

## ORGANIZATION OF SINGING IN HOUSE WRENS

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**Abstract.**—House Wren songs are complex and the repertoires of individuals are large. Most of the songs in this study were composed of nine syllables and they were most frequently made up of only two different syllable types. The number of repetitions of a particular syllable type varied. Syllable arrangement was also variable; particular syllables usually were not found in only one specific part of the song. There was frequent syllable sharing among birds of this population, but little song type sharing occurred. Often, part of the song was shared but the presence of unique syllables produced many different song types and, consequently, distinct song repertoires among birds.

A number of theories have been proposed to explain the evolution of complex songs and large repertoires in birds. In House Wrens large repertoires may be involved in enhancing territorial defense although one hypothesis related to territorial defense, the Beau Geste hypothesis, was rejected. Also, large repertoires may have evolved through female choice.

### ORGANIZACIÓN DEL CANTO DEL REYEZUELO (*TROGLODYTES AEDON*)

**Sinopsis.**—El canto de *Troglodytes aedon* es complejo y con un amplio repertorio. La mayoría de las canciones tienen 9 sílabas, aunque sólo dos de estas son diferentes. La repetición de una sílaba particular varía entre individuos. El arreglo de las sílabas también es variable. No se encontró sílabas particulares que estuvieran colocadas en partes específicas de la canción. Aunque parte de la canción es compartida, la presencia de sílabas particulares da origen a muchas canciones diferentes y por ende a un gran repertorio. Se han propuesto varias teorías para explicar la evolución de complejos de canciones y repertorios en aves. En el ave estudiada es posible que el gran repertorio pueda ser de utilidad en la defensa del territorio, aunque la hipótesis Beau Geste es rechazada. Un gran repertorio puede haber evolucionado como respuesta a la selección de pareja por parte de hembras.

Compared to most other North American wren species, the House Wren (*Troglodytes aedon*) has fairly complex songs and individuals have large song repertoires (Kroodsma 1977). The objectives of this study are to (1) determine song organization and repertoire size of individuals in a local population, (2) determine the degree of syllable and song type sharing in a population, and (3) test the prediction of the Beau Geste hypothesis (Krebs 1977) that song type changes occur concomitantly with perch switches.

### METHODS

Songs of four male House Wrens were recorded at the University of Wisconsin-Milwaukee Field Station, Saukville (Ozaukee County) Wisconsin between 7 June and 23 July, 1982. Songs were recorded at various times of the day (0530-1600, C.D.T.) for any particular individual. Two of the birds had territories in an upland apple orchard, one was located

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in a low brushy area adjacent to an open field, and one occupied an upland area of primarily aspen (*Populus tremuloides*). The territories of Birds I, III, and IV were contiguous. Bird II was located approximately 100 m from the other three. All were probably within hearing range of one another and these were the only House Wrens in the immediate area. Although the birds were not banded, individuals were easily identified by territorial behavior; they tended to sing at or near their own nest sites and only rarely entered another bird's territory.

A Uher 4200 Report tape recorder and an Electrovoice 644 directional microphone were used to record the songs. Information describing singing locations was recorded and distances between song perches were measured, enabling comparisons to be made between song types given and distances moved between songs. Intervals between successive song starts were also recorded. Sonagrams were made with a Kay 6061 B Sona-Graph at an intermediate band width setting (150 Hz).

Identification of syllables was primarily by shape, using frequency and temporal characteristics. Letter symbols were assigned to syllables to facilitate analysis. Sequences of identical syllable types, regardless of the number of repetitions of each type, characterized unique song types. For example, AAAAABBBBBBKKKK and AAAAABBBKKKKKKK were considered to be the same song type but they were not the same as AAAAJJJJKKKKKK.

## RESULTS

*Song description and organization.*—House Wren song consists of two parts. The introductory part is made up of very low amplitude “chatter” notes, but the terminal section contains clearer, louder, “bubbly” notes. As the introductory part of the song in our recordings was too faint to be analyzed accurately, this report deals only with the louder, terminal portion. Several song characteristics (e.g., total syllable number per song, number of different syllables per song, syllable order) varied considerably among birds. Figure 1 illustrates the syllables in the study population and Figure 2 shows several representative songs of four different individuals, demonstrating the ways in which syllables are combined.

Of the 1993 songs analyzed, the total number of syllables per song ranged from 3 to 22, with a mean of 11.49 (SD = 12.06). The mode was 9. The number of different syllable types per song ranged from 1 to 6, with a mean of 2.92 (SD = 3.10) and a mode of 2.

Order and number of repetitions of each syllable type often varied in different songs, even in the same individual. Most syllables were not specific to a particular part of the song. For example, if a certain syllable occurred in the beginning of a particular song and was also present in another song, it did not necessarily occur in the beginning of that other song.

Syllables ranged in frequency from 1.5 to 8.0 KHz. Song duration ranged from 0.33 to 2.48 s ( $N = 220$ ) with a mean of 1.25 (SD = 0.35).

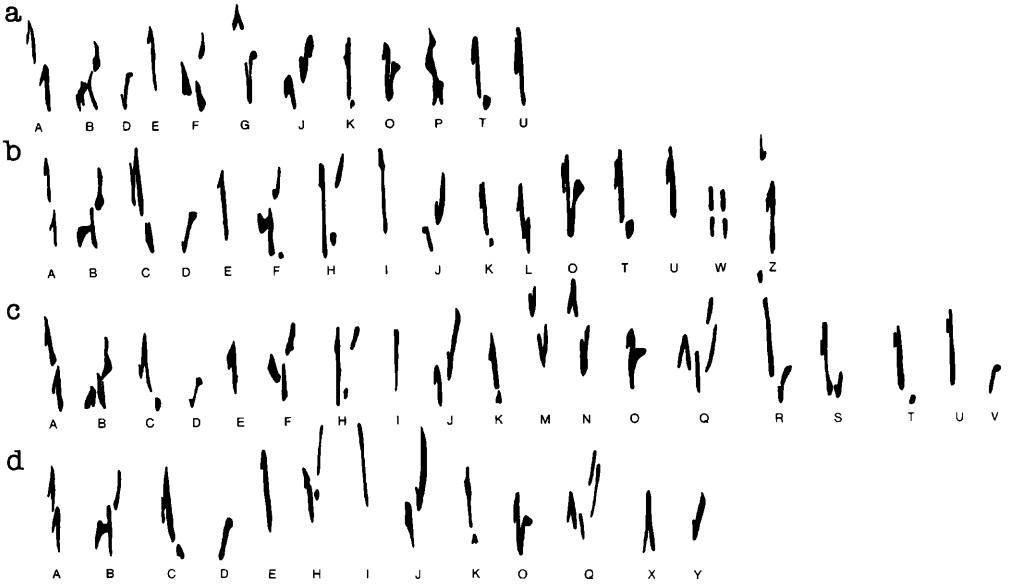


FIGURE 1. Syllables in the songs (terminal, "bubbly" sections only) of House Wrens at the University of Wisconsin-Milwaukee Field Station. (a) Bird I (b) Bird II (c) Bird III (d) Bird IV.

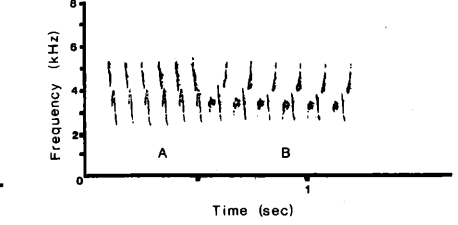
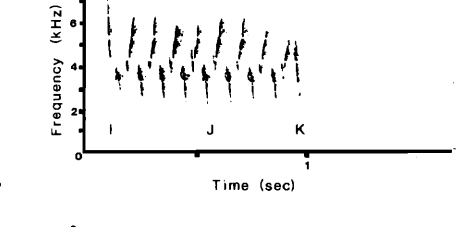
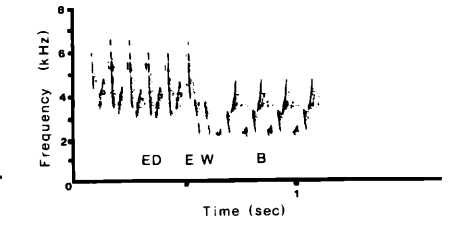
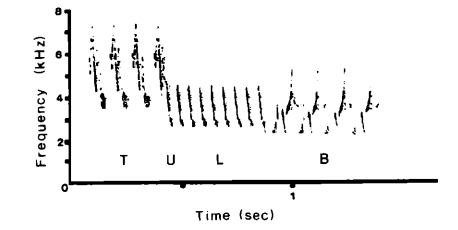
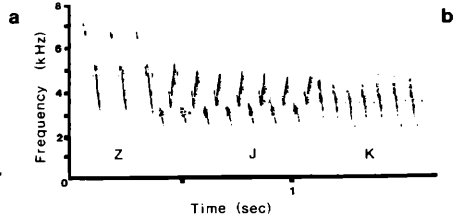
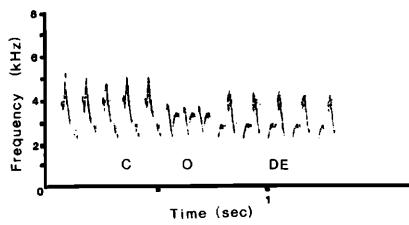
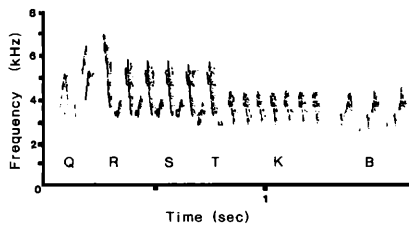
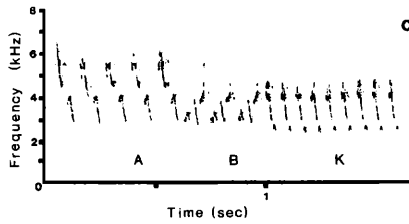
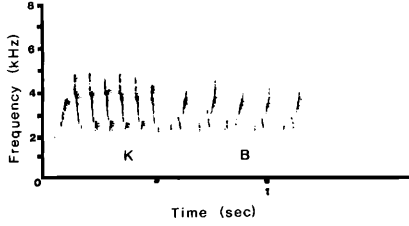
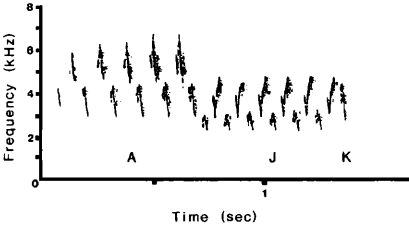
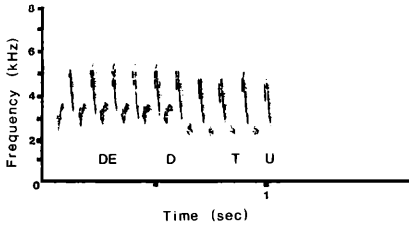
Generally, males sang most rapidly when a female was close to or in the nest.

*Amount of syllable sharing.*—Examination of sonagrams revealed an extensive amount of syllable sharing. Seven of the 26 syllables used by the four birds were common to all. Six other syllables were shared by three out of the four birds. Twelve syllables may have been unique to individuals. Bird I shared 10 of its 12 syllables with at least one other individual, Bird II shared 13 of its 16 syllables, Bird III shared 14 of its 19 syllables, and Bird IV shared 11 of its 13 syllables. Coincidence indices (Dice 1945) were calculated to show degree of similarity of syllable types between pairs of birds. In the equation

$$\text{Coincidence index} = 2h(a + b)$$

$h$  = number of shared syllables,  $a$  = number of syllables of Bird A, and  $b$  = number of syllables of Bird B. Values of the coincidence index range from 0, indicating complete lack of sharing of song syllables of the two individuals, to 1.0, indicating complete sharing. In this study, values

FIGURE 2. Examples of House Wren songs showing the song type variability that may occur both among and within individual birds. (a) Bird I (b) Bird II (c) Bird III (d) Bird IV.



**a**

**b**

**c**

**d**

TABLE 1. Coincidence indices for syllable sharing.

Bird	II	III	IV
I (12) <sup>a</sup>	0.71	0.65	0.56
II (16)		0.74	0.69
III (19)			0.69
IV (13)			

<sup>a</sup> Total number of different syllables.

ranged from 0.56 to 0.74 (Table 1), with a mean value of 0.67 (SD = 0.063), indicating a relatively high degree of similarity between individuals with regard to syllable types.

Unique syllables were generally located at either of the two ends of the songs. Both of Bird I's two unique syllables were located at one end or the other of the 15 songs in which they occurred. Bird II had three unique syllables. Of the 71 songs in which they occurred, they were at the beginning or end in 47 of them. In the other 24 songs, they were near the end and each time they were followed by a syllable type (B) which terminated the song. Bird III had five unique syllables, one of which initiated the song in 39 of the 62 songs in which they occurred. In the other 23, they were near the beginning of the song, being preceded by only one syllable (Q). Bird IV had two unique syllables. Of the 10 songs in which they occurred, they were within the body of the song only twice, and in both cases a unique syllable also began the song.

*Amount of song type sharing.*—Sharing of song types (unique syllable combinations) occurred infrequently. Of the 130 song types that were used by the four birds, 120 were unique. Only one song type was used by all of them and only two were shared by three out of the four individuals. More specifically, Bird I shared 7 of its 33 song types, Bird II shared 9 of its 37 song types, Bird III shared 5 of its 52 song types, and Bird IV shared 3 of its 22 song types. Coincidence indices of the degree of sharing of song types between pairs of birds ranged from 0.03 to 0.17 (Table 2), with a mean value of 0.09 (SD = 0.047). These indices, however, do not take into account songs that were similar but not identical. Many songs differed by the interjection or deletion of only one syllable-type but were still classified as different song types.

*Specific repertoire comparisons.*—Repertoires of four birds were compared. Seven of the twelve more frequently used song types were specific to particular individuals. For example, AJKB was given 91 times, but only by Bird III, and CODE was given 105 times, 103 times by Bird III. The most common song, AB, was given by all of the birds but the percent of the entire repertoire devoted to this song varied from one individual with 6% to others with 12, 24, and 36%.

*Possible influences on song type.*—Change in perch site, change in song type, and interval between successive song starts were tested for interaction using a log-likelihood ratio test (Sokal and Rohlf 1981) on a three-

TABLE 2. Coincidence indices for song type sharing.

Bird	II	III	IV
I (33) <sup>a</sup>	0.17	0.07	0.07
II (37)		0.09	0.10
III (52)			0.03
IV (22)			

<sup>a</sup> Total number of different song types.

way contingency table (Table 3). No significant three-way interaction occurred ( $G[\text{PST}] = 0.056$ ,  $P > 0.50$ ).

All combinations of two of the factors were tested for interaction with the effects of the third factor removed. There was no significant relationship between whether perch site changed and whether song type changed between two successive songs when the effect of time between songs was removed ( $G[\text{PS}\{\text{T}\}] = 0.220$ ,  $P > 0.50$ ), where T = time interval between songs, P = change/no change in perch site, S = change/no change in song type. Also, neither changes in perch sites nor song type changes showed a significant dependence on length of time between songs when the effect of the other factor was removed ( $G[\text{PT}\{\text{S}\}] = 0.570$ ,  $P > 0.50$  and  $G[\text{ST}\{\text{P}\}] = 0.056$ ,  $P > 0.50$  respectively).

#### DISCUSSION

Most North American wren species organize their song bouts into a pattern that Hartshorne (1973) termed "eventual variety" (AAA . . . BBB . . . where A and B are different song types), singing the same song type several times before switching. A few species, including the Marsh Wren (*Cistothorus palustris*) and Sedge Wren (*Cistothorus platensis*) (Kroodsma 1977), have bout patterns that Hartshorne called "immediate variety" (ABCD . . .), in which there is little or no immediate song type repetition. Kroodsma classifies the House Wren as an AAA . . . BBB . . . songster. Since each unique arrangement was considered to be a distinct song type, these House Wrens had several dissimilar song types in a row, resulting in song bouts that were made up of sequences of immediate variety interspersed within the eventual variety pattern.

House Wrens in this study shared many syllables with at least one other bird, but each of the birds also had several unique syllables. Song types were shared infrequently. In many avian species, such as the Tufted Titmouse (*Parus bicolor*), individuals share most or all of their song types with their neighbors (Schroeder and Wiley 1983). Verner (1975) found that male Marsh Wrens in eastern Washington shared most of their song types with each other.

Many hypotheses have been suggested for large repertoires (reviewed by Krebs and Kroodsma 1980). In addition to the possibility of song matching with territorial neighbors, large song repertoires may enhance territorial defense through the proposed Beau Geste phenomenon (Krebs

TABLE 3. Three-way contingency table of the relationships among interval, change of perch, and change of song type.

Time interval	Change of perch	Change in song type		Totals
		yes	no	
Short (0.0-6.0 s)	yes	17	12	29
	no	43	37	80
		60	49	109
Long (>6.0 s)	yes	18	14	32
	no	39	32	71
		57	46	103
Totals		117	95	212

1977) involving deceit of incoming males by the diversity of songs by territory holders. A prediction of this hypothesis is that a bird will switch song types as it moves from one song perch to another. A study of Chaffinches (*Fringilla coelebs*) by Dawson and Jenkins (1983) did not support the Beau Geste hypothesis. Yasukawa (1981) demonstrated that Red-winged Blackbirds (*Agelaius phoeniceus*) do switch songs at different perch sites but he and Searcy (1985) showed that the number of song types is not used to assess male densities. Our study of wrens fails to support the prediction. Krebs (1977) developed the Beau Geste hypothesis to account for repertoire evolution in species with repertoire sizes of 2-20 song types, so it was not surprising that the song switching prediction did not hold true for House Wrens which have very large repertoire sizes.

Thus, although this study does not support one of the key predictions of the Beau Geste hypothesis, that song types change with perch switches, large song repertoires may still be involved in territorial defense through advantages of song matching by territorial neighbors or through reduction of habituation. Large repertoires in House Wrens may also have evolved through their effect on females. For example, the most reasonable explanation of the very low amplitude syllables at the beginning of songs is that these are directed at the mate who is probably in close proximity, rather than at a territorial neighbor that is probably much more distant. In addition, there is the possibility that large repertoires are attractive to females and stimulate them more physiologically than would repetitions of a single song type (e.g., Kroodsma 1976).

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