SONG PATTERNING IN THE ROCK WREN

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Nearly all bird species, and especially those living in a particular geographical region, can be identified by their vocalizations. Several characteristics of singing contribute to specific distinctiveness among the Oscines, but two of the most notable differences among species are the number of different song types per individual and the manner of presentation of those song types during a singing performance. Individuals of a relatively few species possess a single song, and will utter that one song type with very little variation throughout the adult life. Common examples include the Chipping Sparrow (*Spizella passerina*), White-crowned Sparrow (*Zonotrichia leucophrys*), and the Common Yellowthroat (*Geothlypis trichas*) (Borror 1959, Marler 1970, Borror 1967). Most species, however, are more versatile, and individuals possess more than one song theme; singing behaviors are extremely varied, and temporal and sequential aspects of theme delivery may aid in specific recognition. Some species are of the AAA ... BBB ... variety, where one song type is repeated several times before another is introduced: silent intervals between songs are usually four to five times the length of the song. Examples include the Song Sparrow (*Melospiza melodia*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Plain Titmouse (*Parus inornatus*) (Mulligan 1966, Kroodsma 1971b, Dixon 1969). At the other extreme are species in which males sing long sequences with no theme repetition. Such singing might be denoted ABCDEFGHI .... Although intersong pauses may be seven to eight times the length of the song (e.g., Large-footed Finch, *Pezopetes capitalis*, Kroodsma, unpubl. data), they are generally briefer, as in the Long-billed Marsh Wren (*Telmatodytes palustris*; Jared Verner, in press). In some of the more "continuous" songsters (e.g., Brown Thrasher, *Toxostoma rufum*), pauses may be so brief that individual songs are practically unidentifiable. Intermediate between these two singing behaviors, i.e., between the AAA ... BBB ... and the ABCD EFGHI ... songsters, lies a third which might be denoted ABCABC ... GHGHI .... Song themes are rarely repeated in succession, but may occur four to five times in a burst of 10

to 15 songs. Such a unique singing behavior occurs in the Rock Wren (*Salpinctes obsoletus*) of western North America, but to my knowledge has not been described in detail for any other species. An analysis of this "intermediate" behavior is presented here in hopes that it may clarify the significance and evolution of other complex avian singing behaviors.

METHODS

During 4–10 July 1970 near the Cabin Lake Guard Station, Deschutes National Forest, Lake County, Oregon, I recorded 1234 songs of one male (Cabin Lake I, or CLI). Approximately 160 km distant, during 16–20 May 1972, on the Malheur National Wildlife Refuge, Harney County, Oregon, 1276 and 2262 songs were recorded from two males (Malheur I and II, or MI and MII, respectively). In addition, smaller samples from four to five other males were recorded at each location. Several Rock Wren selections from the Cornell Library of Natural Sounds were also analyzed. These included Cut 3 from Big Bend National Park, Texas (recorded by R. C. Stein and R. B. Angstadt), Cuts 4 and 5 from Pyramid Lake, Nevada (C. Sutherland), Cut 6 from Yosemite National Park, California (C. Sutherland), and Cut 7 from Badlands National Monument, South Dakota (R. C. Stein).

RESULTS

DESCRIPTION OF SONG

On first encounter, the songs of the Rock Wren strike the ear as a machine-like volley of harsh grating sounds, but, probably because of the austerity of the surroundings, further acquaintance engenders enthusiasm as the songs become "the sprightliest, most musical, and resonant to be heard in the entire West ... keree keree keree, chair chair chair chair, deedle deedle deedle deedle, tur tur tur tur, keree keree keree trrrrrrrrr" (Dawson and Nice, *in* Bent 1948). The song is thus a trill of serially repeated syllables (fig. 1), with a median of 4.18 syllables/sec (n = 203).
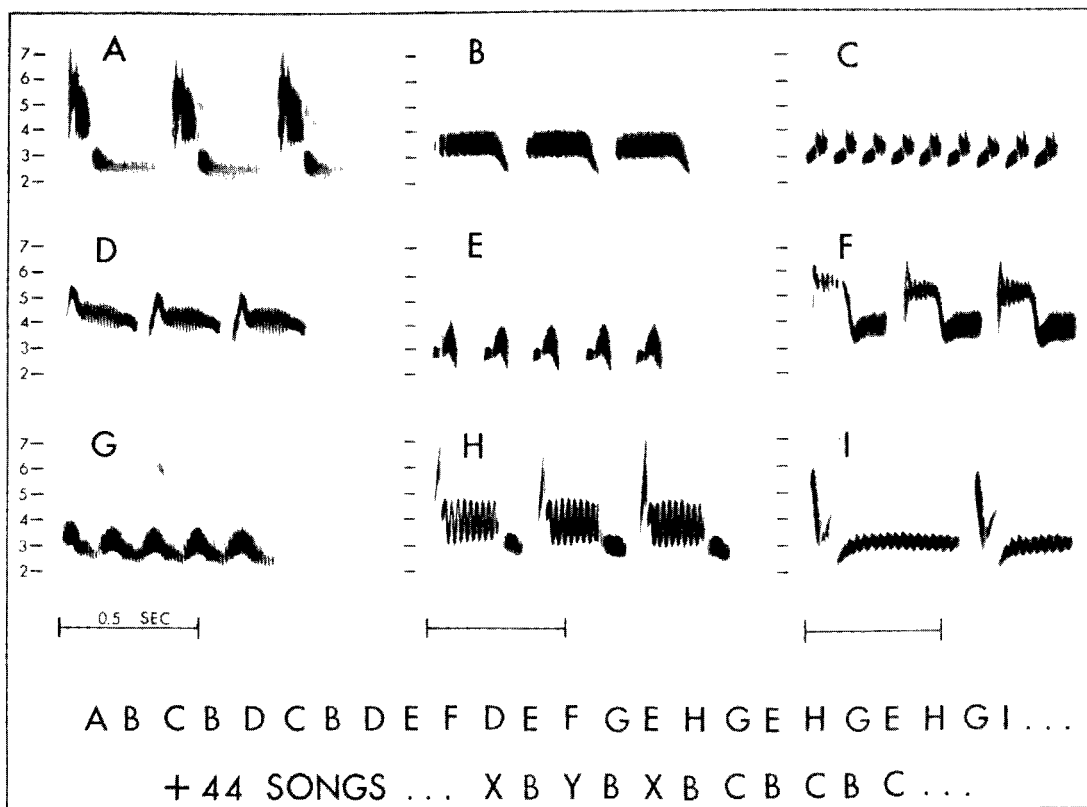
FIGURE 1. Sonagrams of nine song types from the repertoire of MII, with a typical song sequence below. Vertical axis is kHz, horizontal is time. Average song length is 1.4 to 1.5 sec; these sonagrams were shortened for presentation by the omission of one to several syllables.

The duration of the song is approximately 1.5 sec (in Malheur samples, $\bar{x} = 1.43$, n = 3540), while the frequency range averages 3.1 kHz, with an average minimum of 2.7 kHz and maximum of 5.8 kHz (n = 41).

Time intervals between songs are generally two to three times the length of the song: 59% of all intervals were less than 5 sec duration, while 94% were less than 15 sec. For five recordings of 428, 546, 732, 906, and 926 songs from MI and MII, I determined the percent of time actually engaged in singing by dividing the sum of all song lengths by the total duration of the recording. Since intersong intervals greater than 15 sec were usually associated with nonsinging activities such as preening or foraging, these intervals (as well as the previous song) were omitted from the calculation. Considerable differences among the recordings did occur; playback of songs within a male's territory is effective in eliciting song, but the more frequent the playback, the slower the singing rate. It appeared as if the bird sang and then paused, looking for the intruder. Thus, the percent of time actually engaged in song was calculated

to be 19.6 (frequent playback), 23.0 and 23.5 (moderate playback), and 30.0 and 30.6 (no playback).

SIZE OF SONG REPERTOIRE

From CLI, MI, and MII, I recorded 119, 85, and 69 song types, respectively. Successive renditions of a song type were very stable with respect to frequency, syllable structure, and rate of syllable repetition. Two song types in the repertoire of a bird might be very similar in syllable structure and rate of repetition, but consistently different in frequency. The song pairs illustrated in figure 2A differ in frequency by 0.5 to 1.0 kHz. At least two males at Malheur refuge sang the one pair illustrated in figure 2A, and this pair of song types was also found in the repertoire of CLI, 160 km distant. Utterances of song types were very stereotyped, and no gradations between similar song type pairs were found; frequency shifted at times because of a variable tape speed (usually caused by a weak battery), but such variations were readily detectable because all the songs in that portion of the tape were altered similarly.
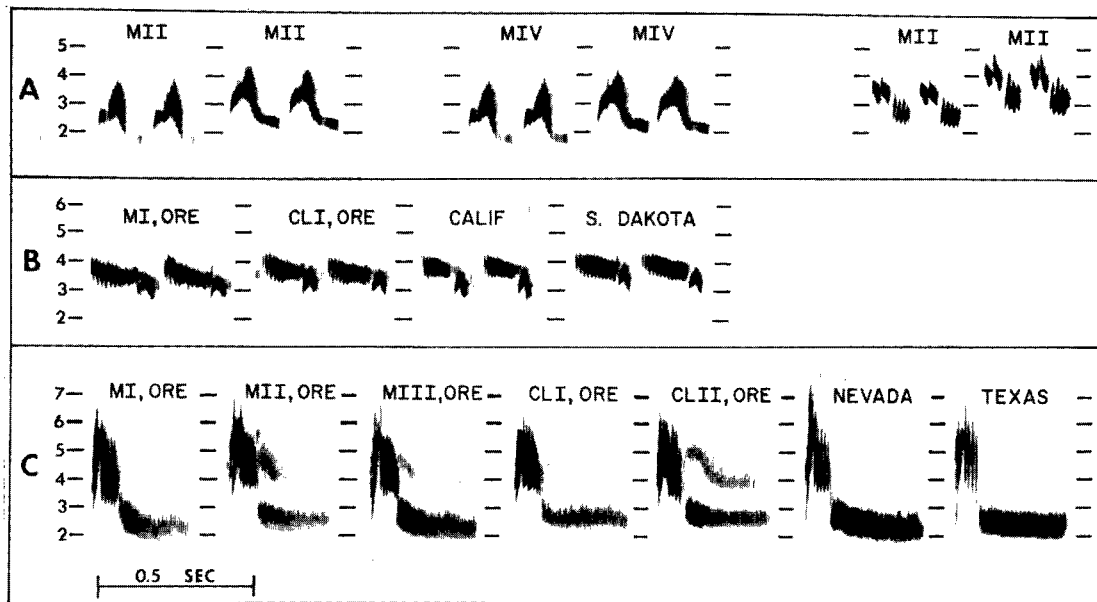
FIGURE 2. A. Similar song type pairs, differing by 0.5 to 1.0 kHz, in the repertoire of MII and MIV. Two syllables of each song type are illustrated. B,C. Widespread occurrence of two syllable types in songs of Rock Wrens.
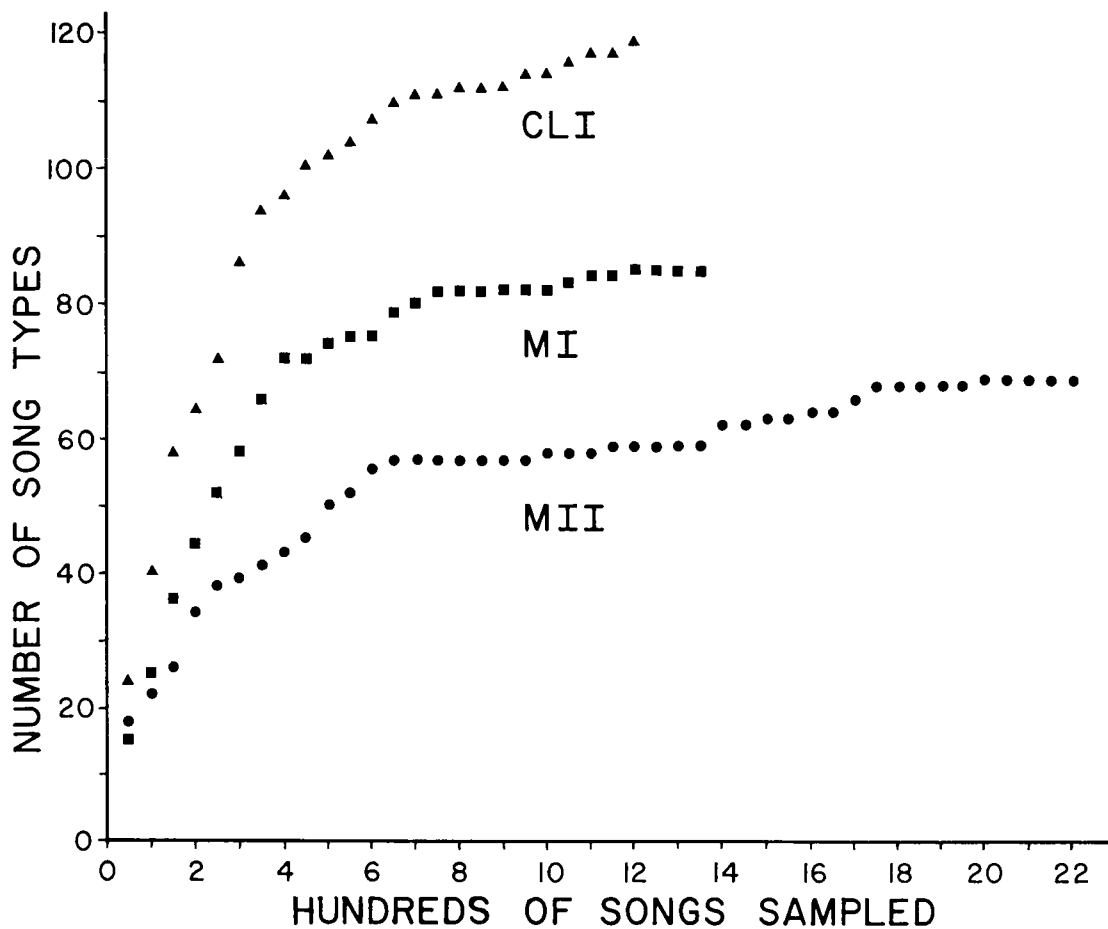

FIGURE 3. The accumulative number of song types appearing in the repertoire of three Rock Wren males at sample intervals of 50 songs.
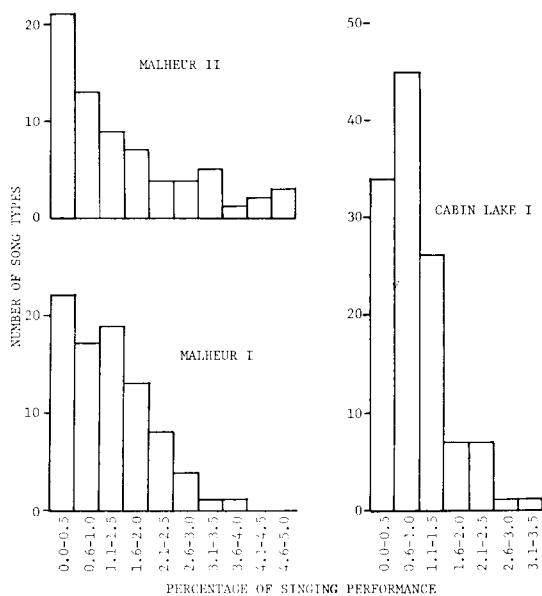
FIGURE 4. Frequency histogram showing the percentage of the total singing performance devoted to different song types in three males. Many song types occurred infrequently, while a few were used quite often.

FIGURE 5. The percent frequency of occurrence for recurrence numbers 0–9 in two lengthy recordings from Malheur II.

When the total number of song types was graphed accumulatively against the total number of songs sampled (fig. 3), the curves were asymptotic to the total repertoire sizes. Recordings of the three birds were collected in sample periods of comparable duration. Thus, the large repertoire size of CLI is not the result of an extended sample period in which the bird was continually adding novel song types. The curves for all three males had begun to level off, although additional sampling would have revealed a few new song types and still larger repertoires than actually recorded. For example, in MII, sampling from songs 1200 to 2262 revealed 10 more song types. A similar percentage increase in new song types to 2262 songs sampled would give CLI a total of 139 song types and MI a total of 99 song types.

Song types were used with differing frequency in a male's singing performance (G-test for goodness-of-fit, $P < 0.001$ in all three males intensively recorded). For example, 50% of the singing performance involved only 24, 26, and 20% of the sampled song repertoire in CLI, MI, and MII, respectively. This favoritism for certain song types is illustrated by the skewed frequency histograms in figure 4.

ORGANIZATION OF SINGING

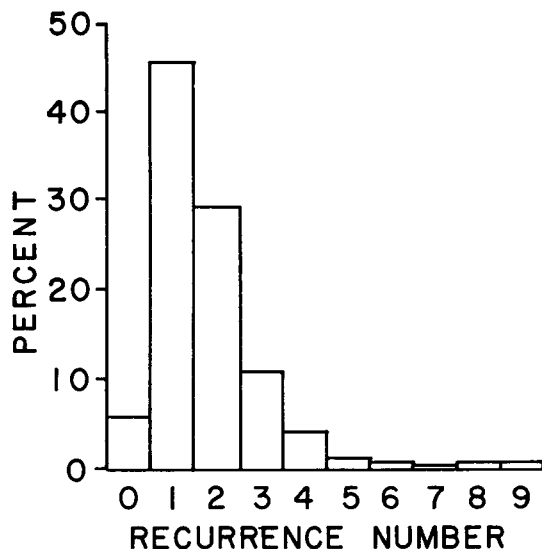If song types are designated by letters, with initial occurrence of each song type italicized, a typical excerpt from a sequence of songs may be depicted ... *A B C B D C B D E F D E F G E H G E H G E H G I* ... (+ 44 songs, approximately 4.5 min) ... *X B Y B X B C B C B C* ... (song types A–I are illustrated in fig. 1). Each letter represents a song of about 1.5-sec duration, while intersong intervals are roughly 3–4 sec.

After a given song type is introduced, the most frequent recurrence numbers (number of songs between successive repetitions of that song type) are one and two (fig. 5), as exemplified by song types B through I in the example above. After a given song type (e.g., B and C above) occurs several times, however, it does not occur again for some time, the actual time lapse varying with the particular song type and the favoritism for song types expressed by the songster. A bout of a given song type may be defined as that period of singing during which recurrence numbers are less than 9. (Nine was selected because it was intermediate between the two modes of distribution of recurrence numbers for frequently used song types. It should also be noted here that bouts of different song types do overlap in time, slightly different from the usual definition for AAA ... BBB ... songsters, where successive repetitions of a given song type would be defined as a bout.) During uninterrupted singing, most bouts occurred over a time period of 30–50 sec and contained one to five occurrences ($\bar{x} = 3.4$, N = 262) of that song type (fig. 6). Recurrence numbers tended to increase in length during a bout, as intervals in the first half of the bout differed significantly in length from those in the
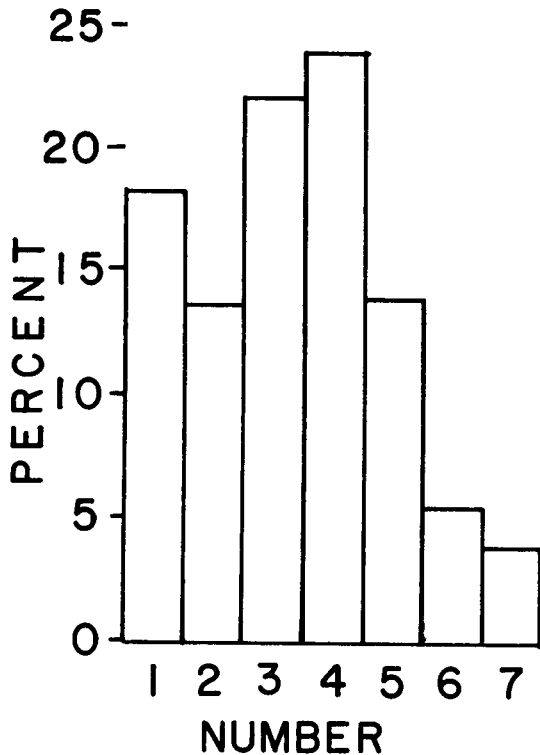
FIGURE 6. The percent frequency of occurrence of the number of repetitions of a song type within a bout. Data from uninterrupted singing performance of MII. Total n = 262.

second half of the bout (Mann–Whitney U-test, N = 46, P < 0.005). The average recurrence number between bouts of a given song type varied considerably and ranged from 64 for the most frequently used song type of MII to values of over 700 for infrequently used songs.

As seen in the above sample sequence of singing as well as in the histogram of recurrence numbers (fig. 5), immediate repetitions (recurrence number = 0) occur infrequently. In 82 of 83 song types where "A-A" sequences occurred, the median intersong interval was greater between like songs than between unlike songs, the difference being statistically significant (1-tailed Mann-Whitney U-test, P < 0.05) in 45 of a possible 62 song types (sample sizes for 20 song types were insufficient for testing at P = 0.05). In fact, average recurrence intervals between successive utterances of a given song type (say A) were 9.3 and 8.0 sec in A-B-A sequences for MI and MII, respectively, compared to 9.6 sec in A-A sequences for both birds. From such a temporal relationship, it is not surprising that the percent of time a bird is engaged in singing is highly correlated with the percent of A-A sequences in the singing performance (corre-

lation coefficient = –0.94, significantly non-zero at P < 0.05; arcsin transformation of percentages used in calculations). The two recordings with no interruptions by song playback contained only 2.1 and 3.1% A-A sequences, probably a more representative example of natural singing in this species.

As suggested by the two bouts of song types B and C in the sample sequence of songs from MII (fig. 1), certain song types are often associated with one another. From a contingency table of song type pairs occurring together, one can calculate the transition probabilities for any sequence, such as A to B, the transition probability being the ratio of the number of times B follows A divided by the total number of occurrences of A in the sample. Figure 7 is a summary of the contingency tables which were prepared for the 30, 21, and 17 most frequently used song types (¼ of the recorded repertoire size) of CLI, MI, and MII. Seqences of MII for only one day (fig. 7, MIIa) are comparable to larger samples (MIIb), indicating that transition probabilities are quite constant from day to day.

Isaac and Marler (1963) found an interesting negative correlation between transition probabilities (the predictability of song type following) and time intervals between syllable type pairs within songs of the Mistle Thrush (Turdus viscivorus). Likewise, Lemon (1971) found in the Red-eyed Vireo (Vireo olivaceus) that certainty of phrase association was correlated inversely with time intervals between phrases, i.e., the shorter the time interval, the more certain the association. Analyses of my data revealed no correlations between predictability of song sequences and temporal patterning.

As in other species, the song of the Rock Wren very likely functions in territorial proclamation and attraction and stimulation of the mate. But perhaps the most striking feature of the singing behavior of the Rock Wren is the large number of different song types at the command of any male. The effect of such a diversity of sounds and the manner of their presentation could be increased stimulation (or reduced attendant habituation) of females or other males. Singing appears to be an exercise in contrasts, and, in fact, a male could achieve maximum contrast with his diverse sound signals (1) if highly associated songs are very different from each other, and (2) if very similar songs (examples in fig. 2A) are dispersed regularly (vs. clumped or even randomly) through time.

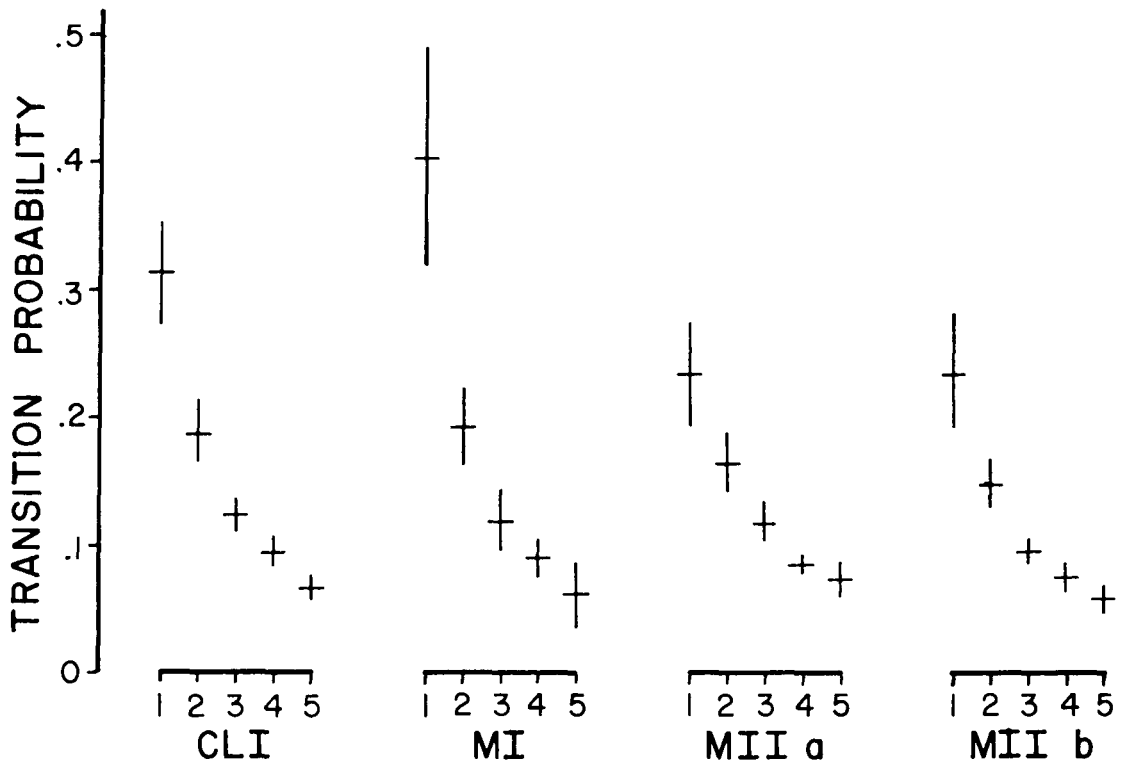In order to test this first contrast hypothesis,

FIGURE 7. Song type transition probabilities for three Rock Wren males. The five largest transition probabilities for the 30, 21, and 17 song types (¼ of total repertoire recorded) used most frequently by CLI, MI, and MII, respectively, are ranked and then averaged (within ranks). The data for CLI are from 2 days, that for MI from 1 day, and that for MII from 1(a) and 3(b) days. Means and their 95% confidence limits are shown.

the 10 most highly associated song type pairs of MII were compared to 22 randomly selected song type pairs. Because of their ease and objectivity of measurement, two measures of contrast in acoustical structure were used, the rate of syllable repetition and the frequency range (maximum minus minimum frequency). The Mann-Whitney U-test revealed a greater contrast between associated song types than between randomly selected song type pairs in both rate of syllable repetition ($P = 0.072$) and frequency range ($P = 0.012$). (Highly associated songs by definition would be used more frequently by the bird than most of the randomly selected song type pairs, but frequency of use of a particular song type was not correlated with the two measures of contrast used here.) Data from MI also supported this conclusion, but sample sizes were smaller and statistical significance could not be demonstrated.

Another indication of the importance of contrast is that bouts of similar song type pairs (fig. 2A) never overlapped and did appear temporally overdispersed; because of the scarcity of such similar song pairs in a

male's repertoire, statistical analysis was not feasible.

GEOGRAPHIC VARIATION

Determining whether songs of different males are of the same song pattern is often arbitrary. However, by using the same criteria throughout a study, an arbitrary classification can yield useful information. I determined the proportion of songs in all recorded samples which were "similar" to the songs in the repertoires of MI, MII, CLI (table 1). Proportions from the local population were then compared to proportions from all other locations lumped together. The data revealed that songs of Malheur birds were more similar to those of MII than were those of other locations (Mann-Whitney U-test, $P = 0.025$), as were songs of Cabin Lake birds more similar to those of CLI than were songs of more distant locations ($P < 0.005$). But the songs of MI appeared rather atypical for Malheur birds, for fewer songs were shared with neighboring males. Thus, even though many song types occurred (or recurred) throughout the geographical range of the species (fig. 2B, C), males at a given location did tend to have

TABLE 1. Percent of songs in sample recordings that were similar to songs in the repertoires of MI, MII, and CLI.

Sample recordings		n, number song types in sample	MI	MII	CLI
Malheur Refuge	MI	85	—	33.2	67.1
Oregon	MII	68	42.6	—	52.9
	MIII	13	46.2	61.5	27.3
	MIV	33	39.4	72.7	57.6
Cabin Lake	CLI	115	49.6	31.3	—
Oregon	CLII	12	33.3	25.0	75.0
	CLIII	26	42.3	34.6	61.4
	CLIV	33	39.4	30.3	57.6
	CLV	8	37.5	12.5	62.5
Cornell Lab	TEXAS	16	25.0	25.0	25.0
Western U.S.	NEVADA	10	30.0	50.0	30.0
	CALIF	4	25.0	00.0	50.0
	S DAKOTA	5	60.0	20.0	40.0

more song types in common with each other than they did with more distant males.

Neighboring males tend to sing shared song types more frequently than they do unshared song types. Of 13 song types recorded from MIII, an immediate neighbor of MII, 8 song types were close matches of song types in the repertoire of MII. These 8 song types were used more frequently by MII than were his other 61 (Mann-Whitney U-test, $P < 0.005$). All attempts to find this same relationship between males with nonadjacent territories failed. In addition, the two neighbors appeared to favor some of the same song type sequences, e.g., the sequence most often recorded from MIII was a sequence of MII with transition probability of 0.27.

Two lines of evidence suggest that the means by which neighboring males come to sing shared song types more frequently than unshared song types is through countersinging of similar song types. (1) Most song types in a male's repertoire are sufficiently distinctive that, while listening to the singing of neighboring males, one can frequently detect matching of song types. (2) Seven playback sessions to MII revealed that songs in the playback tape were frequently matched by the singer. The speaker was placed on the territorial boundary between MII and MIII, and because of insufficient recordings from MIII, songs of MII were used. Natural song sequences were played for several minutes, and each song of MII was recorded on another recorder. Under such conditions, several factors determine the probability of MII matching a song on the playback tape. These include (a) the frequency of occurrence of that song type in the normal singing performance of MII; (b) the transition proba-

bility between the song just sung and the song to be matched on the playback tape; (c) the time elapsed since the last bout of the song type to be copied; and (d) songs of other males within earshot. Of 292 songs presented to MII, 41 were copied; a total of 7.8 songs would be copied by chance considering only (a), the frequency of occurrence of different song types in normal singing. MII did match songs from the playback tape ($P < 0.001$, chi-square test). Little interference from other males (including MIII) was detected, so factor (d) need not be considered. Factors (b) and (c) are crucial, but the limited data prevent any detailed calculation of probability of copying when taking these two factors into account. However, no sequences were absolute, as transition probabilities rarely exceeded 0.5 (see fig. 7), and occurrences of bouts of a given song type were not temporally distributed in a rigidly regular fashion, suggesting that the predicted (expected in chi-square) number of copies would not have been increased significantly. The fact that MII matched the songs from the playback tape suggests that countersinging of similar song types by neighboring males may be an important feature of singing interactions.

DISCUSSION

ORGANIZATION OF SINGING

The cyclic nature of occurrence of different song types in the singing behavior of the Rock Wren is reminiscent of other behavior patterns that tend to occur at regular intervals, a phenomenon which Lorenz (1950) modelled in his "psycho-hydraulic" model of behavior. Inhibitory effects, dependent on performance of a given song type, not totally unlike the

depletion of action specific energy in the Lorenz model, may be used to describe this singing behavior both within and between bouts. Singing of a song type (say A) inhibits immediate repetition of A. This inhibitory effect is dissipated through time at a rate that perhaps increases through the utterance of a second song type, highly contrasted with A. With the frequent recurrence number of one (fig. 5), the time between successive repetitions of a song type is 8–9 sec, a little less than the time between successive repetitions of a given song type if no utterance of a contrasting song type intervenes. Recurrence numbers within a bout increase in length through time, suggesting a gradual buildup of an inhibitory effect (depletion of action specific energy) specific to the song type in question. After several occurrences (usually 3 or 4, fig. 6) of song type A within a short period of time, inhibition builds to a peak, requiring several minutes (5.5 min for most frequently used song type of MII) before sufficient dissipation allows reintroduction of that song type.

Probabilities of song type transition in the Rock Wren are far smaller than in the Long-billed Marsh Wren (Verner, in press), and also smaller than in the Cardinal (*Cardinalis cardinalis*, Lemon and Chatfield 1972). This might have been predicted from the manner in which a Rock Wren presents its song repertoire. The transition probabilities are larger and the sequencing therefore more rigid in the singing of CLI and MI than in the singing of MII. This may relate to the small repertoire size of MII, and it is possible that both repertoire size and sequencing predictability are age dependent. MII sang a great deal and was unpaired, a condition occurring in other wren species more frequently among first year than among older birds (e.g., Bewick's Wren, Kroodsma 1971a).

Selection for such an organization of singing which typically involves immediate variety can best be understood when the singing behaviors and ecologies of other wren species of North America are considered (Kroodsma, unpubl. data). In temperate North America the Winter, House, Canyon, Cactus, Bewick's, and Carolina wrens (*Troglodytes troglodytes, T. aedon, Catherpes mexicanus, Campylorhynchus brunneicapillus, Thryomanes bewickii, Thryothorus ludovicianus*) usually sing the common AAA...BBB... pattern of eventual variety. The Long-billed Marsh Wren sings with immediate variety (ABCDEFG...; Jared Verner, in press) and the Short-billed Marsh Wren (*Cistothorus platensis*) frequently sings a pattern similar to the Rock Wren but also sings the AAA...BBB... pattern (Kroodsma and Verner, unpubl. data). Analysis of 10 years of breeding-bird census data from American Birds reveals that these latter three species which either exclusively or frequently sing patterns of immediate variety are found in habitats of lower avifaunal diversity and occur in greater densities than do the AAA...BBB... singers. Such correlations suggest that frequency and intensity of interaction and perhaps competition for territories and mates among dense wren populations have been selective forces in the evolution of singing patterns of immediate variety.

REPERTOIRE SIZE

Samples of three different males yielded 69, 85, and 119 song (or syllable) types. Few species with such large repertoires have been studied to date. Borror (1964) found 117 "phrase" (= syllable) types in one Gray Catbird (*Dumetella carolinensis*) and 137 phrase types in a Brown Thrasher, and Wildenthal (1965) estimated 244, 213, 66, and 96 syllable types in four different Mockingbirds (*Mimus polyglottos*). Keith Nelson (pers. comm.) described over 160 "recombination units" in Song Thrushes (*Turdus philomelos*), and Jared Verner (in press) found 105–114 song types (N = 6) in typical repertoires of Long-billed Marsh Wrens. Direct comparisons are difficult because of the differing complexity of the unit of measure (syllable, recombination unit, song type); thus, a Rock Wren may have 100 song types (or syllable types), while a Winter Wren may have only 10 song types, but each consisting of many units of complexity comparable to the syllable of a Rock Wren.

Whatever the function of such a repertoire size, the variability from male to male (fig. 3) is often considerable. Males of some species are believed to be capable of learning song throughout life, e.g., the Mockingbird (Laskey 1944), where repertoire size might then be correlated with age. The sensitive period for learning song in the Bewick's Wren ends during its first fall, but young hatched early in the breeding season develop more songs than those hatched later, suggesting that developmental time and the number of songs to which a juvenile is exposed during this period may influence the resultant repertoire size. A small repertoire would indicate a bird hatched late in the summer; such a bird might encounter more difficulty wintering than juveniles several months older (Kroodsma 1972). A greater variety of signals might achieve

greater mate stimulation or be more effective in territorial defense (Nottebohm 1972), and whatever the developmental basis for repertoire sizes, a relationship between variety of signal and reproductive success is worth further study. An attempt to establish a correlation between repertoire size, pairing date, and territory quality was successful in the Mockingbird (Howard 1974); unfortunately, if Mockingbirds do enlarge their song repertoires with age, repertoire size would be age-dependent. Older individuals of most species generally pair earlier and defend better territories, so the cause and effect relationship between large song repertoires and reproductive success remains unsettled.

GEOGRAPHIC VARIATION

Male Rock Wrens at a given location have more song types in common with one another than with more distant birds, but a relatively large number of song types do occur (or recur, as sampling techniques cannot distinguish between the two) throughout the range of the species. The degree to which songs or song elements of distant localities are similar differs considerably among species. In this study 16 of 33 (48.4%) and 11 of 33 songs (33.3%) found in samples outside Oregon were classified as similar to songs from Malheur and Cabin Lake, Oregon, respectively. (Fewer different songs were recorded at Cabin Lake, and this may account in part for the lower percentage overlap.) In the Indigo Bunting (*Passerina cyanea*), over 90% of song elements (the song is more complex and consists of many song elements) occurring in New York and Kentucky samples were also found on a study area in Michigan (Shiovitz and Thompson 1970).

Patterns of geographic variation in song might be related directly to the degree to which the songs or song elements are under genetic control. Lanyon (1960) demonstrated a "remarkable uniformity in vocal characters" among Central American *Myiarchus tyrannulus,* in spite of morphological variation sufficient for some workers to classify one population as a distinct species (*M. brachyurus*); vocal learning among the Tyrannidae has not been described.

Geographical uniformity in vocal characters among flycatchers is perhaps more easily understood than among species where vocal learning has been demonstrated (for examples, see Marler and Mundinger 1971). In such species, considerable divergence in song pattern is often apparent among local populations. However, Indigo Buntings, with little geo-

graphical song variation, demonstrate imitation in song development (Rice and Thompson 1968). Although no ontogenetic study of song with Rock Wrens has been attempted, work with the Bewick's Wren has revealed song learning in young birds (Kroodsma 1974), House Wrens can imitate songs of other species (Kroodsma 1973), two hand-reared Long-billed Marsh Wren males learned songs from tutor tapes only during their first 60 days of life (Kroodsma, in prep.), and evidence from several other species suggests that imitation may play a role in song development of most wrens. But among species where imitation may play an important role in song development, the "biological significance of this geographical similarity in song is not yet fully understood" (Emlen 1971:407).

If song dialects do aid in distinguishing populations, thereby promoting inbreeding and adaptation to local environmental conditions (Nottebohm 1972), perhaps the converse is also true. A lack of marked geographical variation might aid in promoting the overall integrity of the species, and this may be especially valuable among "fugitive" species. If countersinging of similar song types is crucial in male–male interactions, any male which attempts to breed at a locality where his songs are atypical may suffer a disadvantage. Divergence of song patterns between localities might prevent movements, whereas a relative lack of geographical song variation might allow (or be a result of) individual or population movements. Such mobility could be especially critical for survival in climatically unstable habitats or perhaps in seral stages of succession. Songs of the Rock Wren male MI appeared somewhat atypical of the Malheur area, and it is possible that this male had dispersed from some more distant locality. However, a relative lack of geographical variation in songs could be achieved in several ways, and distinguishing between these will require further study of (1) the degree to which individuals of a species produce song through imitation, and (2) the pattern of both individual and population movements in relation to the timing of such imitation.

SUMMARY

The song of the Rock Wren is a 1.4 to 1.5 sec trill of serially repeated syllables; intersong intervals average two to three times this song length. Repertoire sizes of 119, 85, and 69 different song types were recorded in samples of 1234, 1278, and 2262 songs from three Oregon males. A given song type generally occurs three to four times in a burst of 10–15 songs,

the most common recurrence number being 1 or 2. A typical sequence is ... *A B C B D C B D E F D E F G E H G E H G E H G I* ... (+ 44 songs) ... *X B Y B X B C B C B C* .... Populations of wren species singing with immediate variety occur in high densities in habitats of low avifaunal diversity; this suggests that frequency and intensity of interaction and perhaps competition for territories and mates have been selective forces in shaping their singing behaviors.

Recurrence numbers for a given song type tend to increase during a bout and average recurrence numbers between successive bouts of a given song type range from 65 to over 700. Time intervals between immediate repetitions of a song type are greater than those intervals between unlike songs. Song types that are frequently associated during a singing performance differ in syllable length and frequency range more than do randomly selected song type pairs. Not all song types in a male's large repertoire are used with equal frequency; neighboring males tend to countersing with similar song types, and thus songs not shared among neighbors are used less frequently. Song types may occur throughout the geographical range of a species, but males at a given location tend to have more song types in common with each other than they do with more distant males.

ACKNOWLEDGMENTS

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