, whereas the sizeable trill repertoire, generated largely through improvisation, may have evolved as an anti-habituation mechanism in dense, polygynous populations (Kroodsma 1977). Experimentation on the functions of the two portions of Sedge Wren song showing such radical extremes in the extent of individual and geographical variability might prove enlightening.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1976. Thirty-third supplement to the A. O. U. Check-list of North American Birds. *Auk* 93: 875-879.
- BAPTISTA, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). Univ. Calif. Publ. Zool. 105.
- BURNS, J. T. 1977. Social organization of Short-billed Marsh Wrens. Unpubl. M.S. thesis, Minneapolis, Univ. Minnesota.
- CRAWFORD, R. D. 1977. Polygynous breeding of Short-billed Marsh Wrens. *Auk* 94: 359-362.
- DOBSON, C. W., & R. E. LEMON. 1975. Re-examination of monotony threshold hypothesis in bird song. *Nature* 257: 126-128.
- EISENMANN, E. 1955. Species of middle american birds. *Trans. Linn. Soc. N.Y.* 7.
- FICKEN, R. W., M. S. FICKEN, & J. P. HAILMAN. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* 183: 762-763.
- FRETWELL, S. 1977. Is the lady a tramp? *Bird Watch* 5: 1-3.
- HARTSHORNE, C. 1956. The monotony-threshold in singing birds. *Auk* 83: 176-192.
- . 1973. *Born to sing. An interpretation and world survey of bird song.* Bloomington, Indiana Univ. Press.
- HOPKINS, C. D., M. ROSSETTO, & A. LUTJEN. 1974. A continuous sound spectrum analyzer for animal sounds. *Z. Tierpsychol.* 34: 313-320.
- IMMELMANN, K. 1969. Song development in the Zebra Finch and other Estrildid finches. Pp. 61-74 in *Bird vocalizations* (R. A. Hinde, Ed.). London, Cambridge Univ. Press.
- KALE, H. W. II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren *Telmatorhynchus palustris griseus* (Brewster), in Georgia salt marshes. *Publ. Nuttall Ornithol. Club* No. 5.
- KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. *Z. Tierpsychol.* 35: 352-380.
- . 1975. Song patterning in the Rock Wren. *Condor* 77: 294-303.
- . 1977. Correlates of song organization among North American wrens. *Amer. Natur.* 111: 995-1008.
- . 1978. Continuity and versatility in bird song: Support for the monotony threshold hypothesis. *Nature* 274: 681-683.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Physiol. Psychol. Monogr.* 71.
- MEANLEY, B. 1952. Notes on the ecology of the Short-billed Marsh Wren in the lower Arkansas rice fields. *Wilson Bull.* 64: 22-25.
- PETERSON, R. T. 1973. *Field Guide to Mexican Birds.* Boston, Houghton Mifflin Co.
- PETRINOVICH, L., T. PATTERSON, & H. V. S. PEEKE. 1976. Reproductive condition and the response of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) to song. *Science* 191: 206-207.
- RICE, J. O., & W. L. THOMPSON. 1968. Song development in the Indigo Bunting. *Anim. Behav.* 16: 462-469.
- SHERMAN, A. R. 1952. *Birds of an Iowa dooryard.* Boston, Christopher Publishing House.
- THIELCKE, G. 1970. Lernen von Gesang als möglicher Schrittmacher der Evolution. *Z. Zool. Systematik Evolutionsforschung* 8: 309-320.
- THORPE, W. H. 1958. The learning of song patterns by birds, with special reference to the song of the Chaffinch (*Fringilla coelebs*). *Ibis* 100: 535-570.
- VERNER, J. 1963. Song rates and polygamy in the Long-billed Marsh Wren. *Proc. 13th Intern. Ornithol. Congr.*: 299-307.
- . 1965. Breeding biology of the Long-billed Marsh Wren. *Condor* 67: 6-30.
- . 1971. Survival and dispersal of male Long-billed Marsh Wrens. *Bird-Banding* 42: 92-98.
- . 1975. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. *Living Bird* 14: 263-300.
- WALKINSHAW, L. H. 1935. Studies of the Short-billed Marsh Wren *Cistothorus platensis* in Michigan. *Auk* 52: 362-368.
- WELTER, W. A. 1935. The natural history of the Long-billed Marsh Wren. *Wilson Bull.* 47: 3-34.