

SONGS OF THE RUFOUS-SIDED TOWHEE

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The Rufous-sided Towhee (*Pipilo erythrophthalmus*) is one of the more versatile singers among the passerines; each bird has a repertoire of several different songs, and the songs of different birds are often different. I described some of the song variation in this species in an earlier paper (Borrer 1959); the present paper is an expansion of the earlier one, based on considerably more material, and with more concern for the geographic variation in the songs.

This paper is based on a study of 773 recordings (believed to represent 492 birds), with over 10,000 songs; the recordings are from 19 states of the United States and one Canadian province, and represent 9 of the 13 subspecies reported from North America north of México (table 5). Map 1 shows the approximate breeding ranges of these subspecies in the conterminous United States. Most of the recordings are originals, in the tape collection of the Department of Zoology, The Ohio State University; 29 are copies of recordings made by other people: 3 by William W. H. Gunn, 21 by Joan Beltz Roberts, 2 by Donald E. Kroodsmas, and 3 by Jerry and Norma Stillwell (from their phonograph record of western bird songs). Four of the 773 recordings represent subsong and the rest, primary song.

STUDY METHODS

Graphs (sonograms) were made of the vocal patterns represented in the recordings studied, and the patterns identified. My delimitation of these patterns is admittedly subjective. Someone else studying my graphs might recognize a different number of patterns, but my figures on the number of patterns found can at least be considered approximate.

Different introductions are designated by one or two capital letters (with A representing *no* introduction): B, C, D . . . Z, AA, AB . . . AZ, BA, BB . . . , and so on. Different trills are designated by a number (with 1 representing *no* trill). The designations for introductions and trills are purely arbitrary, and the similarity in letters (for introductions) or numbers (for trills) for two or more patterns does not necessarily represent the similarity of these patterns.

In studying the introductions, a number was assigned to each type of note or syllable found. These numbers are not used in this paper, except in table 1, where they are used to show how birds form the different introductions of their songs. The different notes and syllables of the introductions are individually labeled only in figures 1-8, where they are indicated by the

letters A-C—again to show how an eastern bird formed its different introductions.

Song patterns are designated by the letter(s) and number representing the particular introduction and trill they contain. The pattern BA-62 (fig. 4), for example, contains introduction pattern BA and trill pattern 62.

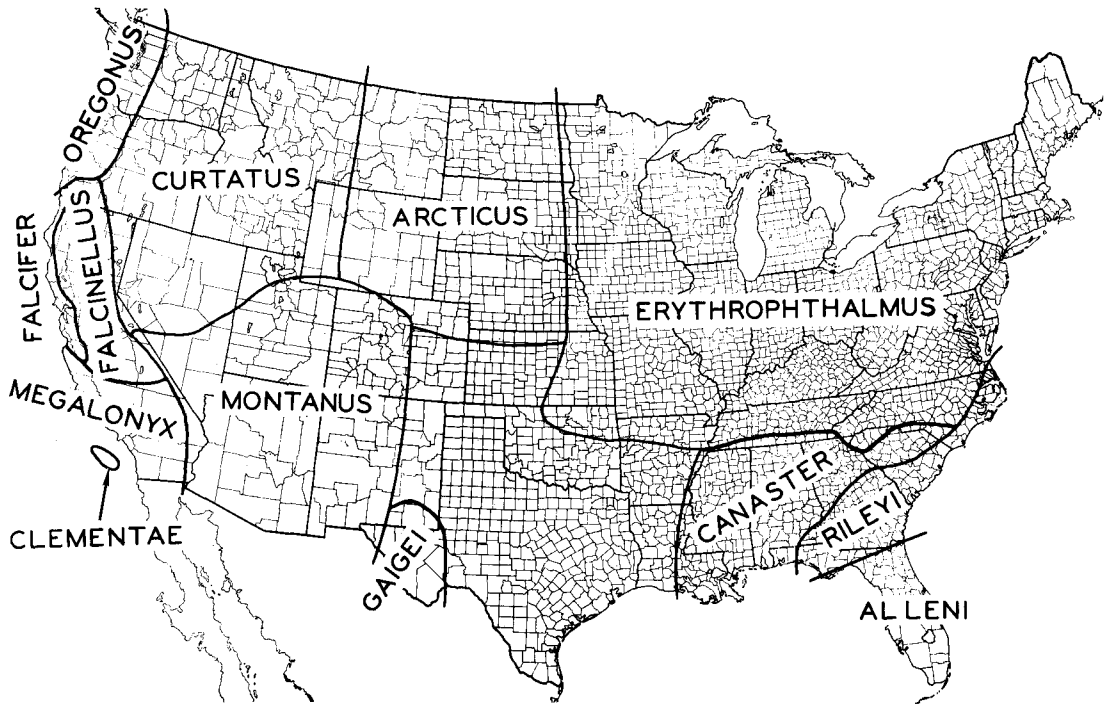
Space does not permit a description or graph of every vocal pattern found, and only a few are shown in figures 1-27. It is not important that the reader know the exact character of each vocal pattern mentioned here, but only that he understand that different letters or numbers represent different patterns.

The song graphs in this paper have been prepared with a Kay Electric Co. Vibralyzer, using the wide-band setting. The hyphenated numbers in the figure legends represent the recording, and the song in the recording, from which the graph was made. The number 6689-10 for figure 1, for example, indicates that this graph was made from the tenth song in recording No. 6689.

THE CHARACTER OF TOWHEE SONGS

A typical song of this species consists of an introduction and a trill. The introduction consists of one or more notes or syllables, of one or more different types, usually uttered slowly enough to count; the trill consists of a rapid series of similar notes or syllables, usually uttered too fast to count, and sometimes uttered so fast that this part of the song sounds buzzy. Some songs lack the introduction, some lack the trill, and a few consist of other introduction-trill combinations (table 8); most of these variations occur only rarely, but some are common in particular areas.

The introduction. Each eastern bird (those occurring east of the Mississippi River, representing subspecies *erythrophthalmus*, *canaster*, *rileyi*, and *alleni*) has a repertoire of several notes or syllables that it may use in the introductions of its songs, and these may be used singly or in various combinations to produce different introductions (or introduction patterns). Table 1 (birds 181, 272, and 10) and figures 1-8 contain examples of the ways a bird's introductory syllables are used to produce different introductions. Each bird appears to have a relatively large repertoire of introductions; the most found in one bird was 13 (bird 272, table 4). Most songs contain from one to three (rarely four or five) syllables in the introduction, and in introductions with two or more syllables these syllables are



MAP 1. Map showing the approximate breeding ranges of the subspecies of Rufous-sided Towhees in conterminous United States.

usually different (table 2). An exception to this was *alleni*; nearly half of the introductions found in this subspecies contained two or more syllables of the same type.

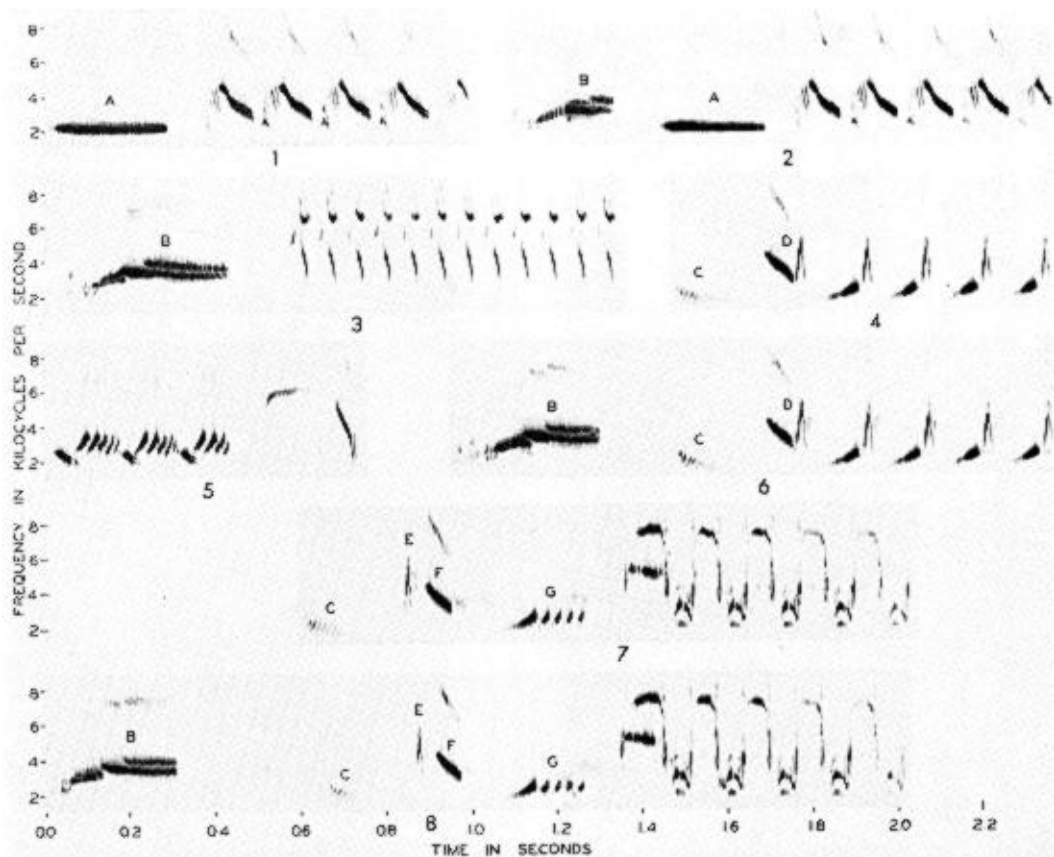
Most western birds (those occurring west of the Mississippi River in North Dakota, Colorado, and Arizona, representing subspecies *arcticus* and *montanus*) form their introductions a little differently—by using different numbers of a given syllable or by using different types of syllables (table 1, birds 483 and 390); only occasionally do they form different introductions by using different combinations of their introductory syllables (table 1, bird 390). The introductions studied contained from one to eight syllables (averaging more in *arcticus* than *montanus*, and more in Colorado than Arizona individuals of *montanus*), and these syllables were nearly always alike (table 2). The largest repertoire of introductions found in a western bird was seven (involving syllables of four types: bird 390, table 1). Examples of western songs are shown in figures 9, 11, 13, 15, 17, and 21.

Most songs of birds of the far west (those occurring in western Montana, Oregon, and California, representing the subspecies *curtatus*, *oregonus*, and *megalonyx*) lack an introduction (figs. 12, 14, 18, 22, and 26); when an introduction is present, it contains from one to four (usually one) notes (table 2). The largest

repertoire of introductions found in a single bird was two.

The character of the introductory syllables varied greatly in the songs studied. They varied in length from a few hundredths of a second to about one-quarter of a second (rarely longer). Most consisted of a single note (steady in pitch, slurred, or with both steady and slurred elements), but some were complex—with both buzzy and musical elements, and sometimes with two or more strong frequencies simultaneously (giving the syllable a harsh or nasal quality). The introductory syllables of western birds were generally more complex than those of other areas. The introductory syllables of birds of the far west were generally musical in quality (as in fig. 24). In some songs of *alleni* (Borrer 1959, fig. 3) and *arcticus* (e.g., bird 390, table 1, and figs. 9, 10, and 11), the "syllables" were actually two-syllable phrases.

The trill. Some trills are uniform throughout—with all the syllables alike, or with the last one incomplete—while others are a little different at the beginning. Trills of the latter type begin with a note or syllable that is a little different from the rest, or with a note that is either continuous with the first repeated syllable or is separated from it by only a few hundredths of a second and is not repeated in the following syllables. A true introduction



FIGURES 1-8. Graphs of songs of bird 181, Blendon Woods, Franklin Co., Ohio. Fig. 1, pattern B-20 (6689-10, 23 March 1964); Fig. 2, pattern X-20 (6709-10, 4 April 1964); Fig. 3, pattern I-60 (6687-3, 23 March 1964); Fig. 4, pattern BA-62 (6201-1, 13 April 1963); Fig. 5, an unusual song, pattern I-18-AE, the introduction (the same as B in Fig. 3) not shown (6444-1, 8 June 1963); Fig. 6, pattern WW-62 (6210-3, 13 April 1963); Fig. 7, pattern BZ-57 (7236-16, 27 July 1964); Fig. 8, pattern BY-57 (7236-17, 27 July 1964). The notes and syllables this bird used in its introductions are indicated by letters A-G; A is introduction B, B is introduction I (also the *chewink* call of this bird), BA is introduction X, CD is introduction BA, BCD is introduction WW, CEF is introduction BZ, and BCEFG is introduction BY. Figures 2 and 6 represent two of the many song patterns of this subspecies that might be paraphrased *drink-your-teeee*.

(as I use this term) is separated from the trill by several hundredths of a second. Some trills that are a little different at the beginning can be recognized as such in the field; in others the difference at the beginning is very slight, and scarcely or not at all recognizable in the field.

The trills found were classified in three groups on the basis of how they began: A, uniform throughout, the first syllable like the rest (figs. 1-6, 9, 11, 12, 14-16, 23, and the second trill in fig. 20); B, with a weak introductory note, or with the first syllable just a little different from the rest (figs. 18 and 26); and C, with a distinct introductory note or a distinctly different first syllable (figs. 7, 8, 13, 17, 19, 21, 22, 24, 27, and the first trill in figs. 20 and 25). A little over half the trills found were of type A, and about a third were of type C; the incidence of type A trills was a

little higher in *alleni* and *arcticus*, and that of type C trills was a little higher in *canaster*.

There was a great deal of variation in the character of the syllables in different trills. Most syllables contained from two to several slurred elements, often both upslurs and downslurs; relatively few consisted of a single slur, and none contained only a single note that was steady in pitch. The slurring was sometimes not very abrupt and the trill had a musical quality; more often, however, the slurring was quite abrupt, often over a considerable pitch range, giving the trill a mechanical or nonmusical quality. Some trills, particularly those of western and far western birds, had several rapidly uttered and abruptly slurred elements in each syllable, giving the syllable a buzzy quality (figs. 9, 11, 14, 15, 16, 21, and 24).

The number and rate of the trill syllables

TABLE 1. Examples of song introductions.

Bird	Syllables in the introduction ^a	Patterns
No. 181	27 (fig. 1, A)	B
Blendon Woods (Ohio)	114-27 (fig. 2, B A)	X
12 recordings	114 (fig. 3, B)	I
196 songs	75-162 (fig. 4, C D)	BA
(<i>erythrophthalmus</i>)	114-75-162 (fig. 6, B C D)	WW
	75-19-49-100 (fig. 7, C E F G)	BZ
	114-75-19-49-100 (fig. 8, B C E F G)	BY
No. 272	None	A
Blendon Woods (Ohio)	27	B
21 recordings	38a-27	CT
444 songs	33	F
(<i>erythrophthalmus</i>)	114-33	AP
	132-32	W
	160	CB
	160-27	VV
	160-33	FY
	160-101	FP
	160-174-89	FQ
	174	CX
	174-90	OO
	178	AA
No. 10	None	A
Myakka River State Park, Fla.	99	M
1 recording	11-99	N
28 songs	11	E
(<i>alleni</i>)	11-11	O
	11-11-11	KK
	11-11-11-11	SS
No. 483	49-49-49-49	JX
Kenmare, N. Dak.	49-49-49-49-49	PO
1 recording	49-49-49-49-49-49	PQ
10 songs	145a-145a-145a-145a-145a-145a-145a	PM
(<i>arcticus</i>)	145a-145a-145a-145a-145a-145a-145a	PN
No. 390	41	JV
Kenmare, N. Dak.	87-194-41	JU
1 recording	154-154-154-154-154-154-154	JW
34 songs	87-194-87-194-87-194-87-194-87-194	JR ^b
(<i>arcticus</i>)	87-194-87-194-87-194-87-194-87-194	IQ ^b
	192-192-192-192-192-192-192	JT
	192-192-192-192-192-192	JP

^a Each number represents a particular note or syllable.

^b Patterns JR and IQ consisted of 5 and 6 2-syllable phrases, and were tabulated for table 2 as 5 and 6 "syllables." Pattern IQ is shown in fig. 10.

varied considerably; in general, the more syllables, the faster they were uttered (table 3). The syllable rate was lowest in eastern birds, averaging 11.1–11.3/sec in three eastern subspecies and 14.7/sec in *rileyi*; only rarely was the rate so fast that the trill sounded buzzy. The syllable rate was higher in western birds (averaging 14.5–21.3/sec, lowest in Arizona birds), and many trills were buzzy in quality. The rate was also high in birds of the far west (averaging 15.4–32.3/sec in the subspecies studied), and many of these trills were buzzy due to a high syllable rate and/or the fact that the syllables themselves were buzzy in quality.

It is probable that all towhees have a repertoire of several trills. The most songs from a single bird were obtained from some Ohio

birds, where the bird with the largest trill repertoire had 11. The most songs obtained from a single bird of another subspecies was 52, and the largest trill repertoire found in a bird of another subspecies was 5 [in an individual of *alleni*; Kroodsma (1971) reported a maximum of 9 in the Oregon birds he studied].

Song patterns. Each eastern bird has a repertoire of several introductions and trills, and these are variously combined to produce a number of different songs or song patterns. Some song parts appear to be used only in a single combination, but some are used in different combinations. In bird 272 (table 4), for example, trill 46 was used with five different introductions, and without an introduction, and introduction VV was used with three different

TABLE 2. Number and types of syllables in the introduction.^a

Syllables in the introduction		Subspecies								
		Eastern				Western		Far West		
		<i>erythrophthalmus</i>	<i>canaster</i>	<i>rileyi</i>	<i>alleni</i>	<i>montanus</i>	<i>arcticus</i>	<i>oregonus</i>	<i>curtatus</i>	<i>megalonyx</i>
1	1	19.8	50.0	71.4	29.4	18.2	4.4	50.0		
2	1	2.5		7.1	11.8	36.4	10.9			100.0
	2	45.8	25.0	21.4	29.4		2.2	25.0		
2½	1						2.2			
3	1	0.6			5.9	18.2	13.0			
	2	2.8			11.8	4.5		12.5		
	3	17.7	25.0				2.2			
3½	1						2.2			
4	1	0.3			5.9	9.1	19.6			
	2	1.2								
	3	0.6								
	4	6.5						12.5		
5	1				5.9	9.1	21.7			
	2	0.3								
	3	0.3								
	4	0.3								
	5	1.2								
6	1					4.5	13.0			
7	1						6.5			
7	1						2.2			
Total intro- ductions		323	4	14	17	22	46	8	0	1
Aver. no. of syllables		2.3	1.8	1.3	2.2	2.7	4.2	1.9		2.0
Aver. no. of types of syllables		2.1	1.8	1.2	1.4	1.1	1.1	1.8	-	1.0

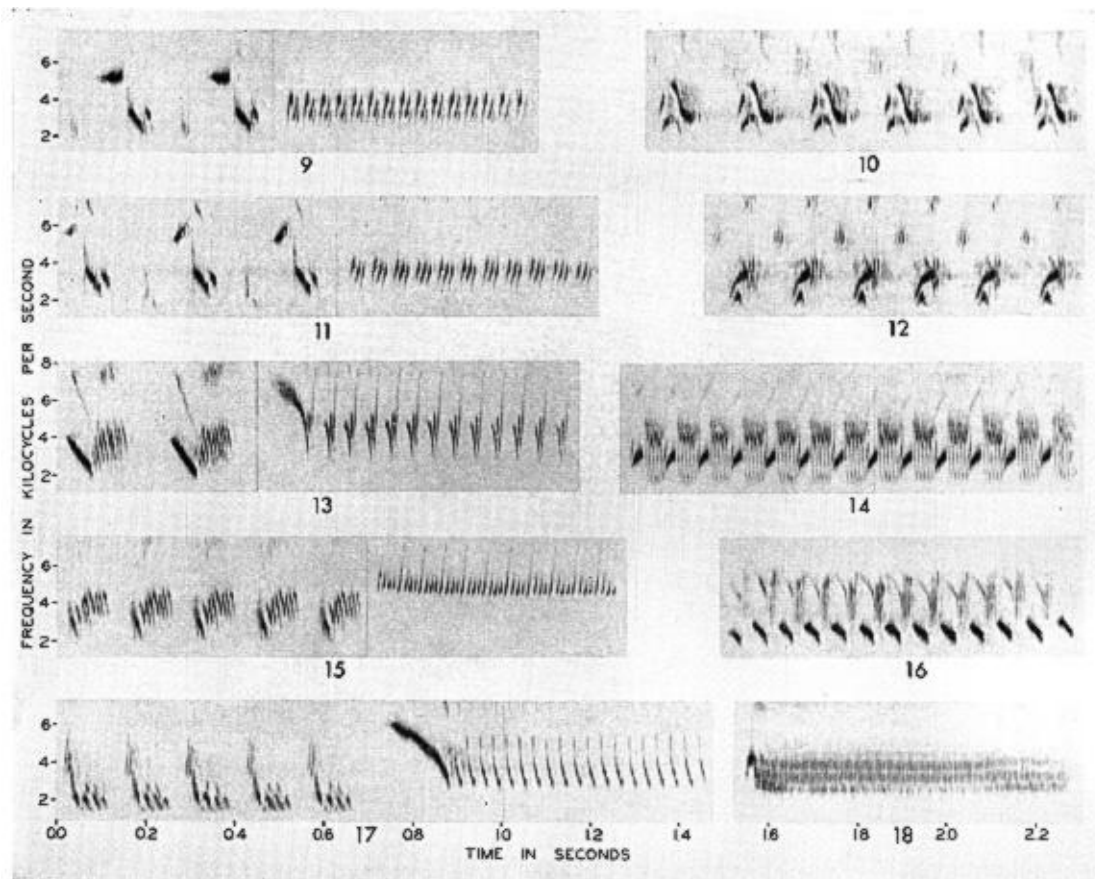
^a The numbers in the table, except those in the three bottom lines, are percentages (of the introductions in the subspecies).

TABLE 3. Number and rate of the trill syllables.

Area	Subspecies	No. of syllables		Syllables/sec ^a		
		Range	Aver. ^a	Range	Aver. ^b	
Eastern	<i>erythrophthalmus</i>	1-18	7.3 ± 0.3	4.4-40.0	11.3 (11.1-11.4)	
	<i>canaster</i>	4-7	5.6 ± 0.5	8.3-14.3	11.1 (9.9-12.6)	
	<i>alleni</i>	3-14	7.5 ± 0.7	6.0-20.8	11.3 (10.1-12.8)	
	<i>rileyi</i>	2-21	9.0 ± 1.0	8.6-43.5	14.7 (13.4-16.2)	
Western	<i>montanus</i>	Ariz.	4-21	10.0 ± 1.4	7.9-89.3	14.5 (12.5-17.4)
		Colo.	8-36	14.6 ± 2.0	11.8-82.0	21.3 (18.6-24.9)
	<i>arcticus</i>	1-48	12.5 ± 1.4	4.8-82.6	19.7 (17.7-22.2)	
Far West	<i>oregonus</i>	3-134	20.4 ± 2.8	4.5-162.0	15.4 (13.8-17.4)	
	<i>curtatus</i>	6-47	19.5 ± 8.2	10.2-80.0	18.9 (13.6-28.4)	
	<i>megalonyx</i>	12-85	35.8 ± 12.8	16.8-111.1	32.3 (24.6-47.0)	
All songs		1-134	8.7 ± 0.3	4.4-162.0	11.9	

^a Based on the series averages; the average number of syllables is given plus or minus the standard error.

^b The range, from the average minus the standard error to the average plus the standard error, is given in parentheses.



FIGURES 9-18. Graphs of towhee songs. Fig. 9, pattern JC-222 (10790-5, Medora, N. Dak., 29 June 1970); Fig. 10, pattern JQ-1 (introduction only, the trill lacking; 10827-2, Kenmare, N. Dak., 3 July 1970); Fig. 11, pattern NA-311 (11369-2, Kenmare, N. Dak., 14 June 1971); Fig. 12, pattern A-236 (trill only, the introduction lacking; 7689-1, Corvallis, Ore., 19 June 1965); Fig. 13, pattern AS-220 (10758-1, Colorado Springs, Colo., 24 June 1970); Fig. 14, pattern A-255 (trill only, the introduction lacking; 7871-1, Corvallis, Ore., 9 July 1965); Fig. 15, pattern IY-212 (10742-18, Colorado Springs, Colo., 24 June 1970); Fig. 16, pattern A-159 (trill only, the introduction lacking; 8115-12, Blacklick Woods, Franklin Co., Ohio, 20 April 1966); Fig. 17, pattern AV-140 (7146-1, Portal, Ariz., 29 June 1964); Fig. 18, pattern A-254 (trill only, the introduction lacking; the fastest trill found; 7866-1, Corvallis, Ore., 5 July 1965).

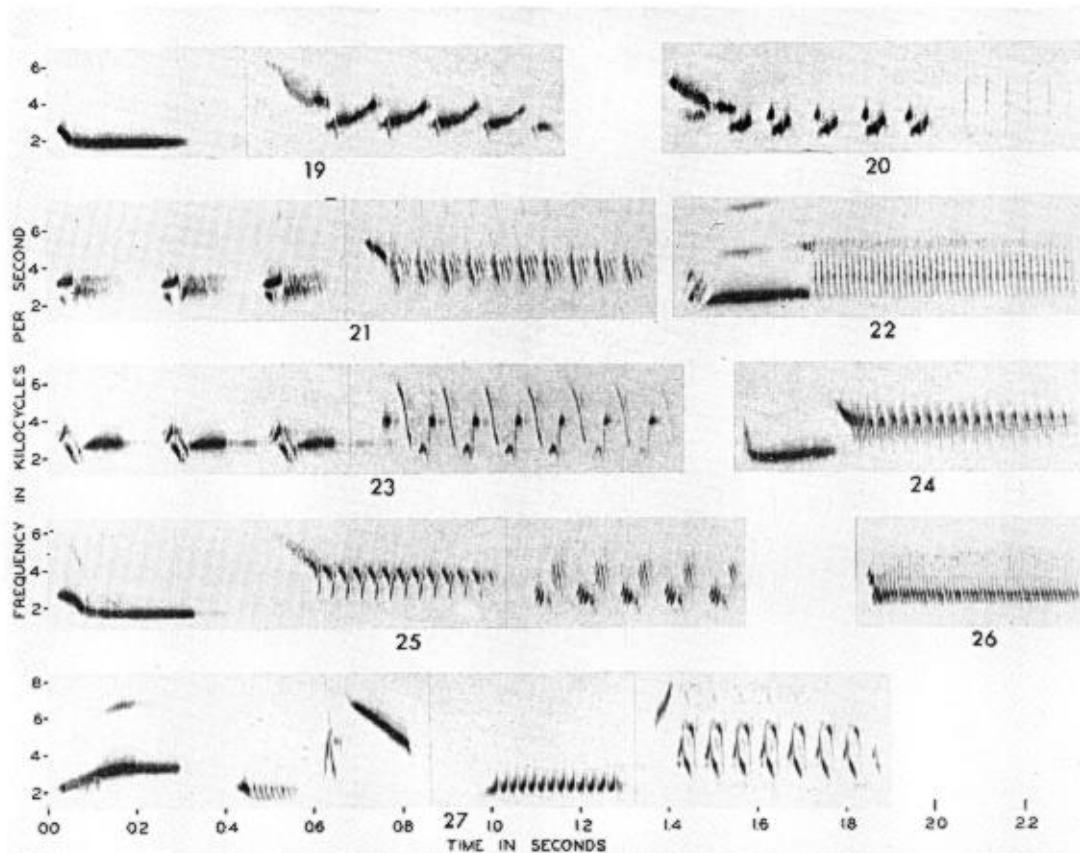
trills and without a trill. Table 4 shows the song patterns found in three birds (all from Blendon Woods, Franklin Co., Ohio), including the two (272 and 203) with the largest repertoires.

The song patterns of western birds are formed a little differently; each type of introductory syllable is normally used with only one type of trill, and the different song patterns containing this trill differ only in the number of introductory syllables. No instance was found in the western songs studied of a given introductory syllable being used with different trills, and only one instance was found of different introductory syllables being used with the same trill (bird 390, table I, which used introductions JU and JV with the same trill).

In the birds of the far west that sang songs containing an introduction, and had a reper-

toire of two introductions, each introduction was used with a different trill. The "introductory phrase" that Kroodsma (1971:303) described in many Oregon songs (he stated that each is always followed by a particular trill) is in most cases so close to the first trill syllable that I would call it the beginning of a type C trill and not a true song introduction (see fig. 22). Different song patterns in a bird of the far west are generally just different trills, as their songs usually lack an introduction.

The numbers of patterns found in the songs studied are summarized in table 5. This represents a great deal of variation, but must be only a very small fraction of the total variation in the species; towhee songs are extremely variable. In areas where the songs normally consist of an introduction and a trill (eastern and western areas), there was usually more variation in the introduction than in the trill.



FIGURES 19-27. Graphs of towhee songs. Fig. 19, pattern F-46 (a common eastern pattern; 8088-1, bird 272, Blendon Woods, Franklin Co., Ohio, 17 April 1966); Fig. 20, pattern A-12-2 (an aberrant pattern: no introduction, and two trills; 1471-4, Clear Creek, Hocking Co., Ohio, 5 June 1955); Fig. 21, pattern AT-139 (7134-4, Portal, Ariz., 28 June 1964); Fig. 22, pattern A-250 (a type C trill, without a true introduction; 7845-4, Corvallis, Ore., 5 July 1965); Fig. 23, pattern CN-47 (an unusual eastern pattern, with three similar syllables in the introduction, and similar to some western songs; 6783-1, Blacklick Woods, Franklin Co., Ohio, 24 April 1964); Fig. 24, pattern NK-259 (7886-1, Corvallis, Ore., 12 July 1965); Fig. 25, pattern F-25-44 (an aberrant eastern pattern, with an introduction and two trills; 10444-2, Delaware Wildlife Area, Delaware Co., Ohio, 18 April 1970); Fig. 26, pattern A-143 (trill only, the introduction lacking; 11542-2, Carmel, Calif., 1 July 1971); Fig. 27, pattern IE-40 (one of the few eastern patterns with five syllables in the introduction; 11683-1, Blendon Woods, Franklin Co., Ohio, 18 April 1972).

Pattern Distribution. A great many of the vocal patterns found were found only in one bird, even in areas where a great deal of recording was done; the data on this point are summarized in table 6. More recordings were made in Blendon Woods than in any other area; yet over half the introductions (61 of 119), nearly a third of the trills (23 of 77), and nearly three-fourths of the song patterns (191 of 265) found there were found in only one bird studied. In many areas, some of the patterns found in only one bird *in that area* were found in one or more birds elsewhere (for example, 21 introductions, 17 trills, and 17 song patterns found in only one Blendon Woods bird were found in one or more birds in other areas). Some of the vocal patterns—107 of the introductions, 108 of the trills, and 118 of

the song patterns—were found in two or more birds.

Of the 107 introductions found in two or more birds, 52 were found in birds 50 miles or more apart (up to 1275 miles); 2 were found in three subspecies and 10 others, in two subspecies. The most common introduction (F; figs. 19 and 25) was found in 62 birds: 57 in Ohio (in all eight of the areas listed in table 5), 1 in Michigan, 2 in Ontario, 1 in Virginia, and 1 in North Carolina. The most widely distributed introduction (B; shows as A in fig. 1) was found in 24 birds: 15 in Ohio, 1 in Michigan, 1 in Ontario, 2 in Maine, 3 in North Carolina, 1 in Florida (*rileyi*), and 1 in North Dakota (*arcticus*).

Of the 108 trills found in two or more birds, 62 were found in birds 50 miles or more apart

TABLE 4. Song patterns of three birds in Blendon Woods (Ohio).

	Bird		
	No. 272	No. 203	No. 181
No. of recordings	21	10	12
No. of songs recorded	444	371	196
Song patterns	A-46	C-691	B-20 (fig. 1)
	B-25	F-1	I-18-AE (fig. 5)
	F-1	U-1	I-60 (fig. 3)
	F-46 (fig. 19)	U-24	X-20 (fig. 2)
	W-25	AA-1	BA-62 (fig. 4)
	AA-44	AA-55	BY-71 (fig. 8)
	AP-1	AA-56	BZ-71 (fig. 7)
	AP-46	BX-1	WW-62 (fig. 6)
	CB-1	BX-44	
	CB-46	CC-1	
	CT-1	CC-5	
	CT-40a	CX-1	
	CX-44	FE-44	
	FP-29	HH-1	
	FQ-1	HH-49	
	FY-1	HH-50	
	FY-46	OO-1	
	OO-49	OO-56	
	VV-1		
	VV-25		
	VV-25a		
	VV-46		
No. of introduction patterns	13	10	7
No. of trill patterns	7	10	5
No. of song patterns	22	18	8

(up to 1720 miles); 10 were found in two subspecies. The most common trill (pattern 47; fig. 23) was found in 42 birds: 41 in Ohio (representing seven of the eight areas) and 1 in West Virginia. The most widely distributed trills were patterns 29 and 50; pattern 29 was found in 13 birds: 9 in Ohio, 1 in West Virginia, 2 in North Carolina, and 1 in Florida (*rileyi*); pattern 50 was found in 19 birds: 14 in Ohio, 1 in Michigan, 1 in Ontario, 1 in Maine, 1 in Kentucky, and 1 in North Carolina.

Of the 118 song patterns found in two or more birds, only 26 were found in birds 50 miles or more apart (up to 1085 miles). The most common pattern (F-46; fig. 19) was found in 14 birds (all in Ohio): 6 in Blendon Woods, 5 in Blacklick Woods, 1 in Darby Creek Park, 1 elsewhere in central Ohio, and 1 in southern Ohio. Fourteen of these 26 song patterns (7 normal, 1 lacking an introduction, and 6 lacking a trill) were found in two or more states, two of them in two subspecies (C-46 in *erythrophthalmus* and *canaster*, 440 miles apart, and CX-1 in *erythrophthalmus* and *arcticus*, 1085 miles apart). The seven normal patterns found in two or more states were:

C-46: in Ohio and Alabama, 440 miles apart (2 subspecies)

F-69: in Ohio and North Carolina, 365 miles apart

V-5: in Ohio and West Virginia, 120 miles apart

X-20: in Ohio (fig. 2) and Maine, 750 miles apart

AQ-50: in Ontario and Kentucky, 300 miles apart

HH-49: in Ohio and West Virginia, 155 miles apart

HH-50a: in Ohio and Virginia, 380 miles apart

Local variation in song in eastern birds is apparently a little different from that in birds of the far west. Kroodsmma (1971) found that Oregon birds exhibited local dialects; the songs of neighboring males were quite similar, but the similarities decreased going only 2 km from a core area. Eastern birds do not exhibit such local dialects; a high percentage of their song patterns occur in only one bird (table 6), and the similarities in song do not decrease (as they do in Oregon) going away from a core area (table 7).

Aberrant song patterns. An aberrant song pattern is any pattern other than the IT (introduction plus trill) type of song commonly heard from the eastern birds of this species. The incidence of such patterns in primary song is shown in table 8.

The most common aberrant patterns were those lacking an introduction (OT and OTT)

TABLE 5. Patterns found in primary song.

Subspecies	Area or state ^a	No. of songs studied	No. of patterns		
			Introd.	Trill	Entire song
	BW	4634	119	77	265 ^{b,c}
	BkW	1318	68	63	150 ^{b,c}
	DCP	277	27	23	33 ^c
	DWA	145	14	13	19 ^c
	CO	454	47	42	83 ^{b,c}
	CCV	363	29	25	46 ^{b,c}
	SO	298	27	23	35 ^c
	NO	215	21	21	31 ^{b,c}
	Ohio total ^d	7704	240	171	593 ^{b,c}
<i>erythrophthalmus</i>	Ind.	9	1	1	2 ^c
	Mich.	54	16	11	24 ^c
	Ont.	23	5	5	6
	N.J.	5	1	1	1
	Pa.	146	10	10	12
	Me.	259	13	17	29 ^{b,c}
	Ky.	19	3	3	3
	W.Va.	102	16	15	22 ^{b,c}
	Tenn.	9	1	1	2 ^c
	Va.	72	10	8	11 ^c
	N.C.	485	55	47	76 ^{b,c}
	<i>erythrophthalmus</i> total ^d	8887	323	232	765 ^{b,c}
<i>canaster</i>	Ala.	20	4	4	4
<i>rileyi</i>	Fla.	152	14	11	18 ^c
<i>alleni</i>	Fla.	105	17	11	23 ^{b,c}
<i>montanus</i>	Ariz.	102	13	10	10 ^{b,c}
<i>montanus</i>	Colo.	89	11	10	14 ^{b,c}
<i>arcticus</i>	N. Dak.	277	46	28	60 ^{b,c}
<i>oregonus</i>	Ore.	515	10	47	47 ^{b,c}
<i>curtatus</i>	Mont.	38	0	4	4 ^b
<i>megalonyx</i>	Calif.	21	1	4	4 ^b
All birds ^d		10206	422	352	950 ^{b,c}

^a Ohio areas: BW, Blendon Woods, Franklin Co.; BkW, Blacklick Woods, Franklin Co.; DCP, Darby Creek Park, Franklin Co.; DWA, Delaware Wildlife Area, Delaware Co.; CO, various areas in or near Franklin Co.; CCV, Clear Creek Valley, Hocking Co.; SO, various areas in southern Ohio; NO, various areas in northern Ohio.

^b Some patterns lacked an introduction.

^c Some patterns lacked a trill.

^d Some patterns occurred in more than one area.

or a trill (IO). Patterns lacking an introduction were relatively rare in eastern birds (3.2% of the total), but were more common in *alleni* (8.7%); they were a little more common in western birds (12.9% of the patterns in *montanus* and 8.3% of those in *arcticus*), and were the common type (72.7% of the patterns) in birds of the far west. Songs lacking the trill were quite rare in the far west (1.8% of the patterns), but were more common in eastern and western birds (10.1% of the patterns in eastern birds, 9.9% in western birds); they were more common in *rileyi* (16.7% of the patterns) than in any other subspecies. Songs of eastern birds that lack the introduction or trill are most likely to be sung by a bird showing some degree of excitement, for example, in response to playbacks of a towhee song on its nesting territory. Other aberrant song patterns (ITT, ITIT, ITI, TIT, TI) were relatively rare, comprising only 4.3% of all the patterns found,

and it is possible that some of the birds singing these songs had not yet completed their song development. Of the 20 aberrant patterns containing two trills (OTT and ITT), 4 had the two trills of the same type, and 16 had the two trills of different types (figs. 20 and 25).

The towhee's use of its song repertoire. The average singing rate in the recordings of primary song varied from 4.5 to 21.2 songs/min, and averaged 9.6/min in all the recordings. The rate was similar in the different subspecies.

A towhee generally sings songs of one pattern for a while, then changes to another. A bird will sometimes sing the same song for 15 min or more, and a listener may get the impression that the bird has only this one song, but if he listens long enough (or the bird sings long enough), he will find eventually that the bird has more than one song in its repertoire.

A towhee occasionally will sing songs of two

Table 6. Patterns in primary song found in only one bird.

Subspecies	Area ^a	% found in only one bird studied			% found in only one bird in the area		
		Introd.	Trill	Song	Introd.	Trill	Song
<i>erythrophthalmus</i>	BW	51.3	32.5	72.1	68.9	52.0	78.5
	BkW	42.7	38.1	79.3	70.6	73.0	92.0
	DCP	55.6	26.1	69.7	85.2	82.6	97.0
	DWA	21.4	15.4	52.6	92.9	92.3	100.0
	CO	46.8	33.3	80.7	78.7	33.3	98.8
	CCV	37.9	20.0	78.3	86.2	68.0	91.3
	SO	51.9	39.1	74.3	85.2	82.6	97.1
	NO	33.3	19.1	80.7	81.0	85.7	100.0
	All Ohio	67.5	52.1	84.0	73.8	59.7	85.7
	Pa.	70.0	40.0	91.7	80.0	70.0	91.7
	Me.	46.2	35.3	86.2	53.9	82.4	89.7
	W.Va.	37.5	26.7	81.8	93.8	86.7	95.5
	N.C.	61.8	48.9	90.8	83.6	83.0	96.7
Subsp. total	71.8	60.8	87.0	73.4	61.2	87.1	
<i>canaster</i>	Ala.	75.0	100.0	100.0	100.0	100.0	100.0
<i>rileyi</i>	Fla.	57.1	81.8	94.4	100.0	90.9	94.4
<i>alleni</i>	Fla.	76.5	81.8	100.0	94.1	90.9	100.0
<i>montanus</i>	Ariz./Colo.	68.2	75.0	91.7	72.7	85.0	91.7
<i>arcticus</i>	N.Dak.	76.1	75.0	96.7	84.8	75.0	98.3
<i>oregonus</i>	Ore.	80.0	89.4	91.5	80.0	91.5	91.5
<i>curtatus</i>	Mont.	—	100.0	100.0	—	100.0	100.0
<i>megalonyx</i>	Calif.	—	100.0	100.0	—	100.0	100.0
All birds		74.6	69.3	87.6	—	—	—

^a The Ohio areas are listed in table 5; some eastern states, from which only a few songs were studied, are omitted (but are included in the total for *erythrophthalmus*).

different patterns more or less alternately; these patterns may differ only in the introduction (a little over one-fourth of the time) or the trill (a little less than one-fourth of the time) or the entire song may be different (about half of the time). Nearly one-fifth of the recordings showed some alternation of pattern; the incidence of such singing was higher in *canaster*, *alleni*, *montanus* (particularly the Colorado birds), and *curtatus*, and lower in *rileyi*.

A bird does not appear to sing its different songs in any particular sequence, and on different occasions generally sings them in different sequences. When singing two patterns alternately, a bird may use the same patterns on different occasions; apparently only some of

a bird's patterns are used in such singing [Kroodsma (1971) found this also in his Oregon birds].

Kroodsma (1971) found that the different song patterns of neighboring birds were often quite similar, and a bird responding to the singing of a neighbor would respond with the pattern in its repertoire like that of the other bird. Such similarities in the songs of neighboring birds were not found in eastern birds, and a bird responding to the singing of a neighboring male may respond with almost any song in its repertoire.

SUBSONG

The preceding comments about towhee song apply to fully developed or primary song; the

TABLE 7. Occurrence of the Blendon Woods patterns that were found in two or more birds.

Patterns ^a	No. of patterns			Miles away
	Introd.	Trills	Songs	
Found in two or more birds studied	58	52	74	
Found only in Blendon Woods	11	10	38	
Found also in BkW	28	25	21	11
Found also in CO or DCP	26	22	11	up to 20
Found also in DWA	11	8	7	20-25
Found also in CCV	12	12	6	35-40
Found also in SO or NO	14	19	8	50-120
Found also in adjacent states	14	10	7	125-330
Found also farther away	17	20	4	400-1720

^a The abbreviations for the different Ohio areas are explained in table 5.

TABLE 8. Aberrant patterns in primary song.

Area	Subspecies	Total patterns	No. of aberrant patterns ^a							
			OT	OTT ^c	ITT ^d	ITIT	ITI	TIT	TI	IO
Eastern	<i>erythrophthalmus</i>	765	18	6	10	9	10	2	3	76
	<i>canaster</i>	4	—	—	—	—	—	—	—	—
	<i>rileyi</i>	18	—	—	—	—	—	—	—	3
	<i>alleni</i>	23	1	1	2	—	—	—	—	3
Western	<i>montanus</i>	31	4	—	—	—	—	—	—	4
	<i>arcticus</i>	60	5	—	—	—	—	—	4	5
Far West	<i>oregonus</i>	47	33	—	1	—	—	—	—	1
	<i>curtatus</i>	4	4	—	—	—	—	—	—	—
	<i>megalonyx</i>	4	3	—	—	—	—	—	—	—
Aberrant patterns	No. ^b	950	68	7	13	9	10	2	7	91
	% of total	21.8	7.2	0.7	1.4	0.9	1.1	0.2	0.7	9.6

^a O, no introduction or trill; I, introduction; T, trill.

^b One IO pattern (CX-1) occurred in both *erythrophthalmus* and *arcticus*.

^c One OTT pattern is shown in fig. 20.

^d One ITT pattern is shown in fig. 25.

recordings of four additional birds studied (all from Ohio: BW, 1; BkW, 2; SO, 1) appear to represent subsong—a stage in song development in which the song patterns are not yet perfected. Only one recording was made of each bird; three of the four recordings were made in areas where a great deal of recording was done (BW, BkW), but none of these birds was found on subsequent visits to these areas. I assume, therefore, that they were birds in migration and nested elsewhere, and that song development in this species is generally completed by the time the birds reach their nesting grounds in the spring.

Subsong differs from primary song in three principal ways: the “songs” are sung at a more rapid rate (an average of about 17/min, compared with 9.6 in primary song), many of the syllables appear imperfectly developed, and many of the song patterns are aberrant. Subsong vocalizations may include some normal songs, but consist mostly of a varied assortment of introductory syllables, trills and trill syllables, and call notes—which are more or less continuous or are combined in what might be considered aberrant song patterns. Many of the introduction and trill syllables in subsong are just a little different from particular syllables in primary song, making it appear that the subsong renditions of these syllables are not quite accurate. What appears to be the same introduction or trill syllable is often a little different in different utterances by the same bird, and sometimes the syllables may vary somewhat through a given trill.

Because of their variation it was difficult to make an accurate count of the number of introduction, trill, and song patterns in the subsong recordings studied, but about two-thirds of the

introductions and trills, and about seven-eighths of the song patterns found were found only in the subsong recordings; the rest were found also in the primary songs of one or more birds. Most of the introductions and trills found in both primary song and subsong were relatively common patterns, found in the primary song of a number of birds (including one or more in the same area); a few were found in the primary song of birds in other parts of Ohio, in adjacent states, or even as far away as Maine and North Carolina. One introduction in a subsong recording made in Blacklick Woods was also found in a recording of primary song of *alleni* (peninsular Florida), and a trill in this same subsong recording was also found in a recording of primary song of *montanus* (Colorado). Most of the song patterns found in both primary song and subsong were found in the primary song of one or more birds in the same area, but two in a Blendon Woods subsong recording were found in the primary song of birds in the Clear Creek Valley (about 40 miles away), and one in the Blendon Woods subsong recording was found in the primary song of a bird in West Virginia (about 120 miles away).

An important problem in relation to song variation is how a bird comes to sing the particular vocal patterns that it sings. Where local dialects occur (as in Oregon), it may be assumed that a bird acquires its vocal patterns by listening to other (adjacent) birds. Such dialects do not occur in the east, and while there is some similarity in the vocal patterns in a given eastern area, there is also a relatively high percentage of these patterns that are unique, that is, they occur in only one bird. It thus appears that while an eastern bird may

sometimes pick up and use, in its songs, introductions and/or trills heard from other birds, it frequently does a considerable amount of improvising, and often develops vocal patterns unlike those of its neighbors.

In the early stages of song development, each eastern bird has a large vocal repertoire, and its song parts (introduction and trill syllables) are put together in all sorts of combinations; as development proceeds, the song parts come to be combined in a fashion characteristic of the subspecies (introduction plus trill). Once a song pattern is developed it is apparently fixed; for 18 of the 488 birds studied (primary song) I have recordings of what I am sure is the same bird (because of peculiarities in its songs) made in two or three seasons—and singing songs of the same patterns. The syllables retained in primary song from sub-song may be influenced by what the bird hears from other birds—in the case of birds of the far west—but such influence does not appear to be very strong in eastern birds.

DISCUSSION

The geographic variation in song in this species involves not only the songs themselves but the nature and amount of local variation. The geographic variation in the songs may be considerable—so much that anyone familiar only with the songs in one section of the country would not recognize most songs in a distant section. Eastern birds appear to have larger song repertoires than western or far western birds; 22 different songs were found in one eastern bird, but the most found in any one bird of the west or far west was 9. The songs of birds of the far west exhibit local dialects (Kroodsmma 1971), but such dialects do not occur in eastern and western birds (see tables 6 and 7). Eastern birds apparently do a great deal of improvising and often develop songs unlike those of their neighbors.

The birds whose songs have been studied fall very nicely into three groups on the basis of song—eastern, western, and far western—but in any given section of the country one may occasionally hear songs that are somewhat atypical for that section, but closely resemble the typical songs in another section of the country. For example, a western song containing several (similar) introductory syllables and lacking a trill is very similar to songs of the far west that consist of a slow trill (and lack an introduction; cf. figs. 10 and 12). Similarly, an Ohio song lacking an introduction is very similar to an Oregon song with a slow trill (and lacking an introduction; cf. figs. 14

and 16), or an Ohio song with two or three syllables of the same type in the introduction closely resembles many western songs (cf. figs. 21 and 23).

My towhee recordings from the north central part of the country (of *arcticus*) come from two areas in western North Dakota—the Des Lacs Wildlife Refuge near Kenmare, and the south unit of the Roosevelt Memorial Park near Medora. Towhees are not common in the Kenmare area, but they are very common near Medora. These songs are quite similar to those I have recorded in Colorado (all recorded near Colorado Springs and believed to represent the subspecies *montanus*), but they are quite different from the songs of *erythrophthalmus* in the east, and those of *curtatus* recorded in western Montana. Morphologically, the birds in the eastern part of North Dakota approach the condition of *erythrophthalmus* (Sibley and West 1959), and it may be that their songs resemble those of *erythrophthalmus*, but I have no towhee recordings from eastern North Dakota where the species appears to be relatively rare as a breeding bird.

My recording in Montana has been done mainly at the Bowdoin Wildlife Refuge in the north-central part of the state, and near Flathead Lake in the western part of the state. I have found no towhees at the Bowdoin Refuge, and there appears to be a sizeable towhee-less gap in eastern Montana. The songs of the birds near Flathead Lake are of the far western type, noticeably different from those of the western type in western North Dakota.

The Rufous-sided Towhee is apparently absent as a breeding bird from large sections of the south-central states (most of Texas, Oklahoma, and Kansas), so that there is a considerable gap between the eastern birds (*erythrophthalmus* and *canaster*) and those to the west (*gaigei* and *montanus*). Strangely enough, the songs of the southern Arizona birds studied appear more like those of eastern birds than do the songs farther north (in Colorado and North Dakota), where there is less of a gap between eastern and western populations.

The recordings of far western birds studied all come from near the Pacific Coast (except those in western Montana). The change from the western to the far western song type apparently occurs somewhere in central Montana in the north, and probably between *montanus* and *curtatus* in the south and southwest. A towhee I heard on the Nevada side of Lake Tahoe a few years ago (but did not record) sang a song like those of the far west.

CONCLUSIONS

The subspecies of the Rufous-sided Towhee whose songs have been studied fall into three major groups on the basis of their songs: (1) eastern birds, subspecies *erythrophthalmus*, *canaster*, *rileyi*, and *alleni*; (2) western birds, subspecies *montanus* and *arcticus*; and (3) birds of the far west, subspecies *oregonus*, *curtatus*, and *megalonyx*. Songs of the first group consist mainly of an introduction and a trill, the introduction with one to three (rarely four or five) syllables that are usually all different, and the syllable rate in the trill rarely so fast that the trill sounds buzzy. Songs of the second group also consist mainly of an introduction and a trill, but the introduction may contain up to eight syllables that are usually all alike, and the syllable rate in the trill is often so fast that the trill sounds buzzy; one of Peterson's descriptions of towhee songs (1961:289), *Chup chup chup zeeeeeeee*, fits these songs. Songs of the third group usually lack an introduction, and the trill is often buzzy: a *chwweeeee* (Peterson 1961:289). Individual eastern birds have a larger reper-

toire of songs than those of other groups, and eastern birds do not exhibit local dialects like those of the birds of the far west.

I have not examined any songs of *gaigei*, *falcinellus*, or *clemente*, but I would expect those of *gaigei* to be similar to the songs of other western birds (group 2, above), and those of *falcinellus* and *clemente* to be similar to those of other birds of the far west (group 3, above).

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