

## STEREOTYPY OF SOME PARAMETERS OF RED-WINGED BLACKBIRD SONG

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**ABSTRACT.**—Parameters of Red-winged Blackbird “conc-a-ree” advertising song were examined for stereotypy. The sample consisted of 538 songs of six territorial males recorded in one breeding season. Sonograms were made and parameters were measured. The range of values of the coefficient of variation for the most variable parameter was 1.8 to 23.3% while the range of values for the least variable parameter was 1.7 to 11.1%. Some aspects of Red-winged Blackbird song are probably subject to strong selective pressure favoring stereotypy.

The communicative functions of song have been examined for many bird species. Through the use of playback experiments, song has been found to convey species identity (e.g., Kroodsma 1974, Shiovitz 1975, Boughy and Thompson 1976), individual identity (Emlen 1971, Brooks and Falls 1975), and to indicate territorial and pair bond status (Emlen 1972, Morse 1970).

In species in which song has been shown to convey both individual and species recognition, different aspects of the song are generally involved (Emlen 1972). Species recognition is facilitated by certain features of song common to all members of that species. When song transmits the identity of the singer, however, idiosyncrasy of some aspect of the song(s) is required. Also, for a song to be effective in transmitting individual identity, the variability in a male's repertoire of song types should be low compared to the variability among different males' repertoires (Krebs 1976). This would facilitate discrimination by listeners (e.g., mates, neighbors or potential intruders).

Among passerine species so far studied, considerable range in song stereotypy has been found. Songs of Indigo Buntings (*Passerina cyanea*) and White-crowned Sparrows (*Zonotrichia leucophrys*) are relatively stereotyped as compared with Mockingbird (*Mimus polyglottos*) song, which is highly variable within and among male repertoires (Howard 1974).

Quantitative analysis of song has focussed principally on determining the extent of song stereotypy within and among populations (Marler and Tamura 1962, Lemon 1971, 1974, Kroodsma and Verner 1979). With few exceptions (e.g., Marler and Isaac

1960a, b), however, little has been published on the extent of stereotypy of an individual's song over a long period of time. The purpose of our study was to quantitatively determine the stereotypy of Red-winged Blackbird (*Agelaius phoeniceus*) songs delivered by marked individuals during one breeding season. We did this by measuring several temporal song parameters from sonograms.

### THE SONG

The “conc-a-ree” advertising song of male Red-winged Blackbirds is delivered throughout the breeding season. It typically contains one or more introductory notes followed by a trill, and is generally less than one second long (Fig. 1). Songs of different males vary in number, spacing, and length of introductory notes, trill modulation and trill length. Furthermore, each individual sings several distinct renditions of the “conc-a-ree” that differ in these parameters. Each rendition, however, appears to be highly stereotyped in temporal patterning and frequency.

### MATERIALS AND METHODS

The songs analyzed in this study were recorded during one Red-winged Blackbird breeding season, March through July 1978. We observed six territorial male blackbirds for over 500 hours and tape-recorded over 8,000 songs from them.

Males #1 through #4 were resident in a four-acre maturing field located in Old Field, Suffolk County, Long Island, New York. This area including the spatial relationship of the males' territories has been described by Smith and Reid (1979). Males #5 and #6 were resident on contiguous territories beside a small lake in Bethel, Sullivan County, New York, 120 miles northwest of Old Field.

Long sequences of song deliveries were recorded for each male. Renditions were identified aurally and identifications verified by sonograms. The six males were found to possess repertoires of from two to seven distinct and different renditions of the “conc-a-ree” song (Smith and Reid 1979).

Sonograms were made on a Kay Elemetrics Vibra-

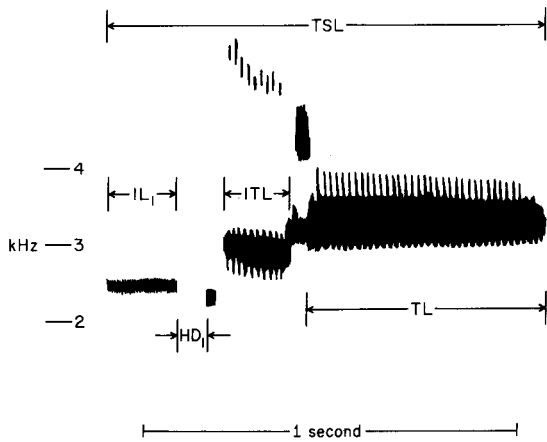


FIGURE 1. The parameters of "conc-a-ree" song of a male Red-winged Blackbird described in the text. IL is the abbreviation for introductory note length; HD for horizontal distance between notes; TL for trill length; TSL for total song length.

lyzer Model 7030A using the F1-1 setting, a 300 Hz filter with the AGC off and the "reproduce circuit" on 80–8,000 Hz. All measurements were made directly from sonograms using the same metric rule and are reported in centimeters (1 cm = .075 s).

Figure 1 shows a typical "conc-a-ree" song and illustrates the parameters we measured. The number of parameters measured varied among renditions due to differences in number of pre-trill notes and limitations in measurement accuracy of some parameters. Where possible we measured the following:

- 1)  $IL_{1...n}$  = introductory note length. Introductory notes are numbered sequentially from 1 to  $n$ , beginning from the left-most (first) introductory note.
- 2)  $HD_{1...n}$  = horizontal distance between notes. These inter-note intervals are numbered sequentially from 1 to  $n$ .
- 3) ITL = introductory trill length. Where a distinct "trill-like" portion of song precedes the final long trill, it was measured from the first distinct black trace to the end of the last distinct mark.
- 4) TL = trill length. This was measured from the beginning of the first distinct black mark to the end of the last distinct black trace of the trill.
- 5) TMR = trill modulation rate. This figure represents the number of distinct black marks over the central two centimeters of the trill.
- 6) TSL = total song length. This was measured from the beginning of the first distinct and routinely present introductory note to the end of the trill portion.

The mean, standard deviation, range and coefficient of variation were calculated for each song parameter measured for each of the 30 renditions.

Because the Kay Vibralyzer has a narrow amplitude response, we made sonograms only when the song recorded was substantially louder than ambient sound level; when sonograms were prepared for measurements, input signals averaged "1–" on the VU meter. This protocol tended to minimize variation in quality of sonograms and reduced measurement errors.

For the Old Field males, sonograms were made of between 18 and 24 deliveries of each rendition for each male, which yielded a total of 479 songs for analysis. Recordings of songs throughout the breeding season composed the sample. The songs of the two Bethel

males were recorded on 2 July. For these males between 5 and 14 deliveries of each rendition, totaling 59 songs, were analyzed.

## RESULTS

Figure 2 presents the renditions comprising each male's repertoire and Table 1 presents their descriptive statistics. The trill portion of the song contains the variable song parameters but some introductory notes also show relatively high variability.

Most of the parameters we measured show a high degree of stereotypy. Of the four to seven parameters measured for each of the 30 renditions, 74% (122/160) have coefficients of variation of 10% or less. Of the 38 with coefficients of variation greater than 10%, 24 are pre-trill and 8 are trill length measurements. The remaining 6 cases with coefficients of variation greater than 10% are total song lengths (TSL), which are not independent of the other measurements.

## DISCUSSION

Values for the short duration parameters are affected to a relatively greater extent by measurement errors (Wiley 1973). This may account for variability of some parameters of the introductory portion of the song. Since 83% of the parameters with coefficients of variation greater than 10% were 1 cm or less in length, a measurement error of just 1 mm could account for these high coefficients of variability. Variability (4.3–16.5%) found for measured parameters of the trill portion of the song is much less likely to suffer from measurement error because of its relatively long duration. Playback experiments have demonstrated that only the trill portion of the "conc-a-ree" song is necessary to elicit full intensity aggressive responses from territorial males (Beletsky et al., in press). Furthermore, playbacks of trills of only half the normal length also elicited full intensity aggressive responses indicating that some aspect other than length is important in this regard. Temporal patterning of introductory notes may be important in coding the identity of the singer or in making other birds more attentive to the subsequent trill portion. Because a male possesses a repertoire of renditions, each of which differs with respect to introductory notes, it seems unlikely that they encode individual identity.

Coefficients of variation ranged from 1.7–23.3% for the measured parameters of Red-winged Blackbird song. Even when only a single parameter is considered, the range of

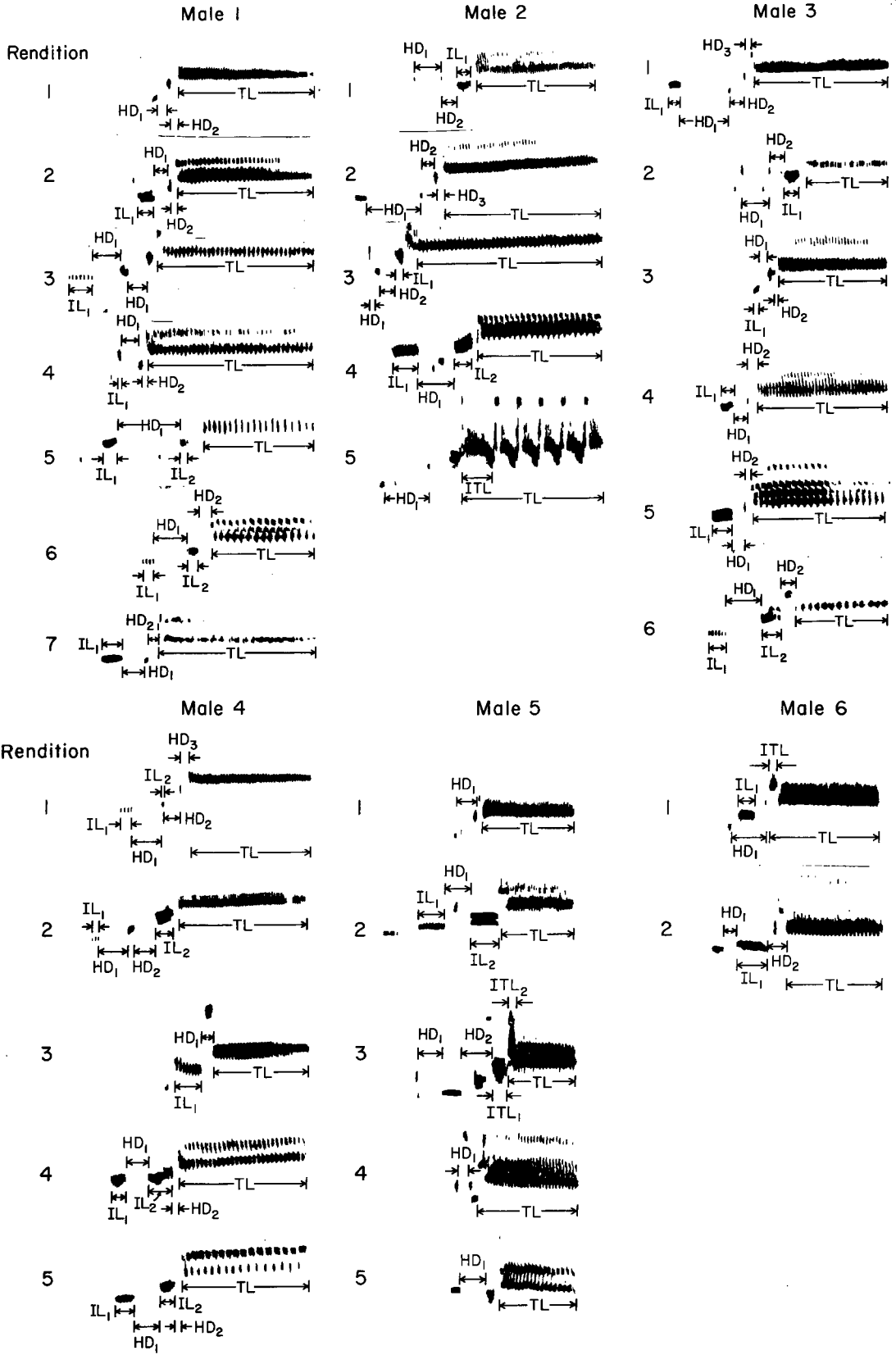


FIGURE 2. The aspects of each rendition measured for each of six males. See Table 1 for measurement values.

TABLE 1. Measurements, in centimeters, for the renditions in Figure 2.

Rendition	Measurement	Male 1 (n = 20)						Male 2 (n = 20)					
		HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>2</sub>	HD <sub>3</sub>	TL	TSL	MR	
1	$\bar{x}$	.6	.5	8.4	10.1	13.0	1.0	1.5	.7	8.4	12.1	14.1	
	sd	.1	.1	.6	.6	.3	.1	.1	.1	1.0	.9	.5	
	cv	16.6	20	7.1	6.0	2.3	10	6.7	14.3	12	7.4	3.5	
	range	5-6	5-6	7.1-9.4	8.8-11.1	12-14	1.0-1.2	1.3-1.6	6-8	6.5-9.9	10.0-13.5	13-15	
2	$\bar{x}$	1.1	.9	.4	7.5	10.3	3.3	.8	.6	8.4	15.0	10.6	
	sd	.1	.1	.1	.7	.6	.2	.1	.1	.6	.6	.5	
	cv	9.0	11.1	25	9.3	5.8	6.1	12.5	16.7	7.1	4.0	4.7	
	range	9-1.4	8-1.0	3-4	6.5-8.9	9.2-11.6	2.9-3.7	6-8	4-6	7.4-9.5	14.0-15.8	10-11	
3	$\bar{x}$	1.8	1.3	1.1	10.8	16.1	.60	.5	1.0	11.4	13.8	7.8	
	sd	.2	.1	.1	.6	.7	.0	.0	1.0	1.0	.9	.4	
	cv	11.1	7.7	9.1	5.5	4.3	16.7	20	10	8.8	6.5	5.1	
	range	1.5-2.2	1.0-1.5	1.0-1.2	9.8-12.0	15.1-17.5	.5-6	.5-6	.9-1.0	9.5-12.6	11.9-15.0	7-8	
4	$\bar{x}$	.4	.1	.3	11.2	13.5	1.3	1.1	2.4	8.0	14.9	5.8	
	sd	.0	.1	.1	.6	.6	1.0	1.0	1.0	.7	.7	.4	
	cv	—	10.0	33.0	5.4	4.4	7.7	9.1	4.2	8.8	4.7	6.9	
	range	4-4	8-1.1	2-4	10.0-12.4	12.4-14.7	1.2-1.3	1.0-1.2	2.2-2.6	6.0-9.4	13.3-15.8	5-6	
5	$\bar{x}$	1.0	1.1	3.6	8.1	15.7	5.1	1.4	9.3	15.5	8.0	8.0	
	sd	.1	.1	.1	.7	.7	.1	.1	2.2	.8	.0	.0	
	cv	10	10	2.8	8.6	4.5	2.0	7.7	23.7	5.2	5.2	8.0	
	range	8-1.1	9-1.1	3.3-3.9	7.0-9.2	14.6-16.7	5.0-5.5	1.3-1.4	8.4-11.4	14.1-17.1	8-8	8-8	
6	$\bar{x}$	1.1	1.2	1.8	.5	6.8	1.1	1.2	1.4	11.4	4.1	4.1	
	sd	.2	.1	.1	.1	1.1	.2	.1	1.1	1.1	.3	.3	
	cv	18.2	8.3	5.6	20	16.2	9.6	7.3	9.6	9.6	7.3	7.3	
	range	.8-1.4	1.1-1.3	1.5-1.9	4-6	5.0-9.0	9.6-13.0	4-5	4-6	4-6	4-5	4-5	

TABLE 1. Continued.

Male 1						
Render-	Mea-	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	MR
tion	sure-				(n = 19)	
	ment				TL	
	$\bar{x}$	1.3	1.3	.5	9.9	4.0
	sd	.1	.1	.1	1.5	.5
	cv	7.2	7.7	20	15.1	12.5
	range	1.1-1.5	1.1-1.5	4-6	5.6-12.4	3-5
					9.0-15.7	

TABLE 1. Continued.

Male 4												
Render-	Mea-	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	HD <sub>3</sub>	TL	TSL	MR	IL <sub>1</sub>	IL <sub>2</sub>	HD <sub>1</sub>	HD <sub>2</sub>
tion	sure-											
	ment											
1	$\bar{x}$	.8	3.2	.8	.3	8.8	14.1	16.8	1.0	.4	1.4	.8
	sd	.1	.1	.1	.1	.7	.7	.4	.1	.1	.1	.1
	cv	12.5	3.1	12.5	33.3	8.0	5.0	2.4	10	25	7.1	12.5
	range	.6-.9	2.9-3.4	.7-.8	.2-.4	7.4-10.1	12.9-15.5	16-17	.8-1.2	.3-.4	1.2-1.6	.7-.9
2	Mea-	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	IL <sub>2</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL
	sure-											
	ment											
3	$\bar{x}$	1.2	1.5	.8	5.6	9.7	13.0	1.1	1.3	1.2	1.2	7.6
	sd	.1	.1	.1	.6	.6	.2	.1	.1	.1	.1	.3
	cv	8.3	6.2	12.5	10.7	6.2	15.4	9.1	7.7	8.3	8.3	3.9
	range	1.1-1.4	1.4-1.5	.7-1.0	4.7-7.0	8.8-11.2	12-13	.9-1.3	1.1-1.3	1.0-1.4	1.1-1.4	7.0-8.2
3	Mea-	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL
	sure-											
	ment											
3	$\bar{x}$	.7	.9	.4	8.4	10.5	1.0	1.8	.7	5.6	8.0	11.1
	sd	.1	.1	.1	.7	.7	.2	.1	.1	.5	.5	.2
	cv	14.3	11.1	25	8.3	6.7	.002	5.5	14.3	8.9	6.3	1.8
	range	.6-.8	.9-1.1	.3-.4	7.0-9.9	9.0-11.8	9-10	1.7-1.9	.6-.8	4.7-6.8	7.2-9.2	11-12

TABLE 1. Continued.

		Male 3						Male 4						
Mea- sure- ment	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	IL <sub>2</sub>	HD <sub>1</sub>	(n = 20) HD <sub>2</sub>	TL	TSL	MR	
														IL <sub>1</sub>
4	$\bar{x}$	.4	.6	.4	7.2	8.9	9.8	1.2	1.7	1.2	.3	9.0	13.4	7.2
	sd	.1	.1	.1	.5	.5	.5	.1	.1	.1	.1	.6	.6	.4
	cv	25	16.7	25	6.9	5.6	5.1	8.3	5.9	8.3	33	6.7	4.5	5.6
	range	.3-.4	.4-.7	.4-.5	6.3-8.1	7.9-9.7	9-11	1.0-1.4	1.5-1.9	.9-1.4	.2-.4	8.0-9.9	12.4-14.5	7-8
5	$\bar{x}$	1.3	.6	.3	7.4	9.8	4.7	1.1	1.2	1.6	.4	7.1	11.4	4.2
	sd	.1	.1	.1	.9	.9	.6	.1	.1	.1	.1	.6	.6	.6
	cv	7.7	16.7	33.3	12.1	9.2	12.8	9.1	8.3	6.3	25	8.5	5.3	14.3
	range	1.2-1.5	.5-.8	.2-.4	5.8-9.4	8.3-11.8	3-5	1.0-1.2	1.1-1.4	1.5-1.7	.3-.5	6.2-8.2	10.5-12.5	3-5
6	$\bar{x}$	1.2	.8	2.2	.5	6.1	11.5	4.4	1.2	1.6	.4	7.1	11.4	4.2
	sd	.1	.1	.1	.1	.8	.8	.5	.1	.1	.1	.6	.6	.6
	cv	8.3	12.5	4.5	20	13.1	7.0	11.4	9.1	8.3	25	8.5	5.3	14.3
	range	1.0-1.4	.6-.9	2.0-2.5	.4-.7	4.3-7.8	9.9-13.0	4-5	1.0-1.4	1.1-1.4	1.5-1.7	.3-.5	6.2-8.2	10.5-12.5

Table 1. Continued.

Measure- ment	Male 5 (n = 5)					Male 6 (n = 11)					
	HD <sub>1</sub>	TL	TSL	MR	MR	IL <sub>1</sub>	HD <sub>1</sub>	ITL	TL	TSL	MR
1	$\bar{x}$ 1.3 sd .04 cv 7.7 range 1.3-1.4	5.5 5.6 10.9 4.9-6.2	10.5 .6 5.8 9.8-11.1	15.8 .5 3.2 15-16	MR	1.0 .2 20 .8-1.4	2.1 .1 8.3 2.0-2.2	.5 .1 20 .5-6	7.1 .5 7.0 6.1-7.8	9.4 .5 5.3 8.3-10.0	—
Measure- ment	IL <sub>2</sub>	IL <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR
2	$\bar{x}$ 1.6 sd .1 cv 6.3 range 1.5-1.8	1.8 .1 5.6 1.6-1.9	4.8 .2 4.2 4.3-5.1	9.9 .2 2.0 9.7-10.3	11.9 .4 3.4 11-12	2.2 .1 4.5 2.0-2.5	1.0 .1 10 .9-1.0	1.2 .1 8.3 1.0-1.5	7.4 .5 6.8 6.7-8.3	11.1 .5 4.5 10.3-12.0	8.4 .5 6.0 8-9
Measure- ment	IL <sub>2</sub>	IL <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR
3	$\bar{x}$ 1.5 sd .1 cv 6.7 range 1.4-1.6	.8 .1 12.5 .8-9	2.1 .2 9.5 1.8-2.3	4.4 .2 4.5 3.9-4.6	10.7 .2 1.9 10.4-10.9	9.0 0.0	9-9	9-9	9-9	9-9	9-9
Measure- ment	IL <sub>2</sub>	IL <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR
4	$\bar{x}$ 4.1 sd .2 cv — range 3.9-4.2	6.9 .4 3.8 6.5-7.3	13.1 .5 5.1 12.5-13.5	9.8 .5 5.1 9-10	MR	—	—	—	—	—	—
Measure- ment	IL <sub>2</sub>	IL <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR
5	$\bar{x}$ 1.7 sd .1 cv 5.9 range 1.5-1.8	5.1 .2 3.9 4.9-5.5	9.1 .2 2.2 8.8-9.4	8.0 0.0	—	—	—	—	—	—	—
Measure- ment	IL <sub>2</sub>	IL <sub>2</sub>	TL	TSL	MR	IL <sub>1</sub>	HD <sub>1</sub>	HD <sub>2</sub>	TL	TSL	MR

variability is large. The parameter that was stereotyped was trill modulation rate (TMR) which had coefficients of variation ranging from 1.7–14.1%. This contrasts with findings on song stereotypy in other species. Chipping Sparrows (*Spizella passerina*) have coefficients of variation of 1.3–1.7% for intervals between the beginnings of successive elements of the song in different individuals (Marler and Isaac 1960a). Coefficients of variation between 8–15% for total song length in Song Sparrows (*Melospiza melodia*; Mulligan 1966) are more comparable to those found for Red-winged Blackbird song (1.8–11%).

The two most stereotyped visual displays reported by Dane et al. (1959) for Common Goldeneyes (*Bucephala clangula*) showed coefficients of variation of 5.1% and 6.1%. Since individual ducks could not be identified, measurements for all individuals were pooled for analysis. These fixed action patterns are characterized by coefficients of variation similar to those for many parameters of Red-winged Blackbird song. Coefficients of variation close to 1% for the duration of the strut display of individual Sage Grouse (*Centrocercus urophasianus*) have been found (Wiley 1973). These highly uniform displays probably represent the limit for stereotypy in birds (Wiley 1973).

The Red-winged Blackbird “conc-a-ree” song consists of two basic components: a variable number of relatively stereotyped introductory notes followed by a trill that varies in duration both within and between renditions. The low coefficients of variation characteristic of many parameters of Red-winged Blackbird song indicate that aspects of displays, both visual and acoustic, are subject to stringent selection pressures which favor extreme stereotypy. Each male retains some variability by being able to select one rendition or another while also showing stereotypy for each delivery. This may satisfy selection pressures favoring both stereotypy and variability.

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