ASSESSING VOCAL VARIETY IN THE WINTER WREN, A BIRD WITH A COMPLEX REPERTOIRE¹

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Abstract. The song of the Winter Wren (*Troglodytes troglodytes*) varies in a complex fashion in both time and space. An average of 21 song types occurred in males recorded on at least two mornings; these song types included many variants. Syllables within songs were not arranged randomly, as those that belong to certain syllable types based on acoustic shape were more likely to be used in the introductory portion of the song. Probabilities of transition among syllable types for consecutive syllables were uneven but consistent between years. The repertoire of song types is probably not fixed but varies in its constituent song types both through the breeding season and between years.

Key words: Song structure; song complexity; song repertoire; Winter Wren; Troglodytes troglodytes.

INTRODUCTION

The complexity of bird song contributes to its aesthetic appeal to the human ear. Evolutionists and behaviorists have constructed hypotheses to account for differences in song complexity within (Lambrechts and Dhondt 1988, Catchpole 1980) and sometimes among (Searcy and Marler 1984) species. The notion that increased complexity has an evolutionary cost is implicit in evolutionary explanations.

If hypotheses about song complexity are to be tested, the term "complexity" requires a quantifiable definition. However, the term has been used variably in the avian acoustical literature. It may represent the total number of different song types or song-type elements produced over a specified period, or it may include the patterning of these elements within or among songs. Mathematically, we may define complexity as the inverse of predictability. That is, complexity should increase as the sum of the squared probabilities of subsequent events (song types or syllables) decreases. It is thus a function of the number of songs or syllables used, their "evenness" in frequency of occurrence, and the existence of rules or constraints for patterning through time (structuring). Most theory about song complexity pertains to repertoire size, i.e., among-song complexity. Within-song complexity, however, determines the amount of variation available for among-song complexity. Additionally, when the

period (day, season, lifetime) is specified, repertoire size is difficult to estimate, as the probability of singing a given song type is often not independent of bout context [see Kroodsma (1982)].

My objective here is to illustrate problems in measuring complexity in the songs of a complex songster using Winter Wrens, *Troglodytes troglodytes*, as an example. To characterize song structuring, I describe patterning through time, both within and among songs and within and among bouts. I then abstract several measures of within-song complexity, among-song complexity, and complexity within a recording session or within consecutive sessions. I also describe how the repertoire changes within season and between years, and how this change might influence the description of complexity.

METHODS

CONTEXT OF RECORDINGS

The study area included 4 ha of early successional coastal spruce-hemlock forest (Greene 1982) and an adjacent 10-ha stand of mature timber in the Cascade Head Experimental Forest of the U.S. Forest Service (Siuslaw National Forest, Oregon). During March of 1984 and 1985, singing male Winter Wrens were captured in mist nets and uniquely marked with a combination of three plastic colored leg bands and an aluminum band. On mornings without rain I recorded the songs of a single male. I usually began recording during the first song bout of the morning (one bout includes all consecutive repetitions of one or more songs without a separation of

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more than 30 sec) and continued until I had recorded at least 100 songs or until the male began foraging, engaging in courtship, or was otherwise interrupted. At least part of this singing occurred before there was adequate light for foraging, so it was not likely to be interrupted by foraging behavior. When recording sessions were interrupted by rain, I continued them on a second and occasionally a third morning. Songs that produced unclear sonograms were not included in the analysis. I attempted to record each male at least twice, separated by at least two weeks, before he began tending nestlings (usually in late April or early May). In some cases the males disappeared before a second recording could be made.

Singing males were classified into 1 of 5 phenological stages on the day of each recording session: 1 = prior to egg-laying by any females on the territory, 2 = during laying by the primary or first female on the territory, 3 = during incubation by the primary female, 4 = nestlings in the nest of any female on the territory, and 5 =after young had fledged from all nests or all nests had been deserted by both parents. Where exact dates of a given nesting event were not known, mean values for these events over the course of the three-year study were used; seven days for laying, 14 days for incubation, and 16 days for the nestling period.

RECORDING OF VOCALIZATIONS AND DESCRIPTION OF STRUCTURE WITHIN SONGS

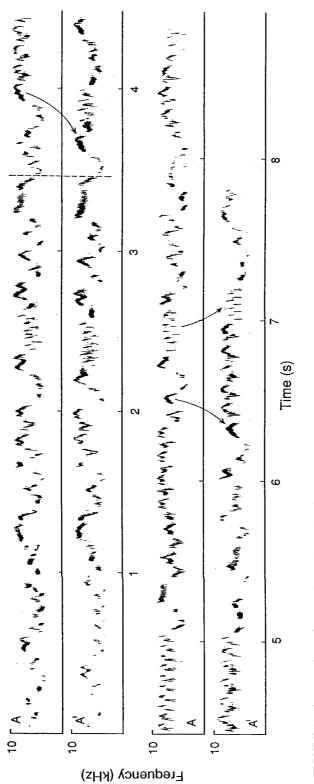
In 1984, songs were recorded on a Uher 4000 Rep-L reel-to-reel recorder with a Sennheiser directional microphone (K3-U/ME 80); in 1985 a Sony Pro Walkman WM-D6C cassette player was used. Songs were digitized using a UNISCAN II real time analyzer and printed on a dot matrix printer. Songs were defined as vocalizations that contained no gaps of ≥ 0.5 sec; gaps within songs were always much smaller than this (see Fig. 1). Within a song, a syllable was a single continuous mark on the sonograph. Occasionally, normally continuous marks appeared to separate into syllables in certain recordings; these retained their classification as single syllables. Syllables were assigned numbers using transparencies of pages of a master catalogue that included all syllables arranged by shape and frequency. Syllable identification was thus independent of context. Each new syllable was given a unique number and

added to the master catalogue. Data from each song was entered into a computer file as a single observation that included its duration, the interval between it and the previous song, and the numeric code sequence identifying consecutive syllables along with the number of consecutive repetitions of those syllables. Because introductory notes were often sung more softly than the remainder of the song, I used the best representation of the notes to identify the introductory syllables and assumed that repetitions of that song contained the same introductory notes.

Although there were too many different syllables for analysis of transitions between syllables, it seemed from visual inspection that there might be rules governing placement of certain shapes of syllables within the song. Consequently, after all syllables had been identified, the syllable catalogue was used to assign each syllable to one of 11 groups, based on the general shape of the syllable and ignoring its frequency (e.g., inverted "v," simple ascending, "m" shape, etc.). Using the terminology of Lynch et al. 1989, I refer to these groups of like syllables as "syllable types." Songs were re-written to a new computer file with syllable type numbers substituted for syllable numbers. This file was used to analyze the locations of syllable types in songs and the frequency of transitions among syllable types within songs.

All transitions among syllable types in each song were summed across all birds within a given year to obtain a matrix whose rows represented the number of all transitions from each possible syllable type, and whose columns represented the number of all transitions to each possible syllable type. Thus, the row and column totals represented the number of times syllables from a given syllable type were sung, less the number of times these were the ending and beginning syllables in songs, respectively.

To investigate whether there were "rules" of transition among syllable types, independent of the commonness of the syllable types, I compared observed patterns of transition to random patterns of transition with the same frequencies of occurrence of the syllable types. I constructed random matrices by beginning with an empty matrix of the same dimension as the observed matrix for that year. A cell was randomly selected and a single transition added to it. For example, the cell selected at random might represent transitions from syllable 3 to syllable 11, and it would





be incremented by 1. This process was repeated, with transitions being added one at a time (unless the addition would violate row or column totals, which represented syllable type commonness) until the total number of transitions in the matrix matched the total number of transitions in the observed matrix for that year.

A measure of dissimilarity between matrices was obtained using a modified distance measure:

$$D_{XY} = \sum_{i=1}^{N} \sum_{j=1}^{N} \sqrt{|(x_{ij}^2) - (y_{ij}^2)|}$$

where x and y are the cells of transition matrices X and Y, respectively, and N is the number of syllable types in each matrix. D values of pairs consisting of 1 random and 1 observed matrix were compared to D values for pairs of random matrices within years. If transitions are distributed randomly, D values should be similar for the two types of matrix pairs. Between-year Dvalues for 1984 and 1985 random matrices were compared to between-year D values for 1984 and 1985 observed matrices to evaluate whether patterns of transition were consistent between years. Random matrices will tend to be "even," with relatively low variance among cells, so that the expected difference between pairs of matrices will be low relative to differences among "uneven" matrices, with high variance among cells. If observed matrices are "uneven," the test is thus conservative for finding similarity between matrices from different years.

Individual songs rather than individual birds were used in the calculation of descriptive statistics for song structure, as song structure of individual birds may change through time. Simple linear regression applied to means for recording sessions was used to test for date effects. For all other statistical tests means for individual birds within classification groups were used in an analysis of variance (ANOVA).

BETWEEN-SONG VARIETY

Wren songs appear to have certain preferred "branch points" (Kroodsma 1980) at which sequences borrowed from other songs or newly constructed sequences can be inserted. An example shows a sequence of two typical songs within a bout (Fig. 1). If a longer series of songs could be included in such a figure, it would be evident that the pattern of syllable usage in consecutive songs cannot be described by looking for preferred "blocks" of syllables, as any such blocks would be broken and joined in a nonrandom fashion as new variants of the song were introduced. That is, a variant of a song may have a new block of syllables inserted or substituted for the ending of the original song, while a subsequent variant may use part of that block of syllables combined with part of another block of syllables that had been used previously. In essence, the patterning through time can be likened to a very complex version of the sequence circles used by Bakker et al. (1983) to describe Bobolink (*Dolichonyx oryzivorus*) song, although Winter Wren songs are more discrete.

This pattern, with its insertions, substitutions, and deletions, is analogous to the structuring of long strings of DNA and RNA. Accordingly, I used a measure of complexity based on mathematical-computational tools developed for the analysis of macromolecular sequences (Waterman 1984, 1986; Galas et al. 1985; Waterman and Eggert 1987). The best possible alignment was obtained using a dynamic programming approach in combination with similarity scoring procedure that penalized for insertions, deletions, and mismatches. High similarity scores between songs sung sequentially represented a structural simplicity through time, while low similarity scores indicated a complex repertoire. Thus complexity (the opposite of similarity) was not measured solely by the number of "different" songs (or syllables), but rather by the amount of difference in syllable type and placement among songs sung sequentially. Because the similarity score for a pair of songs tends to increase with song length, I used linear regression to extract variance due to song length across all songs recorded, prior to using similarity scores in other analyses.

SONG TYPES

For each individual, songs were identified as the same type (sensu Kroodsma 1980, Kroodsma and Momose 1991) if the first 15 consecutively different syllables were in common (38% of the 39.9 consecutive syllable types in the average song). This number was arrived at by visual inspection of coded songs. It appeared from this inspection that songs might share fewer than 10 introductory notes, yet be substantially different throughout, while songs with 15 syllables in common were very similar. In contrast, variants of songs sung consecutively retained at least the first

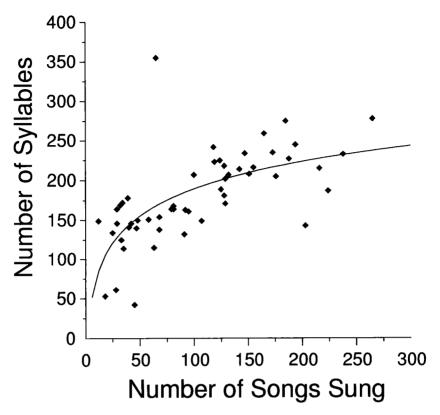


FIGURE 2. Number of different syllables vs. number of songs recorded for each recording session (1-3 subsequent mornings) in 1984 and 1985. Solid line represents a logistic regression on all points (n = 53, $R^2 = 0.420$).

15 syllables; few if any were near this threshold. Thus songs classified as different types were substantially different throughout. The number of song types and song strings sung during each recording session were identified. One song string includes all consecutive repetitions of a song type, including variants, and may include time gaps. "Bouts" of singing do not include gaps > 30 sec.

REPERTOIRE

Vocal variety in songbirds is most often quantified as estimates of individual repertoires. Such estimates assume a fixed repertoire, at least for the sampling period. I refer to the percent of song types sung during a recording session that are repeats of song types from previous recording sessions as REPS, and the number of song types sung during these earlier sessions (the base library) as BASL. If the repertoire is fixed, REPS should increase with BASL. I tested for this by simple linear regression.

RESULTS

BASIC SONG STRUCTURING

What song variety is ultimately available to the wrens, in terms of the syllabic building blocks and their arrangement? Of the recordings made from 10 birds in 1984 and 15 birds in 1985, 6,436 songs were analyzed (Table 1). These contained a combined total of 436 unique syllables; nine of these were sung only once. The number of syllables sung during a recording session by a single bird showed an asymptote at about 225 (Fig. 2), and birds sang an average of 261 syllables (range 137-385) during all recordings within a year. The average number of different syllables in a song was 37.1. Thus males included 16% of their syllable repertoire for a single morning and 10-27% of their syllable repertoire for the season in the average single song. Maximum song length was 98 syllables and the average was 39.9 ± 12.71 syllables ($\bar{x} \pm$ SD; n = 6,436; Fig. 3), or 64.7 \pm 22.57 syllables if repetitions of the

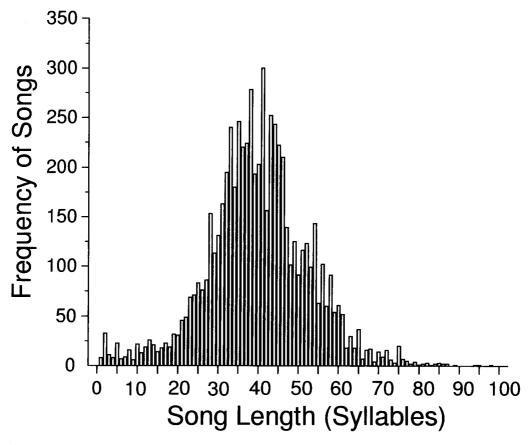


FIGURE 3. Frequency distribution of number of consecutively different syllables (song lengths) in each song recorded in 1984 and 1985.

ed separately. Intervals between songs within a bout averaged 6.5 \pm 3.34 sec ($\bar{x} \pm$ SD; n =5,873), and song duration averaged 5.6 \pm 2.09 $\sec(n = 6,283).$

Any non-randomness in syllable placement within songs would reduce the number of different songs that could be composed with a given set of syllables. I looked for an indication of placement rules associated with syllable shape. The 11 syllable types based on shape showed uneven distributions within songs; some types, such as 1, 3, and 7, were more characteristic of the introductory part of the song while syllable types 2, 4, 5, and 10, as well as those of syllable types 6 and 9 that are typically repeated in trills, tended to be distributed later in the song. Syllable types 8 and 11 had wide distributions (Fig. 4).

Two questions were addressed with matrix comparisons: (1) if a syllable from a given syl-

same consecutive syllable (as in a trill) are count-, lable type is sung, is the syllable type of the following syllable randomly determined, given observed syllable commonness, and (2) if not, are patterns of transition consistent between years. Difference measures (D) between the observed matrices of transitions (Fig. 5) and the random matrices with the same row and column totals were higher than differences between pairs of random matrices for both 1984 ($\bar{x} \pm SD$ of observed-random = $279,110 \pm 662, n = 200;$ random-random = $45,398 \pm 2,655$, n = 100) and 1985 (observed-random = $171,886 \pm 550, n =$ 200; random-random: = $30,747 \pm 1,873$, n =100). Probabilities of transition between syllable types within years are clearly non-random.

> Although the arrangement of syllables in songs is not independent within birds, within years or even between years for birds sampled both years, nearly all (7/446) of the song types sampled were different between years. Because the test for a

Bird	Number of mates ^a	Date ^b	Phenology	Number of songs	Number of song types ^d
		1	984		
1	1	4/16	e – 22	58	6/6
•	-	5/18	e + 11	69	4/4 (0)
		6/2	f+2	129	7/8 (3)
2	1	4/19	e-4	265	15/27
$\frac{2}{3}$	2	4/28	e + 6	155	9/11
5	2	5/19	b + 0 h + 0	28	1/1 (0)
4	1	4/4	e - 11	194	12/19
-	1	5/28, 5/30	i = 3	214	19/24 (2)
5	0		1 + 3	62	• • •
5	0	5/7, 5/8	-	-	4/4
1	1	5/24		95	5/5 (1)
6	1	4/24, 4/26	e + 4	218	8/8
7	1	4/13, 4/14	e – 19	252	28/35
	-	5/25	d + 2	147	9/9 (1)
8	2	4/20, 4/21, 4/22	e – 2	322	16/36
		5/29	i + 8	63	2/2 (2)
9	2	5/2	e – 8	30	5/5
		5/22	i + 5	83	4/4 (0)
10	1	4/3, 4/4	e – 19	127	16/27
		5/17	h + 0	151	15/47 (2)
		1	985		
1	1	4/9	e – 8	165	24/33 [4]
1	1	4/28	h + 4	238	13/17 (0) [0]
2	0	4/5		40	4/5 [0]
	0	4/27	_	92	6/10(1)[1]
3	1	4/6	e - 10	107	6/8 [0]
	1	5/4	d = 10 d + 14	142	14/16 (0) [1]
4	2	3/31	a - 14 e - 15	68	
	2	4/21	$\dot{e} = 15$ $\dot{i} + 0$	125	6/8 [0] 7/10 (0) [1]
11	1	5/5	i + 0 i + 14	216	7/10 (0) [1] 10/19
12	1				
12	1	4/19	e + 9	32	8/8
13	1	4/25	i + 5	112	8/10 (0)
	1	3/29	e – 16	42	6/6
	0	4/24	i + 3	129	10/11 (1)
14	0	4/12	—	39	8/14
		4/29	- ,	327	22/29 (2)
15	2	4/7	e – 6	25	6/6
		5/1	1 + 10	220	20/30 (2)
16	2	5/2	1 + 11	128	10/15
17	1	4/1	e – 19	118	18/24
		5/9	h + 0	144	10/13 (1)
18	1	4/4	e – 11	47	5/6
		4/23	i + 1	140	7/10 (1)
		5/7	i + 14	224	8/9 (2)
19	1	4/2	e – 21	81	8/10
		5/6	i + 7	176	7/7 (2)
20	1	4/13	e + 2	34	6/13
		4/26	i + 6	119	12/14 (0)
21	1	3/28	e – 34	65	35/37
	-	4/3	e – 28	132	9/14 (1)
		4/22	e – 9	91	4/6 (0)

TABLE 1. Number of songs and song types recorded for each winter wren during 1984 and 1985 by date (month/day). One hundred forty-four songs used in other analyses were omitted because the male left the area before he was banded, and 10 songs were omitted because of small sample size on the day they were recorded.

^a Number of mates that laid eggs on each male's territory is indicated. ^b Where recording sessions were interrupted by rain, days were combined as indicated along horizontal lines. ^c Phenological stage for the first recording date is indicated as the number of days (n) added to or subtracted from the date at which the first egg was laid in the primary nest (e + n) or (e - n), or the number of days added to the date at which incubation began (i + n), eggs hatched (h + n), ^d Songs within a song type share at least the first 15 consecutively-different syllables. The number of song types that are repetitions of song types from a previous recording session within year are in parentheses, and those that are repetitions from a previous year are given in brackets.



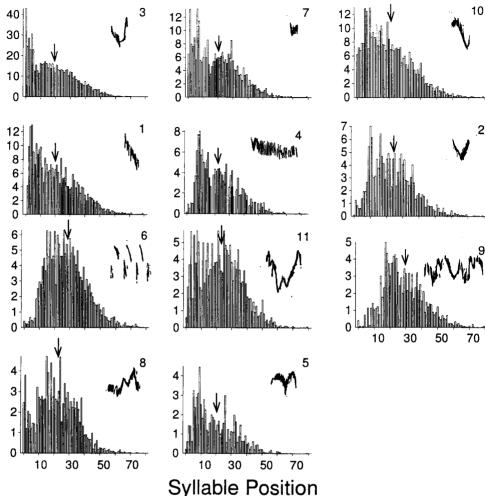


FIGURE 4. Song locations of syllables in each of the 11 syllable types based on shape are arranged left to right and top to bottom from most to least often used. Syllable positions are indicated as "1" for the first syllable of the song, 2 the second syllable in the song, etc. The ordinate indicates the frequency of occurrence of syllables in each location in all songs sampled. Typical syllables of each syllable type are shown on the graph of that syllable type (repetitions are included for type 6).

difference between years in observed patterns of commonness and transition patterns of syllable types is, in effect, based on proportions, nonindependence in song types sampled within years should not bias test results.

The pattern of avoided and favored transitions remained nearly the same between years. The difference measure between the 1984 and 1985 observed matrices, 199,088, was well below the distribution of distance measures between 1984 and 1985 random matrices ($\bar{x} \pm$ SD of random = 199,728 \pm 34.5, n = 200). Clearly, there are structuring "rules." Also, transitional probabilities are not strictly a function of rarity. For example, syllables of type 2 are rarely followed by type 10, the third most common syllable type. They are, however, commonly followed by syllables of type 9, the third rarest syllable type.

STRUCTURING IN TIME

Within-day. Kroodsma (1980) reported 23 and 66 song types sung by two male Winter Wrens. Males of the same species in Japan sang 6–7 song types (Kroodsma and Momose 1991). In this study, the number of song types sung within a season by males recorded on at least two occa-

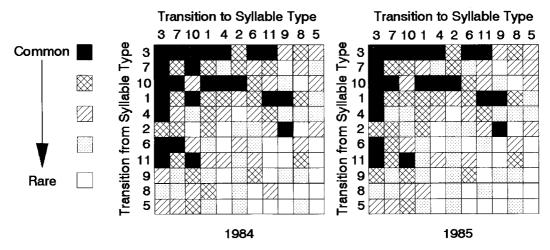


FIGURE 5. A matrix showing the relative frequencies of transition from a syllable of one syllable type to syllables of all other syllable types within all songs that were sampled. Syllable types are arrayed across and down the matrix from most common (syllable type 3; n = 67,621, 41,926 in 1984, 1985) to least common (syllable type 5; n = 6,806, 4,340 in 1984, 1985). Total number of transitions sampled is 250,065 for 1984 and 149,708 for 1985. See Figure 4 for syllable type sampled is 250,065 for 1984 and 149,808.

sions ranged from 8 to 47 with a mean of 21 (from Table 1). Often, consecutive songs within a song type differed in their ending syllables. Frequently these songs alternated, such that if A is one song type, and A¹ the same song type with a different ending, the bird would sing A, A¹, A, A¹, etc. It appeared that there were certain "permissible" breakpoints at which a given song was likely to be modified, and that there were additional permissible breakpoints within the new group of ending syllables. Groups of syllables did not act as rigid blocks, but are broken and joined in a complex fashion (Fig. 1).

Within-season and between-year. If song structures reflect different types of communication, song structure should change through the season as the social context changes. The average number of songs per bout increased through the season (analysis of covariance, df = 24.1 Type I SS = 6,809, P = 0.0002), and the increase in the number of consecutively different syllables included in each song was nearly significant (analysis of covariance, df = 24.1 Type I S = 148, P = 0.0913). There is no apparent relationship with day of the year for song duration, song length (total number of syllables per song) or the percentage of time spent singing (sum of song durations/sum of song durations and intervals). Residuals of a regression of similarity on song length were not correlated with day of the year.

None of the song-variety attributes varied with phenological stage. The difference in absolute song variety was nearly significant, however $F_4 = 2.29$, P = 0.0775), and a comparison of means using LSD indicated that this value was significantly higher during the pre-laying stage than during the incubation or nestling phases (P = 0.05). The rank ordering of the means was pre-laying \geq laying \geq post-fledging \geq incubating \geq nestling. Similarly, Verner (1963) found that singing rates of male Long-billed Marsh Wrens (*Telmatodytes palustris*) declined after laying.

There is little indication that repertoires are fixed. The percentage of song types sung during a recording session that had also been sung during previous sessions (%REP) showed no relationship with the total number of song types that had been sung during the one or two previous recording sessions (BASL) with years combined $(R^2 = 0.0196, F_{(1,18)} = 0.360, P = 0.556)$. %Rep did not vary between years ($\bar{x} = 15.6$ in 1984 and 8.9 in 1985, 2-tailed t test, t = 0.265, df = 18, P = 0.265). Across all samples 10.6% of song types sung in a recording session were types sung during previous recording sessions that year. With this %REP, if the repertoire were fixed and if 10.8 equally-common and randomly ordered song types were sung in the average session (mean over all sessions from Table 1), then the average repertoire would reach an asymptote at 102 song types, and it would take 36 mornings to record 100 song types. Alternatively, the birds could be constantly adding song types to their repertoire as they drop an equivalent number.

DISCUSSION

The song of the Winter Wren varies in a complex fashion through time and space. Songs are built from a large but limited number of syllables. There is some indication that syllables with certain shapes have preferred general locations in each song (early or late). There is no apparent relationship between the commonness of a syllable type and location in the song. Songs are not random assemblages of syllables, nor is the ordering within or among song types random.

Through time, song types and syllables sung by individuals change both within and among seasons. Bout length increases within season, and there is some indication that the number of syllables per song increases as well. After laying the variety of song types sung is lower.

The lack of relationship between the base library of song types and the number of song types from this library used during a recording session indicates that the repertoire is not fixed. Given the amount of variation within song types, it is possible that existing types "evolve" or that new types are introduced either composed de novo from existing syllables and phrases in the repertoire, learned from neighbors, or a combination of the two. In either case, the repertoire of these Winter Wrens is changing continuously as new elements are incorporated. Clearly, however, there are "rules" that underlie the arrangement of syllables from different syllable types whose result is a stable configuration of transition probabilities among syllable types, even as the syllable and song type repertoire changes from year to year. For instance, syllables of type 4 are seldom followed by syllable types 10 or 2 (Fig. 5). Perhaps these syllable types of ascending/descending frequency (see shapes in Fig. 4) just do not sound correct to wrens after syllables of type 4, or perhaps they are mechanically difficult to sing consecutively. In either case, these "rules" should hold at least across the range of the Winter Wren in western North America. The song of the western Winter Wrens differs from that of eastern Winter Wrens in North America (Kroodsma 1980). It should also be difficult to teach young wrens artificial songs with "improper" transitions between syllable types.

This pattern of temporal variation within and among songs presents methodological difficulties in assessing vocal variety. Methods of estimating repertoire size assume that song types occur independently and that the repertoire is fixed. These assumptions are violated if there are uneven probabilities of transition among songs and if new song types are introduced within the period used for estimating repertoire size. The appearance of new song types may be unavoidable, both because recordings over many subsequent days are required to sample a large portion of the repertoire, and because the repertoire is probably not fixed. Further problems are introduced when birds seldom return to previous song types, either within a several-hour period on a single morning, between weeks, or between years (although they do repeat song types, often with flourishes of variation, within song strings).

Other researchers have had difficulty identifying a fixed repertoire. Hailman et al. (1985) described the Black-capped Chickadee (*Parus atricapillus*) as having a "generative" system of calling. The repertoire of "gargle" types may continue to increase after 35 days of two-hour recordings (Ficken et al. 1987, Table 1). Derrickson (1987) reported a repertoire size of 200–300+ for mockingbirds (*Mimus polyglottos*) but indicated that intensive sampling usually produced new, rare song types. Kroodsma and Parker (1977) suggested that Brown Thrashers (*Toxostoma rufum*) may improvise as they sing.

The usual assumption that repertoire size is fixed for an individual (or population) may thus not be justified for very complex songsters. Absolute repertoire size, however, may not be a relevant measure of song complexity.

There are many possible measures of "repertoire size" and vocal variety. Measures chosen to address an hypothesis should be tailored to the relevant structural elements and time frame. For example, if one is interested in measuring the variety of song types presented to a prospective mate during a single morning, the ratio of song types to the number of songs, or a more sophisticated estimate of repertoire size, may be appropriate.

This analysis illustrates that simple measures of vocal variety are not adequate for species with very complex songs. It is likely that additional investigations of song structure based on syllable types will elucidate some of the underlying structure of the songs of complex songsters.

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