# SONG VARIATIONS AND SINGING BEHAVIOR IN THE RUFOUS-SIDED TOWHEE, *PIPILO ERYTHROPHTHALMUS OREGONUS*

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The singing behavior and vocalizations of the Rufous-sided Towhee (*Pipilo erythrophthalmus*) have been described recently by several authors (e.g., Davis 1958; Borror 1959; Roberts 1969). All have recognized variation in the song repertoire of both individuals and populations, yet only the variation in songs sampled from the eastern subspecies (Borror 1959) has received extensive sonagraphic analysis. Here I discuss 1) the song variations observed in the repertoires of four neighboring males of the race *P. e. oregonus*, 2) the similarities of variations among these birds, and 3) the use of variations in the singing behavior of the individual.

## METHODS

Four males defending adjacent territories were mist-netted, color-banded, and released during March and April 1970 at the William L. Finley National Wildlife Refuge in Benton County, Oregon. During April and May, when these males were in full song, I recorded their "primary songs" (Lister 1953). Attempting to obtain their entire repertoire, I recorded the songs of each male during the first hours of intense singing on at least five mornings. In addition, to assess the song variations in the population, 43 recordings were made from other males within a 2-km radius of the core study area. No significant ecological barriers which could have restricted dispersal and gene flow existed within this sampling area.

Recordings were made with a Uher 4000 Report-L tape recorder using a MD405S Cardioid microphone at a tape speed of 7.5 ips. Sonagraphic analysis was conducted on a Kay 6061A Sonagraph, using the wide-band filter. The terminology used in this report follows that of Mulligan (1966).

## RESULTS AND DISCUSSION

### SONG VARIATION IN INDIVIDUALS

Most towhee songs examined in this investigation consisted of a short introductory phrase followed by a trill of serially repeated syllables (fig. 1). The introductory phrase in some songs was lacking (fig. 2, D10), and in others was only a slightly modified trill syllable (fig. 2, A7, D7, A10). Mean song length was 0.83 sec ($n = 100$; range = 0.49–1.05 sec; SD = 0.12 sec); the mean length of the introductory phrase was only 0.06 sec, or 7.2 per cent of the total song length. To the human ear this introductory phrase was often inaudible and the song appeared to consist of a trill alone.

Each sonagram in figure 2 represents a song type, i.e., one of the distinctive songs repeated in a consistent manner in the repertoire of an individual. The male towhees sang a given song type at the rate of 8–15 songs per min for up to 15 min; at times, however, especially during early morning, males alternated two song types, singing first one and then the other in sequence for several minutes at a time. Regardless of the pattern of singing behavior, in successive renditions of a song type the structure of the introductory phrase and the trill syllables were unaltered; only the number of syllables in the trill varied. For example, in 30 renditions of song type D5, the number of syllables in the trill varied from 37 to 55 ($\bar{x} = 46.6$, SD = 4.0). Varying the number of syllables in the trill does introduce a source of variation into the singing behavior; I consider this variation within a song type. Further variation by inclusion or exclusion of a "preliminary note" (Roberts 1969:259) before the song was not observed in the many songs heard in the study area or in the 650 songs recorded and analyzed.

Using these criteria, Birds B and D had a repertoire of seven song types, Bird C, eight, and Bird A, nine (fig. 2). Three other males studied less intensively used four, five, and six song types. While some song types were readily distinguishable in the field, others were less distinctive, and required sonagraphic analysis to determine their occurrence in the repertoire. For example, song types 1 and 10 of Bird C were very similar, yet consistently different introductory phrases and slightly different syllable structure in the trill separated them as two distinct song types.

If some song types were sung only very infrequently, as appears to be the case in Song Sparrows (*Melospiza melodia*) near San Francisco (Mulligan 1966), then each male could have additional song types which were not recorded in this study. For example, in 30 recordings for Bird A, a frequency of occur-



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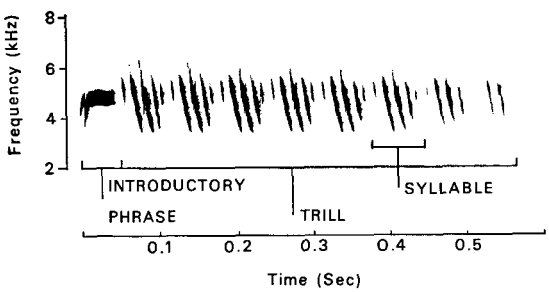


FIGURE 1. Components of a typical Rufous-sided Towhee song recorded at the Finley Refuge. This is song type B8 of figure 2. Vertical axis is frequency, ranging from 3.0 to 8.0 kHz; horizontal axis indicates time, each division representing 0.1 sec.

rence for the nine song types, ranked from most to least frequent, was 5-4-4-4-2-2-2-2-1; all song types except number 5 (fig. 2) were repeated at least once. In Birds B, C, and D all song types were recorded at least twice, and usually three to five times each. Increasing the sample size might have added extra song types, but the potential for variation in individual song repertoires is evident in this sample. Further, if seasonal variation exists in the utilization of different song types (see Davis 1958; Roberts 1969), even greater individual variation could exist.

The variations found within song repertoires of western birds differ from the variations found in eastern birds. Song types of western races generally appear to be simpler than those of eastern races, for they involve less elaborate introductions and often simpler, buzz-like trills. Although his sampling technique did not involve intensive examination of song repertoires in individuals, Borror (1959) found eight song types in one Florida bird. He discerned only three trill types, though; the larger number of song types were derived from differences in the introductory phrases. This form of variation did not occur in the Oregon towhees I studied. The rates of syllable repetition in the trill also vary geographically. In eastern races Borror (1959) found a range of 5–35 syllables/sec; the range I encountered in this study was 6.8–144.7 syllables/sec ($n = 74$; mean = 41.3, md. = 28.8). Most syllable rates (56 per cent) lay between 7 and 35 syllables/sec, the range found in eastern races. Only six were greater than 80, but five of these six were greater than 130 syllables/sec, thus giving the skewed distribution evident from the large difference between the mean and median values.

In this study, intensive tape recording of several individuals followed by spectrographic analysis has suggested that each towhee male may utilize a considerably larger variety of song types than previously reported. In other studies the sampling procedures and analytic methods varied according to the author's objectives. Marler and Isaac (1960:281) mentioned that one individual in Chihuahua, Mexico, used "five basic song types among 24 songs," the types presumably classified by syllable structure in the trills; Bent (1968:587) reported that in 260 songs, an individual male (*P. e. montanus*) sang six "variations" (definition unclear). Borror (1959) found three trill types in one Florida bird (see above), but more recently reported (pers. comm.) two individuals from Ohio with nine and eight trill types (22 and 19 song types, respectively, due to variable introductory patterns). This number of trill variations is identical to the number found in Birds A and C of this study. While studying the towhee on the Hastings Reservation near Jamesburg, California, Davis (1958: 315) recognized by ear "five basic types of song in the repertoire of most individuals." He often heard songs intermediate to those five types, suggesting perhaps greater variation in individual repertoires. Roberts (1969) used spectrographic analysis to examine the same subspecies discussed in this paper, and found that a single captive male sang four types of trills, each recognizable by the rate of syllable repetition. Listening to wild males indicated to her that the trills of individual Oregon towhees were "of only a few readily distinguishable rates." My observations indicate that the song repertoire of noncaptive individual towhee males may be more complex, containing as many as nine song types. Restraining a bird in captivity may simplify its singing behavior, but on the other hand, some wild males may also have a relatively limited song repertoire. One male for which I obtained 22 recordings

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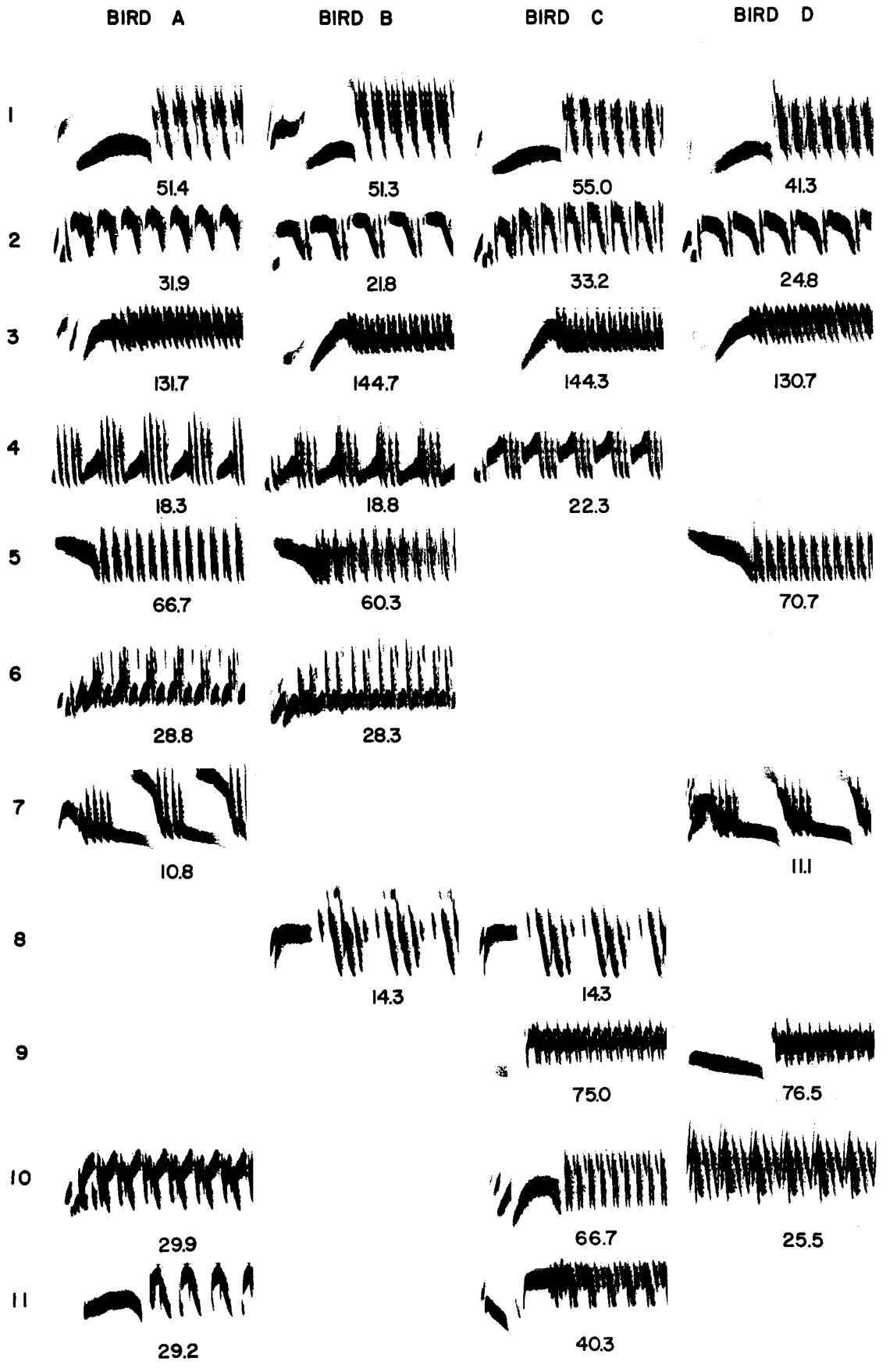
FIGURE 2. Sonagrams of songs of the four male Rufous-sided Towhees with adjacent territories. The columns are song repertoires for individuals; rows contain similar song types. The lower two rows contain those five song types which were similar to none of the other 26 song types. The rows are numbered, and, except for the last two rows, "similar" song types are therefore numbered identically. In the text, a sonagram is referenced by column, or bird (A, B, C, or D), and by row or songtype (1–11); e.g., song type 5 of Bird D is "D5." The numbers below each sonagram indicate the average rate of syllable repetition in the trill. Since a trill consists of many identical syllables, only the introductory phrase and a few syllables (a total of 0.23 sec) are illustrated in each sonagram. The vertical axis is frequency, which ranges from 2.5 to 8.5 kHz.


BIRD A
BIRD B
BIRD C
BIRD D
1
51.4
51.3
55.0
41.3
2
31.9
21.8
33.2
24.8
3
131.7
144.7
144.3
130.7
4
18.3
18.8
22.3
5
66.7
60.3
70.7
6
28.8
28.3
7
10.8
11.1
8
14.3
14.3
9
75.0
76.5
10
29.9
66.7
25.5
11
29.2
40.3

did sing only four song types. Thus, the size of the song repertoire may vary considerably from bird to bird. However, classifying the song types of larger repertoires into classes of several rates of syllable repetition is an oversimplification probably resulting from the relative insensitivity of the human ear.

## SONG VARIATIONS BETWEEN INDIVIDUALS

In addition to these relatively large individual song repertoires, it appears that there may be local or dialect patterns of variation in towhee songs. Of the songs recorded from the four intensively studied males, most (26 of 31) song types of these individuals were "similar" to song types of at least one of the other males (fig. 2). Degree of "similarity" is admittedly at times somewhat difficult to establish, and is a problem encountered when attempting to delineate any continuum into meaningful but nevertheless artificial categories. In the present situation, some song types of different males (e.g., B8 and C8; A3, B3, C3, and D3; A5, B5, and D5) are virtually identical to one another: both the introductory phrases and the syllables in the trill possess identical structure in these song types. With B8 and C8 the rates of syllable repetition are especially convincing. Here there is little problem in classifying the song types as "similar," but other song types are not so readily categorized. Syllable structure may be identical but introductory phrases may differ (e.g., A7 and D7), or both the introductory phrase and the syllable structure might differ slightly (e.g., A6 and B6). The rates of syllable repetition in these two examples reinforce their classification. Because the trill comprised approximately 93 per cent of the total song length, I classified similar song types largely by syllable structure; introductory phrases were used only secondarily. For example, the most heterogeneous grouping of similar song types in figure 2 is that of A2, B2, C2, and D2. The similarities are most obvious in the introductory phrases of A2, C2, and D2 and in the syllable structure of B2 and D2. By syllable structure alone, A11 should be included in this group, for its syllable structure is similar to that of A2; however, the introductory phrase of A2, and not of A11, is similar to that of C2 and D2. Hence, A11 is not included in this grouping. To indicate further problems in classification, the syllable structure of A2 and A11 (as well as of C1 and C10) is so similar that, if they had not been in the repertoire of the same bird, I perhaps would have classified them as "similar."

The similarities among these 31 song types are more evident after examination of the song types from neighboring males and more distant males. Song types in repertoires of males defending adjacent territories are more similar to each other than they are to song types of more distant birds, for upon leaving the core study area, I recorded progressively fewer song types which were similar to those used by the four intensively studied males. Of 11 song types sampled among near neighboring males, 7 (63.5 per cent) were similar, while for distant males, only 3 (10.7 per cent) of 32 song types sampled were similar. I found song types similar to A11, C10, and C11 (three of the five song types not shared by a second bird among the four) in three males neighboring the core study area; this gives further evidence of the similarity of song types occurring in repertoires of adjacent males. These data then suggest a continuous but relatively rapid change in song structure over short distances.

Songs of a species may vary in different localities, with birds of each community all tending to sing similar song types (see e.g., Nottebohm 1969). The existence of dialects in a species is often recognized by recording and analyzing the songs in two such communities. Since juvenile males learn the local song types at the locality where they eventually breed, dialects are perpetuated.

Although I have no direct evidence of song learning in the Rufous-sided Towhee, the similarity of song types among individuals in one locality and the dissimilarities observed over short distances suggest that juvenile male towhees do learn their primary songs from adult towhees. No dispersal data are available for juvenile towhees, but judging from investigations of other passerines, I do not believe 1–2 km to be an unreasonable distance for a young male to wander prior to establishing a territory. If this is true, then the observed distribution of song types must be due to learning in juvenile males.

In perpetuating a dialect system, an adult male must breed in the same locality yearly; with a rapid turnover of song types over distance, even a shift in territory boundaries by two adults could reduce the similarity of song types at that locality. However, site tenacity seems to exist in all migratory and resident subspecies of the Rufous-sided Towhee. Cooke (1942) cited longevity records of eight towhees in different parts of the country, including such extremes of the breeding range as Massachusetts, North Carolina, California, and British Columbia. Each of the eight birds was recaptured at least once at the original banding

site; one individual in New York was recaptured in five successive years. In a Washington study many individuals remained in the same area throughout the year: of 29 banded and recaptured individuals, all were retaken in the locality where initially banded (Bent 1968). Bent also reported that two banded pairs were observed near Portland, Oregon, over at least a one-year period. I observed Bird D on his territory during January 1971, and playback of the *meow* call note (Roberts 1969) elicited an aggressive response. Thus, the towhees in Oregon appear to remain on and defend their territories during the winter.

## SINGING BEHAVIOR

In those avian species with complex dialect systems where individuals possess several song types (e.g., the Chaffinch, *Fringilla coelebs*, Thorpe 1958; the Bewick's Wren, *Thryomanes bewickii*, pers. observ.), neighboring males tend to countersing with similar song types. Spectrographic analysis of the songs given by towhee males during periods of countersinging clearly demonstrates that the birds recognized the various songs and responded to each other with similar song types. For example, during one period of intense countersinging along a territory boundary in which Birds B and D were 10 m apart, each alternated song types 2 and 3. The probability of two males alternating the same two song types by chance at a given time is easily calculated. In this case the repertoire of song types for both Bird B and D is seven; four song types are shared by the two birds. Assuming all song types are used with equal frequency, the probability of one bird alternating two given song types is $2/7 \times 1/6$; four shared song types, taking two at a time, may be arranged in six combinations. Thus, the probability of the observed event occurring by chance alone is $6 \times (2/7 \times 1/6)^2 = 0.014$.

In other instances, all four males sang similar song types simultaneously. With only three song types of a large repertoire shared by all four birds, the probability of such community singing behavior occurring by chance at a given time is again rather remote. When all four birds are singing (usually only during the first one or two hours of morning activity), countersinging of song type 1, 2, or 3 is to be expected by chance $3 \times 1/9 \times 1/7 \times 1/8 \times 1/7 = 0.001$, or 0.1 per cent of total singing time. Even when each bird is alternating two song types, the probability that one of the two is the same in all four birds is still quite small: $P = 3 \times 2/9 \times 2/7 \times 2/8 \times 2/7 =$ 0.014. This event will be expected to occur, at the most, only 1.4 per cent of total singing time. Nonetheless, on 10 May, during a 1-hr observation period when each male sang only five or six song types, countersinging of the same song type by all four males occurred twice (types 2 and 3), for a total period of approximately 10 min. During this same 1-hr period, Birds B, C, and D countersang song type 1 for about 10 min; since Bird A possessed a territory along a fence row and only the end of that territory adjoined those of the others, he was often too distant to be involved.

TABLE 1. Frequency of occurrence of combinations of two song types used in alternation by four male Rufous-sided Towhees.

| | Song type combination | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Bird | 1–4 | 1–9 | 2–3 | 2–7 | 3–6 | 3–8 | 5–7 | 8–10 | Σ |
| A | | | | 2 | 1 | | | | 3 |
| B | 2 | | 1 | | | 1 | | | 4 |
| C | 4 | | | | | 4 | | 1 | 9 |
| D | | 2 | 5 | | | | 2 | | 9 |
| Σ | 6 | 2 | 6 | 2 | 1 | 5 | 2 | 1 | 25 |

Literature reports of the coordination of singing behavior have been somewhat contradictory. Considering the dissimilarities of song types over a short distance, it is not surprising that many authors have emphasized the great variability rather than the similarity of songs which occurs from bird to bird. However, Bent (1968) did report that individual towhee males tended to answer each other with the same song. Roberts (1969) found that by song playback she could influence the song type used by a singing male, but Davis (1958:316) stated that "the particular type of trill used by a singing male does not depend on the trill types used by other males within earshot." The evidence presented here indicates that towhees do recognize and respond to the song types of neighboring individuals; the frequency of occurrence and duration of these community behaviors is far greater than would be expected by chance alone.

The use of two song types in alternation is another interesting feature of the singing behavior. In 25 observations of this behavior, only 8 of 65 possible combinations of two song types were used in alternation (table 1). A larger sample would undoubtedly have revealed others, but the data do suggest that each bird used relatively few combinations. This is especially evident with Birds C and D. Bird A was observed countersinging with Birds B, C, and D only very infrequently, and it is

interesting that neither of the two combinations used by him was observed in the other three males. Further, the three combinations used by Bird B were those same three observed most frequently in the singing behavior of Birds C and D. This constitutes further evidence of the existence of a community singing behavior.

The Rufous-sided Towhee breeds over an extensive range, has many designated subspecies, and possesses an interesting evolutionary history (Sibley and West 1959; Sibley and Sibley 1964). With this in mind, one might expect differences in singing behavior in different portions of the breeding range. As in the Song Sparrow (Mulligan 1966), repertoire size for individuals may certainly vary for races living under different climatic conditions. The song variations described by Borror (1959) in the eastern subspecies are certainly different from those occurring in the relatively simple songs of most western subspecies. Furthermore, Borror (pers. comm.) finds no evidence of local dialects in eastern races. The Rufous-sided Towhee is therefore an ideal species in which to examine the geographical variation in songs and the extent of dialect systems over an extensive range of differing ecologies.

## SUMMARY

Intensive tape recording and sonagraphic analysis of songs of four Rufous-sided Towhee males defending adjacent territories indicate that a male may have as many as nine song types in his repertoire. Marked similarities in song types occur among neighboring birds, but analysis of songs of more distant males reveals a relatively rapid change in song structure over distance. Songs used by the four adjacent males during countersinging indicate that individuals are capable of responding to song types with similar types. These song variations and the singing behaviors of the Rufous-sided Towhee in Oregon are typical of those passerine species in which young males learn their songs and perpetuate local or dialect patterns.

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