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WINTER WREN SINGING BEHAVIOR: A PINNACLE OF SONG COMPLEXITY

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ABSTRACT.—The songs of the Winter Wren in North America are long and complex, but consist of highly organized and repeatable sequences of different song units. Eastern and western populations differ markedly in complexity of song types and overall repertoire size. Two eastern males sang only two song types, while one intensively studied Oregon male sang at least 30 stable song types; temporal and frequency parameters also gave the impression of greater complexity within Oregon songs. At both locations, though, neighboring males sang nearly identical song units or (especially in New York) entire songs, indicating that vocal learning is fundamental to song ontogeny. The complex song of the Winter Wren may be a product of intense sexual selection in a polygynous mating system, but further data on both mating systems and song complexity in different populations are needed before this hypothesis can be critically assessed.

Among songbirds, the typical male song is a vocal display involved in securing the two requisites, an area and a partner, for breeding. Such vocal displays must evolve with other habits, yet the selective forces involved in producing the great diversity of singing behavior among the oscines remain poorly understood. Especially intriguing, of course, are those species where males sing in an extremely elaborate manner.

Near the pinnacle of song complexity lies the Winter Wren (*Troglodytes troglodytes*), a 10–12 g songbird, which probably has "the longest definitely reiterated" song pattern among North American birds (Hartshorne 1973:127). Beyond Hartshorne's (1973) expectations, however, males may have a sizeable repertoire of different song types (Kreutzer 1973). Furthermore, contrary to Armstrong (1963:46), who stated that the song "is probably almost entirely inborn," the nearly identical songs of neighboring males suggest that, as in several other wren species (e.g., Verner 1975), imitation plays a crucial role in song development.

This species is the only wren that occurs outside the New World, and two detailed European studies have revealed a high level of polygyny (Kluijver et al. 1940, Armstrong 1955). Given current understanding of how environmental heterogeneity and productivity affect mating systems (Verner and Willson 1966, Orians 1969), it is likely that breeding habits and mating systems vary geographically, making the Winter Wren an interesting species for the study of how differing regimes affect the evolution of a complex song organization.

In this study, I examined songs of neighboring male Winter Wrens in Maine, New York, and Oregon. My primary objectives were to 1) document exactly how long, complex, and repeatable are the songs of a male from one day to the next, 2) determine the extent to which neighboring males share the same song types, and 3) discuss a striking geographical variability in song complexity which might be related to different breeding biologies.

METHODS

Two males in Oregon (OR-1 and OR-2) and two males in New York (NY-1 and NY-2) were recorded using a Uher M514 microphone, a 60-cm parabolic reflector, and a Uher 4000 Report-L tape recorder at a tape speed of 7.5 ips. Oregon males were studied in McDonald Forest just north of Corvallis, Benton Co.; individuals were color-banded. New York birds were studied on the property of the Mohonk Trust near New Paltz, Ulster Co.; they were not banded, but could be identified easily by location and peculiarities in their song types.

Donald Borror recorded Winter Wrens on Hog Island, Lincoln Co., Maine, during 1953 and 1956 to 1961. Borror used a Magnemite tape recorder, Brush crystal microphone, and 24-inch parabolic reflector; I examined his recording nos. 2040, 2073, 2085, 2087, 2101, 2190, 2850, 2878, 2955, 3466, 4234, 4319, 4748, 4769, 4897, 4802, and 5292 for this analysis. These re-

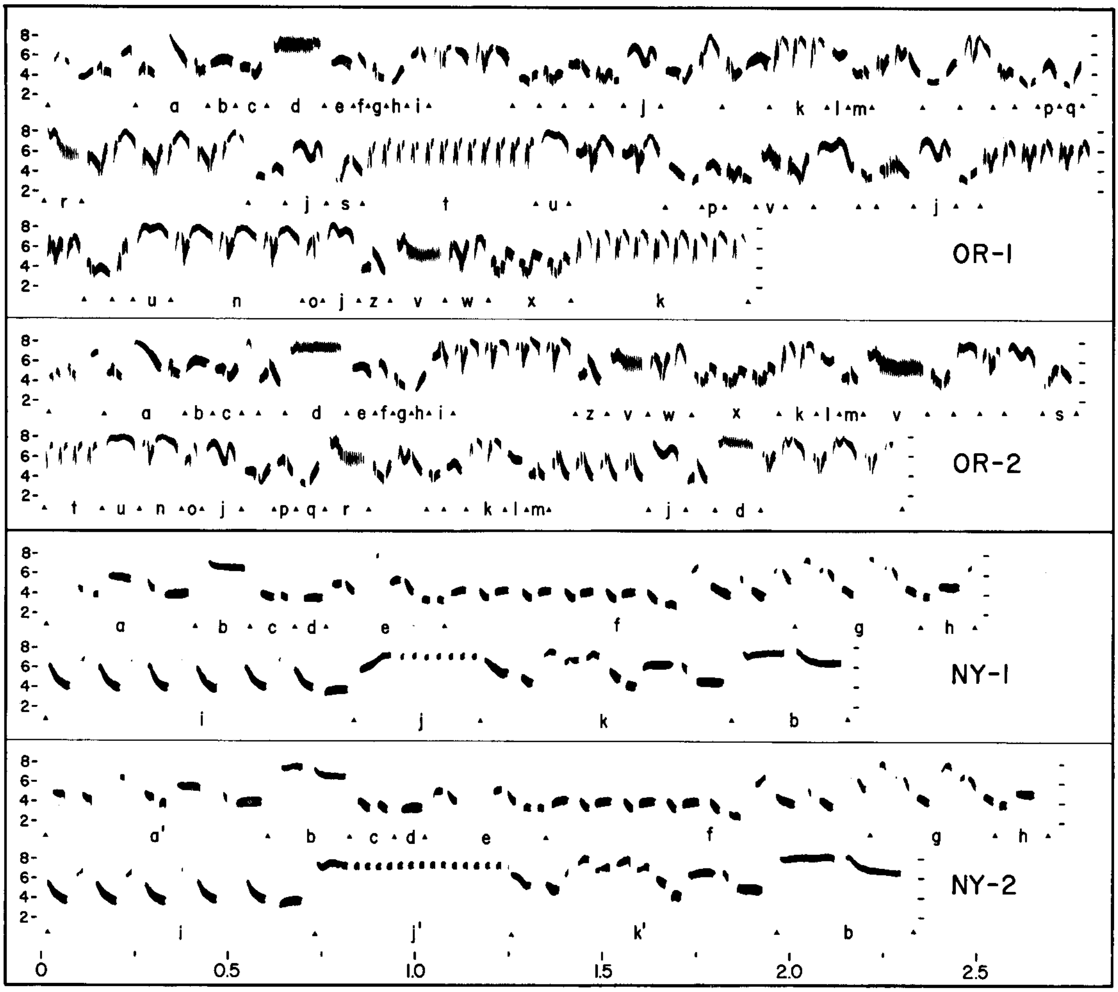

FIGURE 1. Winter Wren songs from Oregon and New York. The abscissa is time (seconds) and the ordinate, kiloHertz. Sample song units, the building blocks from which the song types are constructed, are lettered; these letters indicate similar song units only within, and not between, locations. OR-1: one typical song type from OR-1 (4A of Table 2). OR-2: a typical abbreviated song type from OR-2. Sequences of song units shared with OR-1 and illustrated here are abc, defghi, klm, pqr, stu, unoj, and zvwxk. NY-1: an abbreviated rendition of song type A (Table 1) from NY-1. NY-2: an abbreviated rendition of song type C (Table 1) from NY-2. A comparison of the song types of NY-1 and NY-2 reveals that they are nearly identical.

cordings were made within 400 m of one another, but birds were not marked and the actual identity of individuals in different recordings is unknown.

Analyses of Oregon recordings were initiated on the Kay Sona-Graph at Oregon State University and completed on a continuous spectrum analyzer at Rockefeller University. New York and Maine recordings were analyzed exclusively with the continuous analyzer (see Hopkins et al. 1974).

The song of the Winter Wren is long and intricate, and I attempted to dissect each song into those components that the birds appeared to use as units of recombination in constructing different song types. I wrote song formulas representing the sequences of these building blocks and compared the sequences of those building blocks (hereafter referred to as song units) both within and among males. While a given male was usually consistent in successive renditions of the song units within a given song type, a detailed comparison of the song units in a collection of song types from the same and different males revealed that the structure of some song units appeared to vary continuously (e.g., j of OR-1 and OR-2, Fig. 1). At times, creating song unit categories became necessarily arbitrary, and the limitations of this approach are severe. A more quantitative approach might be advocated (Miller 1979), but in the end there is no information on how the birds categorize these sounds. Other than some minor differences in estimates of song unit repertoire sizes, the basic conclusions of this study would not be altered.

RESULTS

NEW YORK

Of 95 songs recorded and analyzed from NY-1, I found only two basic song types; they were represented by 52 renditions of Type A (see Fig. 1, Table 1) and 38 renditions of Type B (Table 1). Each song type was repeated a number of times (up to 40; successive renditions of a particular song

TABLE 1. Song formulas for song types A and B from New York Winter Wren I (NY-1) and for song themes C and D from NY-2, together with three hybrid song formulas for NY-1 and one hybrid formula for NY-2. Some of the lettered song units are displayed in Figure 1, and the numbers beneath each unit in Types A through D indicate the number of renditions of that particular song type that terminated at the end or during the singing of that song unit. The duration of the median song length is indicated beneath Types A–D.

NY-1, Type A	a	b′	c	d	e	f	g	h	i	j	k	b	c	d	e	f	g	h	i	j	k	b	c	d	e	f	g	h	i	j	k	b
8.8 s								1		1	1	2	1			4		1	2	3	3	28				3					1	1
NY-1, Type B	l	k″	b	c	e	m	g	n	b″	k‴	b	o	b	c	i	b″	k‴	b	o													
9.6 s								1			3	9	2	1		1	1	18	2													
NY-2, Type C	a′	b	c	d	e	f	g	h	i	j′	k′	b	c	i	b″	p	b															
5.2 s						2			5	1	5	60	6	22	3	7	8															
NY-2, Type D	q	k″	b	c	d	e′	f	g	h	i	b																					
5.9 s		1	2	1			2			13	65																					
NY-1, Hybrid BA_1	l	a	b′	c	d	e	f	g	h	i	j	k	b																			
NY-1, Hybrid BA_2	l	k″	b′	c	d	e	f	g	h	i	j	k	b	c	d	e	f															
NY-1, Hybrid AB	a	b′	c	d	e	f	g	h	i	j	k	b′	o	b	c	i	b″	k‴	b	o	(3 renditions)											
NY-2, Hybrid CD	a′	b	c	d	e	f	g	h	i	j′	k′	b	c	i	b″	p	b	c	d	e′	f	g	h	i	b							

type are here called a bout) with remarkable consistency before the second song type was introduced. On 30 April 1974, for example, I recorded six bouts of Type A and five bouts of Type B during a five-hour period. In addition, occasional songs (5 out of 95 songs, or 6%) began with elements of one song type and ended on the elements of the other; they were interspersed among renditions of the two basic song types. Because these songs were not repeated in succession as were the two primary song types, I have classified them as hybrid songs (Table 1).

In the 204 songs recorded and analyzed from NY-2, again only two basic song types were represented (Fig. 1, Table 1). As with NY-1, a song type was repeated many times before the other type was reintroduced. I recorded Type C 119 times in six separate bouts, and Type D 85 times in six bouts; only one song was a hybrid, created by adding a portion of Type D to the end of Type C (Table 1).

For the two males, I classified a total of 25 song units. Sample classifications are illustrated in Figure 1 and "similar" song units in the repertoires of neighboring males are undoubtedly homologous in the sense that they are good imitations or slight improvisations (or miscopies) which occur during the process of vocal learning. Where consistent but relatively minor differences did occur among the song units of New York males, I indicated such variations with "primes" (e.g., a and a′ in Fig. 1 are very similar, but two extra notes in the a′ were consistently present).

Examination of the song formulas for the two males gives the impression of great similarity in the repertoire of song units used by the two males. Ten song units were shared by NY-1 and NY-2 (b, b″, c, d, e, f, g, h, i, k″). Other song units were similar between the males (variants of units a, b, e, j, k), leaving only units l, m, n, and o of NY-1 and units p and q of NY-2 as distinctive units unique to one of the two males.

Not only were song units similar between the two males, but their sequences of use were also similar. Types A and C from NY-1 and NY-2, respectively, differ in only a couple of notes in the a, j, and k song units (Fig. 1), and the sequence b c d e (or e′) f g h i was the major portion of NY-2 Type D as well (Table 1).

In the four hybrid songs of Table 1, the song unit transitions joining segments of the two different song types are l-a, k″-b, b′-o, and b-c, respectively. These song units are the same or very similar to other pairs of

TABLE 2. The number of renditions of each song type and the number of occasions (different occasions were separated by at least 30 min, with other song types occurring during the intervening time) on which I encountered that particular song type. Each of 10 (1–10) introductory phrases was paired with from 3 (A–C, Intro. #5) to 10 (A–J, Intro. #1) different song conclusions.

Introduction	Conclusion	Number of renditions	Number of occasions
1	A	17	3
	B	4	1
	C	3	2
	D	3	2
	E	23	5
	F	1	1
	G	22	4
	H	5	2
	I	1	1
	J	2	1
2	A	24	6
	B	13	4
	C	12	2
3	A	18	3
	B	3	1
	C	1	1
	D	3	2
	E	3	1
	F	1	1
	G	1	1
	H	3	2
4	A	36	4
	B	2	1
	C	6	1
	D	2	1
	E	13	3
5	A	2	1
	B	2	1
	C	1	1
6	A	30	4
	B	2	1
	C	7	3
	D	24	3
	E	1	1
7	A	16	3
	B	1	1
	C	1	1
	D	5	1
	E	1	1
	F	1	1
	G	2	1
	H	1	1
	I	8	2
8	A	40	6
	B	1	1
	C	1	1
	D	1	1
	E	1	1
	F	7	2
	G	1	1
	H	13	2
9	A	41	5
	B	4	1
	C	2	1
	D	1	1
	E	2	1
	F	5	2
	G	2	2
10	A	55	4
	B	6	1
	C	1	1
	D	2	1
	E	2	2
	F	1	1
	G	1	1
	H	1	1

song units (l-k in Type B, with k very similar to unit a, k″-b in Type B, b-o in Type B, and b-c in Types C and D, respectively), which are common transitions within song types. These song unit transitions are therefore natural branching points for two song types to be linked together, for the commonly used sequences of song units remain intact.

The median song lengths of NY-1 and NY-2 differed (see Table 1). Different motivational states may affect song duration, for males on territory early in the season can sing for several minutes continuously, and songs may become shorter during the season as males become more occupied with nesting activities (see also Kreutzer 1973). For example, Type C of NY-2 was shortened considerably over just a six-day period: on 30 April 1974, only 19 of 52 (36.5%) renditions had been terminated at or before the second b song unit, while on 6 May, 46 of 67 (68.7%) had been terminated by that point (Table 1).

HOG ISLAND, MAINE

I analyzed about 200 songs from Borror's Hog Island recordings. Although the individual male being recorded cannot be identified, the data are in general consistent with my New York data.

1) A given song type is repeated with great accuracy from day to day, presumably by the same bird at the same place. From 14 June 1956 to 17 July 1956, Borror recorded at roughly the same location on six separate days; only one basic song type was found in all six recordings.

2) Song repertoires include from one to three song types. The male recorded in 1956 probably had only one song type. Recordings from three days in 1957 all contained one song type as well. Five recordings in 1961 contained two song types, and data from 1959 suggested that an individual might have as many as three song types in his repertoire.

TABLE 3. Data on song programming by OR-1 from 05:30 to 08:30 on mornings of 4 and 5 April 1970. A total of 22 bouts were recorded where variations on 1 of 10 introductory phrases were sung (see also Table 2).

Sequence of introductory types (read down)	No. songs recorded	Estimated total songs*	No. renditions of each song variation									
			A	B	C	D	E	F	G	H	I	J
4 April 1970												
4	6	27	6									
6	27	81	3	15	6	2	1					
3	23	69	15	1	1		3		2	1		
10	10	34	8						1	1		
1	15	39		6								9
8	13	39	11	1			1					
2	13	25	3	10								
5	3	6	2		1							
9	19	52	12	1	1	1	2		2			
10	13	34	12						1			
1	8	23	6		2							
2	5	12	4	1								
5 April 1970												
4	9	39			8		1					
8	27	77	10	12	4				1			
10	15	46	13		1	1						
1	22	54	9	5						1	1	6
6	12	38	6	5			1					
7	13	32	4			5	1	1		1	1	
2	17	49	8	7	2							
4	3	8	3									
9	15	33	12	1	2							
1	7	14		1					3			3

* I counted all songs, but because I recorded only every second or third song, I had to estimate the total number of songs in a given session; the actual number of songs may vary by as much as ±2.

OREGON

From the Oregon males (OR-1 and OR-2), I recorded and analyzed 518 and 178 songs, respectively. Like the New York and Maine males, the Oregon males tended to repeat a given song type several times before switching to another. However, unlike the New York males, the Oregon males had large repertoires of song types, each consisting of many song units. Instead of the 19 and 16 song units that I classified as building blocks of NY-1 and NY-2, respectively, I distinguished 92 and 82 song units that were used by OR-1 and OR-2. As indicated in a typical song type from both OR-1 and OR-2 (Fig. 1), the song units were much briefer than the New York song units: for OR-1 and OR-2, each song type contained an average of 40 and 33 *different* song units respectively, while NY-1 and NY-2 used only 12 and 11.5.

Classifying song types and writing song formulas for such versatile songsters soon became a nightmare. OR-1, for example, had only 10 different introductions of one half second duration, and he tended to sing many songs (up to 80) in succession using one of these introductory phrases. However, as the male proceeded further into what was frequently a 10-s song, an increasingly large number of song variations developed; a given introductory phrase could be followed by three (A–C, Introductory phrase #5 in Table 2) to ten (A–J, Intro. #1) different conclusions. In song 4A of OR-1 (see Fig. 1), for example, the song diverged at roughly 2.0, 2.3, 4.5, and 7.5 s; at these branching points, OR-1 added a different conclusion, thereby creating song types 4B, 4C, 4D, and 4E (see Table 2).

In order to determine how these song types were used during a singing session, I recorded and analyzed every second or third song of OR-1 during the first three hours of singing on the mornings of 4 and 5 April 1970 (Table 3). In a total of about six hours, this male sang 831 songs organized into 22 bouts during which variations on a given introductory phrase were sung. The second bout of each day contained the largest number of songs, 81 and 77 songs, respectively. The median number of songs/bout was 36 ($\bar{x}$ = 38), and a median of three song conclusions/bout were sampled for each introductory phrase.

Since nearly half of the total repertoire of song units for a male occurs in each song type, the large repertoire of song types is created simply by recombination of song units and favored sequences of those song

TABLE 4. Frequency of occurrence of selected song unit transitions in the repertoire of OR-1 and OR-2 song types.

Song unit preceding	Song unit following	OR-1	OR-2
k	end of song	30 (51)*	12 (50)
	l	13 (22)	9 (38)
	vv**	13 (22)	3 (12)
	ww, xx, yy**	3 (5)	0
s	j	14 (64)	7 (54)
	t	7 (32)	4 (31)
	zz**	1 (5)	2 (15)
t	end of song	13 (76)	3 (21)
	u	4 (24)	11 (79)

* Number of occurrences followed by percent of total in parentheses.
** Not illustrated in Figure 1.

units. For example, the last 1.5 s of 5A and 9E (Table 2) consist of the song units between (but not including) i and l of 4A (the OR-1 song displayed in Fig. 1), and the last 3.6 s of 8H (Table 2) consist of the sequence of song units s-t-u through w-x-k in 4A (OR-1, Fig. 1). As with the New York males, some "hybrid" song types were created by linking two longer phrases via a favored song unit transition.

Overall, I recorded 66 different song types from OR-1; 22 of these occurred only once, another 12 occurred only twice, and 32 occurred three or more times in the sample of 518 songs. Many of the less commonly used songs were analogous to the hybrid songs of the New York males, but 30 song types occurred often enough that my sampling (see Table 3 footnote) encountered at least two successive renditions.

The singing of the other Oregon male, OR-2, was equally complex. In 178 songs, I found 23 song types. Eight additional song types, mostly hybrid, were also found: of these, seven occurred only once and one was sung twice. Only eight unique half-second introductions were used in the 178 songs.

A detailed examination of the song units, song formulas, and transition matrices for all song types permitted three conclusions for the two Oregon males: 1) a male used a song unit in relatively few contexts (Table 4), 2) neighboring males shared the same song units (Fig. 1), and 3) neighboring males tended to use the song units in the same sequences (Table 4 and Fig. 1). Of all the song units in the repertoire of the two Oregon males, I classified 80 as shared by both birds; this shared component represented 87% and 98% of the total classified repertoire of OR-1 and OR-2, respectively. While the shared units were extensive, most shared sequences of those song units lasted less than two seconds (representative examples in Fig. 1).

Thus, while neighboring males in New York and Maine shared entire song patterns to a greater degree than did the Oregon males, these Oregon males appeared to stress individual variation by recombination of shorter song units. This greater complexity of song organization in the Oregon males is further illustrated by examination of temporal and frequency characteristics within individual songs (see Fig. 1). The Oregon songs contain more notes/second (median = 36) than do the New York songs (median 16; Mann-Whitney *U*-test, $P < 0.001$); furthermore, frequency modulations dominate the Oregon songs, whereas the New York and Maine songs tend to emphasize rather pure tones.

DISCUSSION

GEOGRAPHICAL VARIATION

The contrast in the song organization between the eastern and western North American populations is extraordinary. This contrast exists not only in the total repertoire size of different song types used by individuals, with the number of patterns in the West at least an order of magnitude greater than in the East, but also at the level of the individual song. Temporal and frequency parameters suggest that the variety within a western song is far greater than that within an eastern song.

In Europe, Kreutzer (1973) found a median of five song types per male; there, too, individual song types were created by recombining the same song units in different sequences, but whether some of these song types were rarely used hybrid songs is not discernible from Kreutzer's data. With respect to frequency and temporal parameters within songs, the songs of wrens in France appeared very similar to those in New York.

Hall-Craggs (unpubl. data) found striking differences in the song structure of *T. t. troglodytes* when compared to several of the island subspecies (*islandicus, borealis, zetlandicus, fridariensis, hebridensis,* and *hirtensis*). Entire repertoires were not recorded for most males, but the variety within songs appeared greater on the island than in the nominate subspecies: in *T. t. troglodytes*, 68% of the repeated units (i.e., syllables) within the song consisted of a single continuous note, while in the island subspecies, 64% consisted of two or more notes.

How can the geographic variation in the complexity of song organization be explained? Several hypotheses that must be considered include: 1) sexual selection (intra-sexual and/or epigamic, e.g., Howard 1974, Kok 1975), 2) sound propagation and territory size in different habitats (Wiley and Richards 1978), 3) the sound milieu and the coevolution of vocal behavior among sympatric species (Brown 1977), 4) the song season and duration of residency on territory (Mulligan 1966), 5) founder effect and/or age of populations (Bitterbaum and Baptista 1979), and perhaps 6) mere chance variation.

Unfortunately, more data on the breeding habits of the many wren subspecies are necessary before any of these hypotheses can be examined critically. European populations of the nominate subspecies are highly polygynous (Kluijver et al. 1940, Armstrong 1955), yet no data on mating systems of North American populations are available. If the complex song of this wren is a product of intense sexual selection in polygynous mating systems, then between-population variation in song complexity should reflect a corresponding variation in mating systems. Data on the song complexity of males in monogamous populations [e.g., the islands of St. Kilda or Shetland in Great Britain (Armstrong 1955)], as well as data on the mating system of western North American populations where songs are complex and repertoire sizes especially large, would be important to test this hypothesis.

In North America males in some western populations tend to have larger song repertoires than those in eastern populations. Good evidence documents this trend in at least five species other than the Winter Wren: House Finch (*Carpodacus mexicanus*; Mundinger 1975, Bitterbaum and Baptista 1979), Song Sparrow (*Melospiza melodia*; Mulligan 1966, Harris and Lemon 1972, Eberhardt and Baptista 1977), Fox Sparrow (*Passerella iliaca*; Martin 1979, pers. comm.), Rufous-sided Towhee (*Pipilo erythrophthalmus*; Kroodsma 1971, Ewert 1978), and the Long-billed Marsh Wren (*Cistothorus palustris*; Verner 1975, Kroodsma and Pickert, unpubl. data). The meadowlarks are a counter-example, though, for Eastern Meadowlarks (*Sturnella magna*) have much larger song type repertoires than do Western Meadowlarks (*S. neglecta*; J. B. Falls, pers. comm.). In the Winter Wren, House Finch, Song Sparrow, Rufous-sided Towhee, and the Long-billed Marsh Wren, eastern and western populations tend to be migratory and sedentary, respectively. As Mulligan (1966) speculated, perhaps the duration of the song season and the time on a territory have important consequences for repertoire size. Until critical parameters of the breeding biology of these species can be examined, though, the full significance of the geographical variation in song complexity and repertoire size cannot be assessed.

COMPLEXITY OF SINGING BEHAVIOR

The complexity of the Winter Wren singing behavior can be viewed at several different levels. For an Oregon male, a song may consist of over 300 notes. Not only are the exact note sequences of one of these song types repeatable from minute to minute and day to day, but a male may sing 30 or more of these highly complex and very stable song patterns. Of the 32 song patterns encountered three or more times in my total sample from OR-1, during each of two three-hour recording periods on successive April mornings, I sampled only 17 types. Thus, a male requires several hours and perhaps a couple of days to present even his more commonly used song types.

At a finer scale, however, if one examines the song units from which the many song types are composed, a male may use roughly 40% (40 of 92 = 43% for OR-1, 33 of 82 = 40% for OR-2) of his total repertoire of song building blocks during the first song. The various favored combinations and permutations of those song units are not exhausted for several hours, though, and it is this overall diversity of combinations that makes the Oregon males appear so proficient and gives the (human) impression of tremendous variety.

At the other extreme, the two New York males, with only two song types apiece, tended to use both within any 10- to 15-minute period, and they used 60 to 80% of their song units during the first song. European birds sing with slightly greater complexity than the New York males but do not rival the complexity of the Oregon males.

A comparison of the Winter Wren song repertoire to that of other species must be made at several levels, including the song-type repertoire size, song-type length, variety within and the contrast between song types, and the sequential organization of song types. Unfortunately, because of technical aspects of analyzing vocalizations, our knowledge of avian vocal behavior is strongest for the relatively simple songsters. The White-crowned Sparrow (*Zonotrichia* *leucophrys*), for example, usually has only one song type per male, and has probably been the subject of more bioacoustic studies than any other species. Many other emberizids also have limited repertoires, and the singing behavior of several of these species is quite well known (see recent review in Martin 1979).

With the advent of continuous spectrum analyzers, the behavior of complex songsters is becoming more accessible; yet, to date, there are relatively few studies in which the overall complexity of described vocal behavior rivals that of the Winter Wren. Among some continuous songsters, the total repertoire of song types may number in the hundreds or even thousands; in the Mockingbird (*Mimus polyglottos*), Wildenthal (1965) estimated a maximum repertoire size of 244 syllable patterns in one Kansas male, while Kroodsma and Parker (1977) found that Brown Thrashers (*Toxostoma rufum*) are capable of singing over 2,000 different song phrases and may even improvise as they sing. A number of impressive songsters also exist among the Sylviinae and Turdinae. The Song Thrush (*Turdus philomelos*; Marler 1959), Mistle Thrush (*Turdus viscivorus*; Isaac and Marler 1963), Blackbird (*Turdus merula*; Hall-Craggs 1972, Thielcke-Poltz and Thielcke 1960, Todt 1970 a, b), and Nightingale (*Luscinia megarhynchos*; Todt 1970c, 1971) may have as many as 100 songs or song phrases in a typical repertoire. The Sedge Warbler (*Acrocephalus schoenobaenus*) sings (on average) 20-s songs of 10 different syllable types chosen from a repertoire of as many as 51 syllable types; syllable sequences are clearly non-random, but predictable and stable sequences of these syllables are used in reconstructing repeatable song patterns (Catchpole 1976). Wrens other than the Winter Wren are also excellent songsters: the Rock Wren (*Salpinctes obsoletus*; Kroodsma 1975), the Long-billed Marsh Wren (Verner 1975), and Short-billed Marsh Wren (*Cistothorus platensis*; Kroodsma and Verner 1978) may all have more than 100 song types per individual; songs are relatively brief (1 to 2 s) and generally occur in non-random sequences.

Among the Mimidae, Turdinae, and Troglodytidae discussed above, songs (or phrases) are relatively discrete, brief, and repeatable from one occasion to the next; sequences of these songs tend to be non-random and probably follow, at the very least, a first order Markov series. Songs of the Sedge Warbler (Sylviinae) are much longer but the sequences of song units comprising the song, while non-random, probably seldom reoccur. What is most remarkable about the singing of the Oregon Winter Wrens, then, is neither the total repertoire size of song units (perhaps up to 100) nor the length of the songs (to 10 s), but rather the sequential organization of these many song units into a large number (over 30) of highly organized and very long repeatable songs. The internal organization of the songs and the occasional "hybrid" songs are probably facilitated by the fact that each of the many song units occurs in relatively few contexts (Table 4). Even if a single song unit occurs in only two contexts, the total number of permutations (or song patterns) that could be produced in a string of 60 such song units is astronomical. Clearly, the impressive performances of the (Oregon) Winter Wren are highly organized. Future data on other complex songsters may reveal that this wren is not exceptional, but for the moment, its singing style places it near the pinnacle of avian singing behavior.

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