

SINGING BEHAVIOR AND THE GONAD CYCLE OF THE RUFIOUS-SIDED TOWHEE

By JOHN DAVIS

Although the Rufous-sided Towhee (*Pipilo erythrophthalmus*) is a common species over much of western North America, its singing behavior has never been described in detail, and even the published descriptions of its song are brief and inadequate. In this study, singing behavior was observed in the population resident at the Hastings Reservation, two and one-half miles east of Jamesburg, northern Monterey County, California. The gonad cycle was determined for populations resident within a radius of three miles of the Reservation, to see whether any aspects of singing behavior were correlated with events in the gonad cycle. The subspecies with which this paper is concerned is *Pipilo erythrophthalmus megalonyx*, which reaches its northern limits of distribution in northern Monterey County.

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MATERIALS AND METHODS

Most of the material presented has been taken from my field notes, written at the Hastings Reservation between September 22, 1953, and October 13, 1957. In addition, field notes recorded by the following workers at the Hastings Reservation were used: Lowell Adams, John E. Chattin, Floyd E. Durham, Richard J. Hitsch, Everett W. Jameson, Enid A. Larson, Jean M. Linsdale, Alden H. Miller, George M. Scheibner, Charles G. Sibley, Lloyd P. Tevis, Jr., P. Quentin Tomich, Howard Twining, and Henry G. Weston, Jr.

The testis cycle was established for 120 males collected within three miles of the Hastings Reservation between January 5, 1955, and May 10, 1956. Testes were removed in the field within ten minutes after death, measured to the nearest 0.5 mm., and fixed in Bouin's fluid. They were subsequently prepared by the paraffin technique, sectioned at 7.5 or 8 microns, and stained either with Galigher's or Harris' hematoxylin and eosin. The reproductive cycle was established for 68 females collected during the same period. Each was autopsied in the field, and the ovary and oviduct were examined macroscopically. When the ovary showed any sign of activity, the largest follicle was measured to the nearest 0.25 mm. The presence or absence of an incubation patch was also noted.

To indicate the various stages of activity of the testis, the seven stages outlined by Blanchard and Erickson (1949:266) were used, with the exception that their stages 1 and 2 are considered as a single stage 1-2. The stages are as follows:

- Stage 1-2. Resting spermatogonia only.
- Stage 3. Increase in spermatogonia. First primary spermatocytes.
- Stage 4. First primary spermatocytes in synapsis.
- Stage 5. Predominance of primary spermatocytes in synapsis.
- Stage 6. First spermatids.
- Stage 7. Breeding.

To assess the reproductive state of females, the four stages of ovarian development described by McCabe (1943:551-2) were used, and incubation patches, when present, were classified according to the four stages described by Bailey (1952:125-7). In addi-

tion, a subjective estimate of the development of the oviduct was made. The four stages of reproductive development are as follows:

Inactive. Ovary uniform, non-granular. Oviduct thread-like and barely visible. Incubation patch absent.

Low development. Ovary rather granular, some oöcytes definitely enlarged. Oviduct ranges from minimum size to moderately enlarged. Incubation patch absent.

Breeding. Oöcytes moderately enlarged to discharged. Oviduct greatly enlarged. Incubation patch present, stage I (defeathered), stage II (vascularized), or stage III (edematous). Any female with a stage I incubation patch was termed "breeding," as it was assumed that such a female would have laid even though it had not done so at the time of collection. Recent laying could be established by the presence of ruptured follicles.

Postbreeding. The ovary is markedly granular or "gravelly" (McCabe, 1943), with many hard, degenerating oöcytes which are mostly yellow or cream-colored. The oviduct is small. A stage IV (recovery) incubation patch is present.

The age of each individual was determined on the basis of the criteria outlined by Davis (1957). Two age groups are recognized in this study. They are first-year, including those birds taken between the end of the postjuvenile molt and the beginning of the first postnuptial molt, and adult, indicating those birds which have completed at least one postnuptial molt.

MALE GONAD CYCLE

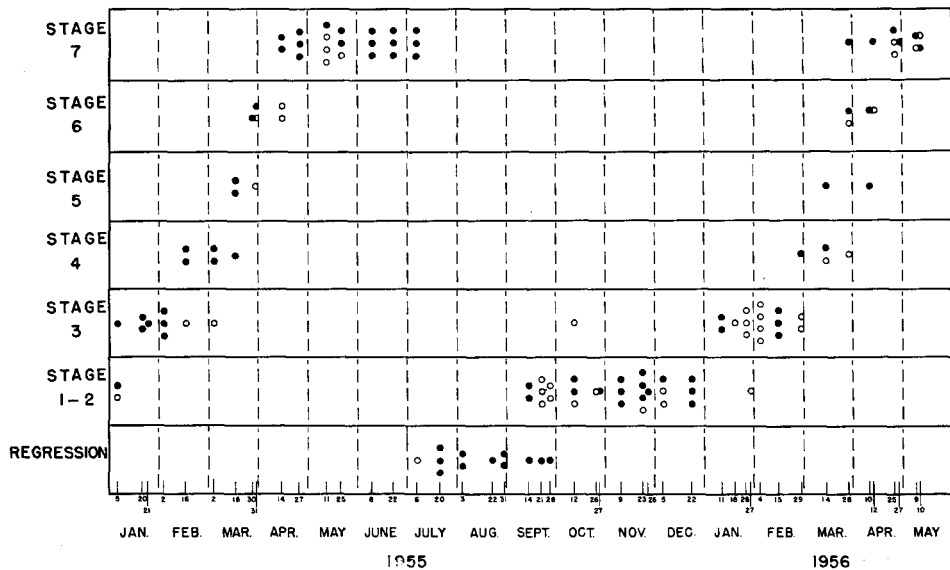


Fig. 1. Testis cycle of *Pipilo erythrophthalmus* based on specimens collected near the Hastings Reservation between January 5, 1955, and May 10, 1956. Dots represent adults; circles represent first-year birds.

THE GONAD CYCLES

The testis cycle.—The male gonad cycle for the period from January 5, 1955, to May 10, 1956, is presented graphically in figure 1. Spermatogenic activity starts in early January. Breeding condition may be reached as early as March 28, but most males reach this stage at about the middle of April. Regression from breeding condition may start as early as July 6 in some individuals, and it is apparently under way in all males by

July 20. Regression is complete in most males by the middle of September, although one collected on September 28 was still in the terminal stages of regression. Through the fall and early winter the testes of most males are in an inactive condition, although in the testes of some individuals there is a slight proliferation of spermatogonia. During this period, the testes of only one male, a first-year bird collected on October 12, reached stage 3. Thus, in the fall, there is no recrudescence of spermatogenesis in adults or initiation of spermatogenic activity in the great majority of first-year males.

Table 1

Stages of Gonadal Development Attained by First-year and Adult Males Collected on the Same Day

1955			1956		
Date	Age	Stage	Date	Age	Stage
Jan. 5	Immature	1-2	Feb. 29	Immature	3
	Adult	1-2		Immature	3
	Adult	3		Adult	4
Feb. 16	Immature	3	March 14	Immature	4
	Adult	4		Adult	4
	Adult	4		Adult	5
March 2	Immature	3	March 28	Immature	4
	Adult	4		Immature	6
	Adult	4		Adult	6
March 31	Immature	5	April 10	Adult	5
	Immature	6		Adult	6
	Adult	6		Adult	7
April 14	Immature	6	April 12	Immature	6
	Immature	6		Adult	7
	Adult	7			
	Adult	7			
July 6	Immature	Regression			
	Adult	7			
	Adult	7			
	Adult	7			

Throughout the period of spermatogenesis there is a definite tendency for adults to precede first-year birds in the attainment of stages 4 to 7. This can be seen in table 1. In only one case does any first-year bird precede any adult. During the period from April 10 to 12, three adults were in stages 5, 6, and 7. A single immature was in stage 6, at the average stage of the three adults and more advanced than one of them. It is apparent that on any given date most adults have reached a more advanced stage than have first-year birds. As regards the onset of regression, the material is inadequate to determine any differential between adults and first-year males. On July 6, three adults were still in stage 7, but the testes of a first-year male were regressing. On July 20, one adult was in the earliest stages of regression. Bundles of sperm were still present, but the average number of sperm per bundle was lower than in breeding testes. The left and right testes measured 13×7 and 11×8 mm., respectively. The testes of two other adults taken on this date were well into regression, with no mature sperm present. The left testes of these males measured 4×2 and 8×5 mm.; the right testes measured 2.5×1.5 and 6×6 mm.

The situation is suggestive of that described for the Redwinged Blackbird (*Agelaius phoeniceus*) by Wright and Wright (1944:51), in which development of the testes in adults preceded that in first-year birds by about three weeks. The differential between age groups is not as well documented in the towhee because of the small samples of first-

year birds, these being indistinguishable from adults in the field. Nevertheless, the general schedule of spermatogenic activity in the towhee suggests that of *Agelaius* and contrasts with that described for the White-crowned Sparrow (*Zonotrichia leucophrys*). Regarding *Z. l. nuttalli*, Blanchard (1941:57) stated that "immature birds stay in the winter condition [stage 1] longer on the average than do the adults," but she included them in her graphs of behavior and development. Of *Z. l. gambelii*, Blanchard and Erickson (1949:266) stated that the testis cycle of first-year birds was identical with that in adults except for slight differences in testis volume, and they found "no evidence to suggest that immatures were consistently behind the adults in the achievement of comparable histologic stages . . ." In this regard the testis cycle of the Rufous-sided Towhee more closely resembles the cycle of the icterid *Agelaius phoeniceus* than that of its fellow emberizine, *Zonotrichia leucophrys*.

Table 2

Lengths of Testes in Millimeters at Different Stages of Gonadal Development					
Stage	Age	Mean Left testis	Range Left testis	Mean Right testis	Range Right testis
1-2	Adult	1.92 (12)	1.5-2.0	1.65 (10)	1.5-2.0
	Immature	1.06 (9)	1.0-1.5	0.94 (9)	0.5-1.0
3	Adult	1.82 (11)	1.5-2.0	1.64 (7)	1.0-2.0
	Immature	1.42 (12)	1.0-2.0	1.12 (13)	1.0-1.5
4	Adult	3.19 (8)	2.5-4.0	2.57 (7)	2.0-3.0
	Immature	2.50 (2)	2.0-3.0	1.75 (2)	1.5-2.0
5	Adult	4.33 (3)	3.0-5.0	4.12 (4)	3.0-5.0
	Immature	4.00 (1)	3.50 (1)
6	Adult	7.17 (3)	5.0-8.5	6.50 (3)	5.0-7.5
	Immature	6.67 (3)	5.5-7.5	5.83 (3)	5.0-6.5
7	Adult	11.95 (19)	10.5-13.0	10.41 (16)	8.0-12.0
	Immature	10.06 (8)	9.0-11.5	8.43 (7)	7.0-10.0

Testis size.—For any given stage, adults tended to have greater testis lengths than those of first-year birds (table 2). This parallels the situation described for *Agelaius phoeniceus* and *Zonotrichia leucophrys*. Reference to table 2 will show that simple measurements of greatest length will not differentiate between adult testes in stages 1-2 and 3, the mean lengths for these stages being nearly equal. The means for the testes of first-year birds in these stages are farther apart, but there is still considerable overlap in testis length between the two stages. Adult testes in stage 4 are considerably larger than those in stage 3. From the small samples available, it would appear that any adult with a left or right testis 2.5 mm. long is in stage 4. From stage 4 through stage 7, testis length in both age groups shows a steady increase. The testes of adults average slightly longer than those of first-year birds throughout, and the left testis always averages longer than the right, the usual situation in birds. Any adult with a left testis 10.5 mm. or longer, and a right testis 8.0 mm. or longer, is in full breeding condition. The corresponding figures for first-year birds are 9.0 and 7.0 mm. Three general groups can be safely differentiated on the basis of testis length: stage 1-2 and 3; stages 4 to 6; and stage 7.

Intertubular tissue.—In order to estimate the relative abundance of Leydig cells in the intertubular tissue, the following classes of abundance were used:

Rare. 1-3 Leydig cells per section.

Occasional. 5-10 cells per section.

Fairly common. Up to 3 cells per 500 \times field.

Common. 5-15 cells per 500 \times field.

Very common. 20 or more cells per 500 \times field.

In 35 males collected between August 3 and December 22, what appeared to be fully developed Leydig cells were rare in the testes of 12 birds (August 3 [2], September 21 [2], September 28, October 12, November 9 [2], November 23, December 5, and December 22 [2]). Such cells were occasional in the testes of five birds (September 28, October 12 [2], November 26, and December 22). In the testes of the remaining 18 birds, small numbers of partly enlarged and somewhat rounded cells were found, apparently similar to those described by Miller (1954:18) for the Golden-crowned Sparrow (*Zonotrichia atricapilla*) and considered by him to be possibly developing Leydig cells. In the material at hand, it was not possible to differentiate consistently between spermatogenically inactive testes which lacked or possessed Leydig cells (stages 1 and 2 of Blanchard and Erickson, 1949).

In January and early February there was a definite increase in the numbers of Leydig cells in both first-year and adult birds. Of 18 males collected between January 5 and February 4, Leydig cells were fairly common in the testes of 15, occasional in one, and rare in one; they were common in the testes of a first-year male collected on February 4. Of five males collected on February 15 and 16, Leydig cells were common in the testes of four, and fairly common in the fifth. The testes of a sixth male contained heavy deposits of fixative which precluded making an accurate count. Leydig cells were common in the testes of three birds collected on February 29. Thus, a definite further increase in the numbers of Leydig cells occurred between February 4 and 15 and continued at least until mid-March.

The female cycle.—The factors influencing the ovarian cycles of passerines are poorly understood. Some evidence from other studies suggests that psychic factors may be of importance in bringing about progression of the cycle; such factors might be the presence of an adequate nest site and food supply and the presence of a male (see Burger, 1949:225–226; Marshall, 1951:253–255). In collecting the females used in this study, it was realized that the collecting of a male might have a deterrent effect on the progression of the ovarian cycle of his mate. Therefore, an effort was made to avoid collecting females on successive trips at localities at which males had been taken previously. In addition, records were kept in the field as to whether each female collected was or was not paired. Females were considered paired if accompanied by a male, if a male sang or foraged nearby, or if a male and female responded in company to the squeaks and imitated Pygmy Owl calls used to draw towhees from brush to exposed perches. Of the 29 females collected in 1955 and 1956 from March, when ovarian development was first visible macroscopically, through July, when breeding had ceased, 18 were paired. There is no proof that the other 11 females were or were not mated, as very little time was spent observing the birds before they were collected. All females collected in the critical period from mid-April to mid-May were paired (see fig. 2), and it is felt that the collecting of males did not interfere with the cycles of the females used in this study. It is of interest that in the six pairs of which both members were collected, both male and female were in the same age group. Three adult females were paired with three adult males, and three first-year females were paired with three first-year males.

The female reproductive cycle is presented graphically in figure 2. In 1955, the cycle was more uniform than that of 1956, in that after the first adult in a stage of low development had been collected, on March 2, all females collected subsequently were in this stage of reproductive activity until the onset of the breeding season. In 1956, a first-year female collected on February 29 was still in the inactive stage. The first female collected in a stage of low development was taken on March 14, but two others taken on the same day were inactive. All three were first-year birds. On March 28, an adult

had an enlarged oviduct, and many oöcytes had enlarged to 1 mm., but a first-year bird taken on the same day was still inactive. It may be that first-year females leave the inactive stage more slowly than adults, and that the discrepancy between the cycles of 1955 and 1956 was caused by the preponderance of first-year females collected in 1956. It will be noted (fig. 1) that in the males, also, the samples collected in the spring of 1956 contained a much higher proportion of first-year birds than did the samples collected in the spring of 1955. This was to be expected, since the same collecting areas were used in both years. Apparently, in 1955, most of the established adults were shot off and replaced by birds of the year, and a shift from a preponderantly adult to a preponderantly first-year population took place. In attempting to equate the cycles for 1955 and 1956, only females of the same age should be compared. In 1955, the first immature showing low ovarian development was collected on March 16, and in 1956, on March 14. The first breeding adult was collected on April 27 in both years. The small samples indicate that the timing of the cycles was similar in 1955 and 1956.

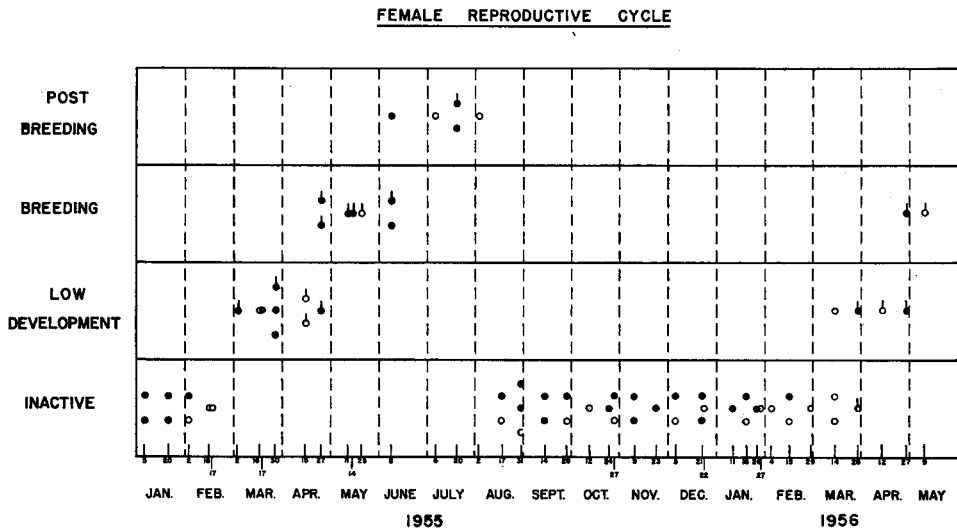


Fig. 2. Reproductive cycle of female *Pipilo erythrophthalmus* based on specimens collected near the Hastings Reservation between January 5, 1955, and May 9, 1956. Dots represent adults; circles represent first-year birds. Symbols with vertical line above represent paired individuals.

In 1955, the first males in breeding condition were collected on April 14, and all adult males collected after this date were in breeding condition. The first breeding females were collected on April 27. Thus, in 1955, adult males reached breeding condition about two weeks before the adult females. In 1956, the first adult male in stage 7 was collected on March 28. However, April 12 was the date on and after which all adult males collected were in breeding condition. The first breeding adult female was collected in 1956 on April 27. Again, the males preceded the females by about two weeks. The discrepancy between the males and females was thus noticeably shorter than that reported for the House Sparrow (*Passer domesticus*) in southern California (about four weeks; Davis and Davis, 1954:343) and for the Song Sparrow (*Passerella melodia*) in the San Francisco Bay region (about four to six weeks; Johnston, 1956:32).

SINGING BEHAVIOR

First and last song dates.—Singing is first heard in most years between the middle of January and the first week in February. Records at the Hastings Reservation show that first singing was heard on the following dates: February 6, 1938; January 18, 1939; February 2, 1940; February 1, 1942; January 29, 1943; January 17, 1951; January 15, 1954; January 31, 1955; February 1, 1956; and February 15, 1957. In 1954, singing was widespread in the general population by February 17, when eight males were heard during one morning's observation. On February 16, 1955, at least ten males were heard during a full day's observation. Thus, in 1954, 34 days elapsed between the first record of singing and the date on which singing was heard commonly; in 1955, this period was 17 days. However, the dates in each year on which song was first considered as being widespread are only one day apart.

Last summer song was heard in 1954 on August 3 (one bird, two minutes); in 1955, on August 7 (one bird, one trill); in 1956, on August 2 (two birds; one sang an awakening song of two trills); and in 1957, on August 4 (one bird, 18 trills). Brief singing heard on August 12, 1956 (one trill), and on August 10, 1957 (one bird, two trills), was not considered as pertaining to regular late summer singing, as these were isolated records preceded by an absence of song of ten and six days, respectively.

In September and October, brief periods of song were occasionally heard, indicative of a slight recrudescence of singing involving only a small percentage of the total male population. On September 14 and 15, 1942, single males in different areas were heard singing. In 1953, song was heard on September 22 (one bird, for about one minute), 23 (one bird, four trills), and October 10 (one bird, three trills); in 1954, on September 4 (one bird, two trills), 20 (one bird, for about one minute), 28 (one bird, for two minutes), and October 4 (two birds; one sang "several" trills, and the other sang four trills); in 1955, on September 14 (one bird, two trills), 17 (two birds; one sang for about two minutes, and the other sang two trills), 18 (one bird, three trills), 24 (one bird, four trills), October 2 (one bird, five trills), 11 (one bird, 15 trills), and 15 (one bird, one trill); in 1956 on September 15 (one bird, four trills) and 29 (one bird, seven trills); and in 1957 on September 8 (one bird, two trills) and October 13 (one bird, four trills). In 1955, one of the birds heard on September 17, and males heard on September 18 and 24, and on October 2 and 11, sang in the same general area, and these records may all apply to the same individual. Counting each record as applying to a different male, only twenty-two were heard in six years. On the 15 birds for which trills were counted, the average was only 4.1 trills per individual. Of the four birds for which the amount of singing was expressed in minutes, the average song period was only 1.5 minutes. Autumn song, although of regular occurrence, is thus brief and it is limited to only a few individuals.

Song form.—The song of the Rufous-sided Towhee is usually a simple trill of 0.4 to 0.6 seconds duration, sometimes preceded by a sharp *chip* note. Five tests on the range of audibility of birds singing from trees at the edge of an open field showed that the mean distance at which trills could be heard by the human ear was 750 feet (range, 700 to 800 feet). The trills themselves, however, may show considerable variation, not only from bird to bird, but within the song repertoire of the individual. Most published descriptions of the song of the Rufous-sided Towhee do not indicate its true variability. For example, Peterson (1941:183) characterizes it as a "drawn-out, buzzy trill, *chweeeeeee*," or in some races as a *chup chup chup zeeeeeeeeee*. Grinnell and Storer (1924:478) render the song as *tu-wheeze*. Hoffmann (1927:313) describes it as a "*bree*, long drawn out." Dawson (1923:395-6) described variation in towhee songs and listed

several phonetic versions of songs which he had heard. He felt that this variation was geographic, and indeed, this may be true; yet, he gave no indication of the wide variation of song in the individual or within a limited population.

There are five basic types of song in the repertoire of most individuals treated in this study. These are as follows:

1. The basic trill. This is a simple, flat trill, without metallic overtones, and it is the most frequently heard song in the population treated here.

2. The chip trill. This song consists of a sharp, clear *chip* followed by a trill. Very rarely, an individual may precede a trill by two *chip* notes. Nearly always, the *chip* is followed by a basic trill.

3. The dry trill. This is a very hard, flat trill, which has the quality of the buzzing of an insect.

4. The metallic trill. This is a simple trill with definitely metallic or "tinny" overtones.

5. The warbled trill. This is a musical trill in which the individual notes are rather widely separated and easily distinguishable. It is the only trill that may be termed "musical" by human standards. It represents the widest departure from the basic trill.

Since most songs are basic trills, and since basic and chip trills make up nearly all song early and late in the season, they are considered the fundamental types of trill in the repertoire.

In addition to the usual complement of five types of trill, males often sing intermediates between two types, such as basic x metallic, basic x dry, and so forth. Since there is considerable individual variation in the basic trill, a great deal of listening to a given male is required in order to differentiate his trill types and the intermediates between them. The most valuable information is derived from the shifts from one type to another that often occur within a period of steady singing.

The complexity of singing is further increased by the tendency of some individuals to alternate two types of trill, singing first one, then the other, in perfect sequence, for minutes at a time. Such periods of alternation, interspersed with periods of singing a single type of trill, are restricted in most instances to the first 30 to 45 minutes of early morning song, although occasionally alternation may be heard at other times of the day. Such alternation usually involves basic trills and one of the other four types. One male, out of sight, alternated full-strength basic trills with half-strength basic trills. Since males invariably sing while facing straight ahead, it does not seem likely that this male was alternately shifting position to face toward, then away from the observer.

A number of aberrant, highly distinctive trills were heard in the course of the study. Some of these were variations of one or more of the usual types, while others were completely unrelated to any of the usual types and were not recognizable modifications of any of them. Such aberrant trills were important mainly in that they appeared to be characteristic of particular individuals singing in the same areas on successive years, and they served to identify particular males from one year to another.

The amount of singing devoted to each of the five usual types of trill can vary from individual to individual, or within the singing of a given individual from day to day. In 2986 minutes of the singing of a nesting male during 13 days of observation in 1954, there was considerable daily variation in the amount of singing time devoted to the different trills. In this period, an average of 47.7 per cent of this male's daily song output was composed of the basic trill (range, 28.2 to 72.4 per cent), and 9.5 per cent was composed of chip trills (range, 2.8 to 24.3 per cent). These two types of trill, considered the most generalized in the repertoire, accounted for an average of 57.3 per cent of the

bird's singing (range, 47.8 to 81.6 per cent), and on only one day did the combined percentage fall below 50 per cent. The two days on which the most chip-trilling was done (21.6 and 24.3 per cent) were those days on which the least basic trilling was done (33.6 and 28.2 per cent). In 2186 minutes of singing by another nesting male the following year, possibly the same bird heard in 1954, an average of 45.8 per cent of song was basic trilling (range, 33.2 to 62.2 per cent), and 17.9 per cent was chip-trilling (range, 2.6 to 45.4 per cent). These two types combined accounted for an average of 63.7 per cent of all song (range, 48.6 to 82.8 per cent), and on only one day did the combined average fall below 50 per cent. In 557 minutes of singing by an unmated male, 62.8 per cent was composed of basic trills and 26.9 per cent was composed of chip trills for a combined average of 89.7 per cent.

The particular type of trill used by a singing male does not depend on the trill types used by other males within earshot. At times, two males singing near each other might sing the same type of trill, but when one changed type, the other did not do so. Nor did singing males shift trill types to match the songs of other males starting to sing near them. Singing males will often shift trill types without any apparent reason. Such shifts may occur within one period of steady singing; at other times a bird which has used one type of trill through several singing periods separated by intervals of several minutes may resume singing after such an interval with another type of trill. Usually the change from one type of trill to another within a single period of steady singing is abrupt, but occasionally a gradual transition may be made. A few examples of the latter will suffice. A male singing basic trills during several song periods from 7:52 to 9:23 a.m. resumed singing basics at 9:28.5 a.m. At 9:31.5 he twice sang chip trills after every third basic, then alternated basic and chip trills three times (six songs), after which he sang chip trills steadily. Another male sang warbled trills during several song periods from 9:56 to 10:46 a.m. At 10:46 he alternated warbled and chip trills three times (six songs) and then sang chip trills during several periods until 11:34 a.m. Another male made a transition from steady basic trilling to steady chip-trilling as follows: basic, chip, basic, chip, basic, chip, basic, chip, chip, chip, basic, followed by steady chip trills.

The reasons for shifts in trill types are obscure. Frequently, as I approached a singing male, the bird would become silent when I came close to him and would then resume with another type of trill after I had passed. This happened so often that it seemed as though disturbance to the singer may be one cause of shifting song types. In most instances, no disturbance was evident to me when a male, watched from a distance, shifted trill types, although the singer may have seen sources of disturbance of which I was unaware. However, it does not seem likely that the gradual transitions from one trill type to another, described previously, resulted from disturbance. Hartshorne (1956) suggested that there is a "monotony-threshold" in the singing of most passerines, and that when singing is nearly continuous, the singer will vary his performance to avoid monotony. However, he defines discontinuous singing as that in which the actual song occupies at most only 30 per cent of the total performance time, with a pause between songs two and one-third times the duration of the song itself (70 per cent of performance time). Since individual songs of the Rufous-sided Towhee last only 0.6 seconds, at most, with an average pause between songs of about six seconds, the song itself occupies only 9.1 per cent of the total performance time, and singing is thus highly discontinuous. Such singing, according to Hartshorne, would not require variability to avoid monotony, and the reasons for the frequent shifts in song type are not clear. No male, at any time of year, was ever heard to run through his entire repertoire of songs before repeating a trill type given previously.

As the song season progresses, singing becomes more complex as additional trill

types are included in the repertoire. All trills heard in January and early February were either basic or chip trills. In 1955, the first dry trill was heard on February 14, the first warbled trill on February 24, and the first metallic trill on March 8. In 1956, the first warbled trill was heard on February 13, the first dry trill on March 20, and the first metallic trill on March 24. In 1955, the first alternation of trill types was heard on April 5, and in 1956, on April 19. Conversely, toward the end of the song season and during the period of fall singing, the performance becomes less complex. Of 51 periods of singing heard from July 20 through October 13, 48 were composed of either basic or chip trills, one was composed of metallic trills, one was composed of warbled trills, and one consisted of alternating metallic and warbled trills (four songs). In addition to being almost entirely limited to basic and chip trills, the singing heard in mid-winter, late summer, and fall is often of low volume, and the individual trills are often abrupt and not of full length. During the latter part of July, and in September, very aberrant trills were sometimes heard. On July 27, 1956, an awakening song consisted of five very abrupt, whistled *pweet* notes, and on July 31, the same bird sang an awakening song consisting of whistled *wheep* and *wheet-wheet* notes. On September 4, 1954, a male gave a loud, harsh note, followed 10 seconds later by a basic trill. On September 17, 1955, a male gave three or four very peculiar *tseep* notes, then an aberrant trill, indescribable, and then he sang basic trills. On September 29, 1956, a bird sang six basic trills and then an aberrant *che-che-che*. It may be that such performances represent singing by birds of the year.

Threat song.—Although some suggestion of threat is implied in most, if not all, of the singing of the Rufous-sided Towhee, the term "threat song" is reserved for the rapid, subdued singing of males in close proximity, often resulting in combat. Such song is characterized by very low volume, and it is sometimes barely audible. It is steady and the rhythm is very rapid, with intervals between songs of no more than one second. Often, the trills are abrupt and incomplete. When two males are near each other both may sing in this fashion, and the trills come so rapidly that at times the singing seems nearly continuous. Males may sing in this fashion for several minutes before a clash results, or a male may sing threat songs on his way to attack another male, or such singing may be heard during a chase. A persistent attack made by one male against another lasted for 35 minutes, with the pursuing male singing very softly much of the time. The pursued bird sang infrequently, possibly because he carried a dead oak leaf in his bill during at least the last 26 minutes of the running combat, still retaining it when he finally flew off. Howard (1952:77) has described the habit of males carrying dead oak leaves during territorial disputes of the Blackbird (*Turdus merula*). Not all attacks are accompanied by typical threat song. They may be completely silent, or they may be accompanied by singing of normal strength and rhythm.

Nice (1937:57) describes a similar type of low, rapid singing in the Song Sparrow (*Passerella melodia*); in that species it occurs in males newly arrived on the breeding grounds when they attempt to take up territories near already established birds. She also notes that a bird singing in this fashion will frequently hold one wing straight up in the air and flutter it. This habit has also been noted in the Rufous-sided Towhee at the Hastings Reservation, but it apparently occurs in males which are already established on territory. The six instances of wing-raising display noted in towhees occurred on April 24, May 8 (2), May 21, May 30, and July 15. Since nesting usually starts during the last week in April, all these instances fall within or beyond the nesting period. Linsdale (MS) noted two displays; the pursuing male displayed in one instance, and the pursued male in the other. Three displays were given by a color-banded male known to be mated. In one case, this male displayed when another male started to sing nearby;

he then flew closer to the singing male and sang loudly and steadily in return. This same male started to display on July 15 when a full-grown juvenile flew in and landed near him, but he checked his movement before his wing was fully extended. Once he displayed when no other towhee was evident to me, but a short time later he was fighting with and driving off another male. In the sixth instance an unbanded male, singing, suddenly started to move through nearby brush, pausing several times to raise and flutter one wing. I saw no other towhee, but the male under observation traveled about 30 feet through the brush before returning to his original station and resuming his singing. Low, rapid, aggressive singing and the wing-raising display are common to the Song Sparrow and the Rufous-sided Towhee, but they seem to occur under different circumstances in the two species.

A peculiar, rapid, musical twitter, rising and falling, was given by a nesting male chasing another male on four separate occasions. I had heard this twitter previously from other fighting males, but it was so unlike any other performance given by a Rufous-sided Towhee that I did not associate it at the time with that species. Almost a year later another male, color-banded, gave the same twitter as he pursued a male invading his territory. Although it is not heard frequently, this vocalization is apparently given during combat by a small proportion of the male population.

Posture.—In the normal singing posture, the tail may be slightly cocked above the dorsum or held in line with it. The same individual may sing with the tail in either position. The wings are usually held against the sides of the body although a few males sang with them folded over the dorsum. At each song the bill is opened, the tail is depressed slightly, and the head is thrown back. Some males sang muted trills while holding insects in their bills, which were thus not opened to the full extent at each song. Males invariably face forward while actually singing, and the eyes are kept open. Towhees singing from the ground while foraging always look straight ahead to sing, interrupting their foraging to do so. This is probably because the songs of the Rufous-sided Towhee are so brief. The Winter Wren (*Troglodytes troglodytes*), with a song lasting five or six seconds, turns its head from side to side while singing (Armstrong, 1955:58), as do the Grasshopper Warbler (*Locustella naevia naevia*), with a trill sometimes sustained for as long as two minutes, and the Nightjar (*Caprimulgus europaeus europaeus*), with a sustained trill sometimes continuing for five minutes (Witherby, Jourdain, Ticehurst, and Tucker, 1948).

Song perches.—Song perches of the Rufous-sided Towhee are highly variable and males may sing from the ground while foraging or from as high as 50 feet up in tall trees. By far the greatest number of singing perches noted were in trees, especially in live and valley oaks, but to some extent in willows and sycamores. Shrubs of various kinds may be used, especially coffeeberry, with some records for elderberry, coast ceanothus, poison oak, and chamise. Of 1579 song perches recorded, 1239 were in trees, 196 were in shrubs or brush, 133 were on the ground while foraging, and 11 were on the ground, not foraging. Towhees may sing from exposed perches, such as bare limbs or the tops of trees or shrubs, but usually they sing from leafy cover where they are at least partly concealed. Intermittent singing from the ground while foraging was noted in all months from February to August. Much of the early song noted in February was intermittent and came from the ground. Although the singer was not always seen, sounds of foraging between songs indicated that he was foraging at the time. Song heard early in the season and in the fall tended to be delivered from somewhat lower perches than that heard from March through July. Not including song from the ground, the song perches of four males heard in January averaged 10.75 feet above ground, and those of six males heard from September through November averaged 13 feet up. The average elevations of singing

Table 3

Height in Feet of Singing Perches of a Nesting Male During Incubation Period

Date	Number	Height
May 6	9	25.0
May 8	9	25.4
May 10	8	23.2
May 11	17	21.1
May 12	11	21.6
May 13	35	19.2
May 14	26	17.4
May 15	25	15.9

Table 4

Height in Feet of Singing Perches of an Unmated Male

Date	Number	Mean height	Range
Apr. 9, 1956	11	23.3	0-45
Apr. 11, 1955	15	25.1	0-40
May 17, 1955	76	21.9	0-50
June 21, 1955	41	17.7	0-40

males recorded on 511 occasions from March through July ranged from 15.8 feet in June to 23.3 feet in April. The status of a given male during the breeding season appears to have some effect on the average height above the ground from which he sings. It will be seen that the mate of an incubating female sang from increasingly lower elevations as the incubation period progressed, with an especially pronounced change during the three days prior to hatching (table 3). The unmated male for which data are given (table 4) appeared to sing from increasingly lower elevations as the breeding season progressed. Further, in the nesting male, singing from the ground while foraging increased noticeably during the last four days of the eight days after hatching on which observations were made. The number of song periods from the ground per hour during the first four days after hatching were 0.49, 0.00, 0.21, and 0.09, but during the last four days the frequency increased regularly as follows: 0.54, 0.67, 1.33, and 1.70. Since the number of trips which he made per hour to the nest with food for the young varied only slightly during the eight days of observation, the increased amount of singing from the ground did not result from more frequent foraging periods, but it may have resulted from a switch from foliage foraging to ground foraging.

Intervals between songs.—The intervals between songs, when singing is steady, are surprisingly regular, and they vary within narrow limits. Some individuals were heard singing for several minutes at a time with perfectly regular intervals between songs, indicating a well-marked, inherent sense of timing in this species. Singing, while fairly steady, may be very irregular when it is carried on by birds foraging or preening between songs. However, even when engaged in other activities between songs, a male may maintain perfectly regular intervals. One male, watched for five minutes, dressed his back and breast feathers between songs, but he faced ahead and sang at perfectly regular intervals of four seconds. The following sequence of the numbers of songs per minute sung by one male will indicate the regularity of singing over a period of time. In seventeen minutes, he sang: 10, 11, 10, 9, 11, 11, 10, 10, 11, 10, 9, 10, 11, 8 (switched trill types midway in series), 10, 10, and 11 songs per minute. During one 32-minute period, he sang: 13, 13, 12, 13, 13, 13, 12, 12, 12, 13, 12, 12, 13, 12, 12, 12, 12, 11, 12, 8 (Scrub Jays, *Aphelocoma coerulescens*, screamed nearby during this series), 11, 11, 12, 11, 11,

10, 10, 9, 10, 8, 9, and 7 songs per minute. The definite decrease in singing during the last seven minutes may well have been due to fatigue, perhaps actual fatigue of the syringeal muscles.

Six hundred and thirty-eight timed intervals between songs ranged from one to 28 seconds in length. The mean was 6.2 seconds, and the median was five seconds. Of the 638, 505 (79.2 per cent) fell between four and eight seconds. There seemed to be little seasonal variation in interval length. Combining with the timed intervals figures derived from counts of number of songs per minute, and allowing 0.6 seconds for each song, the following monthly figures result: January, 20 trills, average interval, 5.8 seconds; February, 329 trills, 6.0 seconds; March, 535 trills, 5.8 seconds; April, 338 trills, 6.2 seconds; May, 962 trills, 6.8 seconds; and June, 835 trills, 5.4 seconds. The monthly variation falls well within the range of individual variation within any one month, and there are no pronounced shifts during the song season. Since the figures were derived from birds observed at all times of day, and since fatigue may possibly lengthen the intervals between songs, the monthly averages are surprisingly close.

Table 5

Singing of an Unmated Male for Eight Hours, May 24, 1956

Hour	Number of songs	Per cent of time singing	Average interval
8:15-9:15 a.m.	642	95.8	5.1
9:15-10:15	567	93.3	5.6
10:15-11:15	418	91.7	7.6
11:15-12:15 p.m.	412	88.3	7.4
2:25-3:25 p.m.	409	84.2	7.4
3:25-4:25	291	70.0	8.4
4:25-5:25	413	86.7	7.3
5:25-6:25	238	64.2	9.4
Totals	3390	84.3	7.3

On May 24, 1956, the singing of an unmated male was recorded for eight hours, from 8:15 a.m. until 12:15 p.m., and from 2:25 to 6:25 p.m. In this time he sang a total of 3390 trills. In the first four hours the percentage of each hour spent singing decreased steadily, as did the number of songs per hour, while the average interval between songs lengthened steadily (table 5). In the afternoon, singing decreased further in the first two hours, rose in the third hour, and fell off sharply in the last hour. There are three ways in which a bird can decrease the amount of singing that it may do at different times of the day. First, it may keep the intervals between songs the same but devote less time per hour to singing; second, it may devote the same amount of time per hour to song but lengthen the interval between songs; or third, it may use a combination of both methods. It will be seen that in the morning, the relative (not actual) percentages of singing time per hour decreased by only 7.8 per cent from the first hour to the last, but the average interval between songs increased by 45.1 per cent. This method of decreasing song output might be advantageous as it tends to spread singing over each hour fairly regularly, thereby avoiding lengthy periods of silence. Thus, the announcement of the presence of this male to other birds of either sex within earshot was rather steady, although the actual number of songs per hour declined noticeably. In the afternoon, the relative percentages of each hour spent singing, during the hours of most and least song, differed by 26 per cent, and the average interval between songs increased by 28.8 per cent, indicating that a combination of both methods was used. This resulted in a number

of lengthy periods of silence, as much as 14.5 minutes passing without any song, whereas the longest period of silence in the morning was only four minutes. The song output was less intense in the afternoon, not only in terms of the number of songs per hour and time spent singing, but in the less even distribution of song during the period of observation.

Amount of singing.—In January and February, when the song season begins, and again in the last half of July and in early August, when the season comes to an end, periods of singing are brief and they are separated by lengthy intervals. The same is true of singing heard in September and October.

Table 6

Numbers of Singing Males Counted on Early Morning Censuses, 1956

Date	Number of singing males	Date	Number of singing males
March 22	4	June 5	10
24	8	7	7
31	8	9	10
April 2	6	11	5
5	5	21	11
9	3	23	10
12	4	26	10
16	3	29	10
19	8	July 3	7
21	10	7	9
24	9	10	7
28	12	13	8
May 1	10	17	7
3	10	20	2
7	11	24	2
12	13	27	2
15	11	31	1
19	10	August 2	0
22	10	7	0
25	11	9	0
29	10	14	0
31	14	18	0

By the third week in March, most males are in full song, and on March 19, 1956, one male sang steadily for 44 minutes. In the first half of April, there is a decrease in singing. Some males which had been heard in certain places became silent at this time. This decrease is reflected in the results of a series of early morning censuses of singing males, starting on March 22, 1956 (table 6). By the third week in April, the numbers of males recorded on the censuses began to rise, and they reached a high level by April 28, at which time nesting activities got under way in most of the population.

During the breeding season, the amount of singing by a given individual seems to depend on whether or not he is mated, and if mated, on what his position in the nesting cycle may be.

The greatest amount of singing was done by an unmated male observed on May 24, 1956 (table 5). In eight hours, he sang 84.3 per cent of the time. Another unmated male, observed on April 11, 1955, sang 77.9 per cent of the time between 5:07 and 8:12 a.m. In this period only one other male sang, for two minutes, or 1.1 per cent of the time, and no song was heard from a nearby area in which two towhees, one a male and a second of undetermined sex, had been seen foraging 10 feet apart at 6:15 a.m. On May 17, 1955, the same unmated male was followed for 13 hours and 13 minutes. He sang 63

per cent of seven hours and 13 minutes in the morning, and 17 per cent of six hours in the afternoon. The latter figure is abnormally low, as the singing of this bird and birds of other species in the area was cut down by a strong wind which blew during much of the afternoon. During the morning, two other males sang persistently until 8:00 a.m., then sporadically until 9:00, and after this, one sang briefly a few times during the next three hours and ten minutes, when observations ended. On June 21, 1955, the same male was followed for eight hours and 35 minutes. Between 4:46 and 10:01 a.m., he sang 226.5 minutes (74.2 per cent of the time) and between 3:20 and 6:50 p.m., he sang 100.5 minutes (47.9 per cent). During the entire period of observation, he sang 63.5 per cent of the time. In the morning, three other males were heard. One sang 15 minutes (4.9 per cent), one sang 2.5 minutes (0.82 per cent), and the third sang 17.5 minutes (5.7 per cent). In the afternoon, two males sang, one for one minute (0.48 per cent) and one for 9.5 minutes (4.5 per cent). This unmated male was heard on many days, and at all times of day, when he was the only towhee singing within earshot.

On April 9, 1956, the same unmated male, identified by several aberrant types of trills first heard in 1955, was observed from 5:57 to 7:57 a.m.; during this time he sang 109 minutes (90.8 per cent). On April 19, he was noted accompanying a female. On the 19th, 21st, and 28th, he was observed for a total of 5 hours and 16 minutes, mainly in the early morning, and in this time he sang only 36 minutes (11.4 per cent). Unmated males apparently sing much more persistently than mated males.

The reactions of a male which had lost its mate seem to be somewhat different from those of a male unmated to begin with. On April 15, 1955, I collected two females from mated pairs occupying narrow, brushy draws about one-quarter of a mile apart. Be-

Table 7

Amount of Daily Singing by a Nesting Male, 1954

Date	Observation period (minutes)	Per cent of time singing
May 6	636	18.8
7	729	34.8
8	898	40.4
10	851	45.1
11	660	45.0
12	856	30.8
13	686	37.0
14	841	33.9
15	904	32.8
	Post-hatching	
17	861	21.5
18	687	15.0
19	867	16.3
20	698	13.3
21	854	15.6
22	873	34.8
24	855	37.9
25	669	50.1

tween 5:40 and 9:05 a.m., the only singing heard in the area was done by one male, for about two minutes, after I had shot his mate. On April 19, I returned to the same area. Between 7:50 and 8:30 a.m., "Dismated" male A sang 5.5 minutes and called 17 times. Between 8:49 and 9:17 a.m., at the other draw, no evidence of male B was noted. Upon my returning to male A, between 9:38 and 11:17 a.m., he sang 159 times and called 157 times. The only other towhee heard during this time called for a total of about four min-

utes. No other towhee song was heard. Avian activity was very low, and aside from the persistent calling and singing of a Bewick Wren (*Thryomanes bewickii*), only brief periods of singing and calling were heard from six other species. The great amount of calling in relation to singing, as opposed to the slight amount of calling done by unmated birds, suggested that this male had not only become more vocal after the death of his mate but that he was still searching for her four days later.

The singing of a nesting male observed between May 6 and 25, 1954, is presented in table 7. Hatching occurred on May 16. On May 6, this male sang only 18.8 per cent of the time. His singing steadily increased from May 7 through May 11, and then it fell off irregularly through May 15. Following hatching, his singing was noticeably depressed from May 17 through May 21, and it then rose steadily from May 22 to 25. The rise in the amount of singing seemed to correlate with decreased attendance at the nest by the female. From May 17 to 21, the female's attendance ranged from 63.1 to 88.6 per cent. On May 22, her attendance was 54.9 per cent, and on the 24th and 25th it was virtually nil.

Table 8

Amount of Daily Singing by a Nesting Male, 1955

Date	Observation period (minutes)	Per cent of time singing
May 26	587	38.5
28	493	50.9
30	552	30.8
June 1	265	42.6
2	451	45.5
4	567	62.8
6	542	62.9
	Post-hatching	
7	552	48.9
9	515	37.9

Seven days of the singing of a nesting male, between May 26 and June 9, 1955, are presented in table 8. In this nest, hatching occurred on June 7, and the nest was destroyed on June 10 or 11. The amount of time spent singing varied irregularly between May 26 and 30, rose sharply from June 1 to 6, fell 14 per cent on June 7, and fell another 11 per cent on June 9. On this last day, the male sang 24.8 per cent of the time between 5:05 and 9:00 a.m. At that time, a Scrub Jay flew to a point just above the nest and peered down at it. The male, on his way to the nest with food, flew off calling, but his mate dashed in and drove off the jay. At 9:01, the male began to sing, and until 11:40, when observations ended, he sang 66.7 per cent of the time, a figure comparable to that noted on June 4 and 6. When I resumed observations at 4:41 p.m., he sang 25.4 per cent of the next two hours, a figure comparable to that of the early morning. His overall performance for the day probably would have been about 25 per cent had it not been for the appearance of the jay and the male's greatly increased singing following the extreme danger to the nest.

Another male with young in the nest, observed on May 16, 17, and 19, 1956, for a combined total of 10 hours and 10 minutes, sang 17.4, 15.2, and 10.2 per cent of the time, respectively. There appears to be a definite tendency for males to sing more persistently during incubation than when young are in the nest. Nice (1943:119-120) found that this was true of male Song Sparrows.

The decrease in the number of singing males recorded in the censuses of June 7 and

11 may correlate with the presence of recently fledged young, although on June 9 the number heard was normally high (table 6). In early July there is a noticeable decrease in the numbers of males heard singing. Not only is this reflected in the census counts, but on some days no towhees were heard at all in areas where males had been heard to sing previously. On July 3, 1954, only one bird was heard in three hours and 45 minutes, and on July 9, none was heard in four hours and 35 minutes. On July 12, 1956, no towhee was heard in eight hours and eight minutes. During the first two weeks in July, most of the singing is confined to brief periods. By July 20, 1956, the census figures showed an abrupt decline, and on August 2 the last song of the summer was heard, but it was not in the census area. This situation contrasts sharply with that described by Marshall (1957:117) for Rufous-sided Towhees in the pine-oak woodland of southern Arizona and northern Sonora. He stated that in this area, "singing increases greatly in July and August as contrasted with April through June . . ." although he noted that juveniles were abundant in late July and August, suggestive of nesting in June. If these birds did nest in June, then June and July would bear the same relation to the nesting season at the Hastings Reservation as July and August in the area studied by Marshall. No increase in singing was noted at the Reservation in June, and July was definitely a period of steadily decreasing song output.

Time of first vocalizing.—First vocalizing is here understood to mean either the first calling or singing of the day, whichever comes earlier for any particular individual. The Rufous-sided Towhee was one of the early species to become vocal in the area studied. On the average, from February 25 to October 3, this species was the seventh to call or sing. However, this rating is very general and serves merely to establish the Rufous-sided Towhee as a relatively early riser, and it should not be assumed that there was any rigid schedule in the order of first vocalizing in the species present. From mid-winter to early fall there were pronounced shifts in the time of first vocalizing of one species relative to another. The so-called "bird clock" was not operative over the entire period of time; rather, there was a series of "bird clocks," each evident during a particular segment of the entire study period.

In general, Violet-green Swallows (*Tachycineta thalassina*) and Western Bluebirds (*Sialia mexicana*) were by far the earliest birds heard, with the swallows usually the first species recorded. On those mornings when the bluebirds preceded the swallows, it seems likely that the latter had actually been active first but that the flock, twittering on the wing, came into earshot after the bluebirds had been heard. These observations agree with those of Weydemeyer (1934:251), who noted that Western Bluebirds were the second species to sing in the early morning at Fortine, Montana, being preceded only by Tree Swallows (*Iridoprocne bicolor*).

The next group of species to become vocal included the Western Flycatcher (*Empidonax difficilis*), Mourning Dove (*Zenaidura macroura*), Western Wood Pewee (*Contopus sordidulus*), California Quail (*Lophortyx californicus*), and Rufous-sided Towhee, more or less in that order, but all heard within the span of a few minutes. They were followed by the Brown Towhee (*Pipilo fuscus*) and the Bewick Wren. Scrub Jays, Wrentits (*Chamaea fasciata*), Plain Titmice (*Parus inornatus*), Hutton Vireos (*Vireo huttoni*), Red-shafted Flickers (*Colaptes cafer*), Nuttall Woodpeckers (*Dendrocopos nuttalli*), Anna Hummingbirds (*Calypte anna*), and the other species present had not ordinarily become vocal by the time I left the area.

Considering the middle group of five species, the exact order of awakening was seldom the same on any two consecutive mornings. In addition to the variation in the order of vocalizing from one morning to another, there were shifts in precedence that appeared to be seasonal. The relations of the Rufous-sided Towhee to the other four species and

to the Brown Towhee are shown in figure 3. From February 25 to May 15, this species preceded *Lophortyx* on every morning but one, when the two sounded off virtually simultaneously. On May 25 and 28 the two exchanged precedence on successive mornings of observation. From May 29 to June 29, *Lophortyx* was the earlier of the two, with only one exception. The quail in the area became silent after June 29. Mourning Doves were first heard in the study area on March 29, and from that date through July 8 the order of precedence was quite irregular. From July 9 until August 9, *Zenaidura* was without exception the earlier of the two to vocalize. After August 9, the doves stopped calling entirely, although their presence in the area was indicated by flight sounds up to October 3.

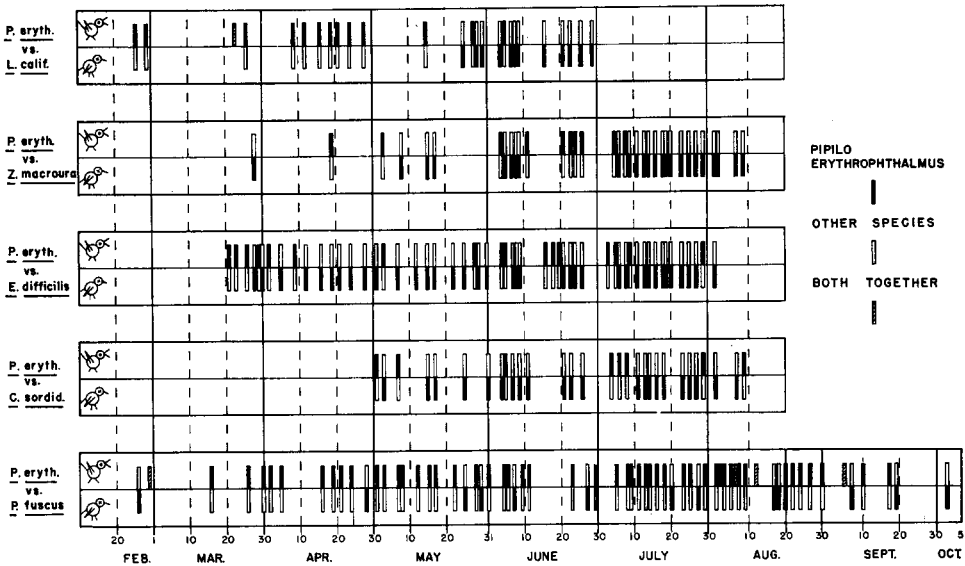


Fig. 3. Separate comparisons of the earliness of first vocalization of the day of *Pipilo erythrophthalmus* and the first vocalizations of: *Lophortyx californicus*, *Zenaidura macroura*, *Empidonax difficilis*, *Contopus sordidulus*, and *Pipilo fuscus*. In each daily comparison the earlier species is above the line. Records were made in 1955 and 1956 at the Hastings Reservation.

The relations of the towhee to the two species of tyrannids are rather similar. The Western Flycatcher was first heard in the study area on March 22, 11 days after its earliest recorded arrival at the Reservation (Linsdale, 1947:238). From March 22 to 27, the towhee preceded the flycatcher. From March 29 to April 9, there was a noticeable transition period, following which the flycatcher was the earlier, with relatively few exceptions, until it was last heard on August 1. The Western Wood Pewee was first heard on May 1, 16 days after its earliest recorded arrival at the Reservation (*loc. cit.*). Unlike the Western Flycatcher, which had arrived earlier in the study area, the pewee at once entered a transition period relative to the towhee, between May 1 and 7, and then became generally earlier until August 9, when it was last heard.

In relation to the Brown Towhee, the Rufous-sided Towhee was predominantly the earlier until August 12; from this date until October 3, the two species varied considerably in relation to each other, and on the 14 mornings of observation during this period they were exactly even in their order of first vocalizing.

As the Rufous-sided Towhee became relatively late in its vocalizing, other species

were recorded. Scrub Jays were heard only between July 25 and October 3, Wrentits between August 7 and September 2, and a Plain Titmouse on July 25 and 31.

From these observations it seems apparent that, with regard to the species in the study area, the bird clock operated in rather general fashion, and that a particular "clock" could apply only to a certain part of the study period.

Table 9
Relation of Time of Last Songs and Last Calls to Sunset, 1955-1956

Date	SONGS		
	Number	Mean	Range
April 29-May 28	6	20.9	15-28
June 4-30	10	24.5	16-33
July 1-13	3	21.0	19-24
July 18-August 16	6	10.5	4-16
	CALLS		
April 29-May 28	7	23.1	16.5-29
June 4-July 13	3	25.7	24-28
July 18-August 16	13	12.4	2-24

Time of last vocalizing.—Between April 29 and August 16, 25 records were made of the time of the last song of the day, and 23 records were made of the time of the last call of the day. The relation of these songs and calls to sunset are shown in table 9. All of the records pertained to males, as judged by the fact that calling came from particular points at which song had been heard a short time previously, or that it came from a territory occupied by an unmated male. The only pronounced seasonal difference that appears is that the time of last vocalizing from July 18 on was noticeably earlier in relation to sunset. This shift occurred during the period when awakening song came markedly later in relation to both morning civil twilight and sunrise, and it suggests that after the middle of July, the daily activity period of the Rufous-sided Towhee becomes shorter in relation to both sunrise and sunset. Interspecific variation in the cessation of the day's activities relative to sunset appears to be high. For example, Nice (1943:106-107) found that there was little seasonal variation in the time of occurrence of the last note (either song or *tchunk*) of the Song Sparrow in relation to sunset from December to May, and again in October. Armstrong (1955:257, fig. 38), on the other hand, found considerable seasonal variation in the roosting times of the Winter Wren. Most of his records were based on a male. Roosting time came relatively earlier to sunset in May, June, and July. Since the dates of first eggs of the Winter Wren at Cambridge, England, where Armstrong's observations were made, ranged from April 15 to May 8 (*op. cit.*: 162), it would appear that the wren roosted relatively early in relation to sunset shortly after the onset of the breeding season, whereas the towhees, as judged from the time of last vocalization, did not cease daily activity at a relatively early time until after the breeding season was over. As is true of other passerines, towhees start their daily activities earlier in relation to sunrise than they cease these activities after sunset, as judged by the time of first and last song (fig. 4, table 9).

With regard to the time of last vocalization of the Rufous-sided Towhee in relation to other species, my records are too few to allow any detailed comparison. On the few occasions when detailed records were kept of the order of last vocalizing of all the species within earshot, those that were the latest to be heard included the California Quail,

Mourning Dove, Acorn Woodpecker (*Balanosphyra formicivora*), Western Flycatcher, Western Wood Pewee, Scrub Jay, Rufous-sided Towhee, and Brown Towhee. Since all but the jay and the woodpecker are among the first birds to vocalize in the morning, the few records tend to support the statement that "in general, the earliest risers are the latest to bed" (Nice, 1943:109).

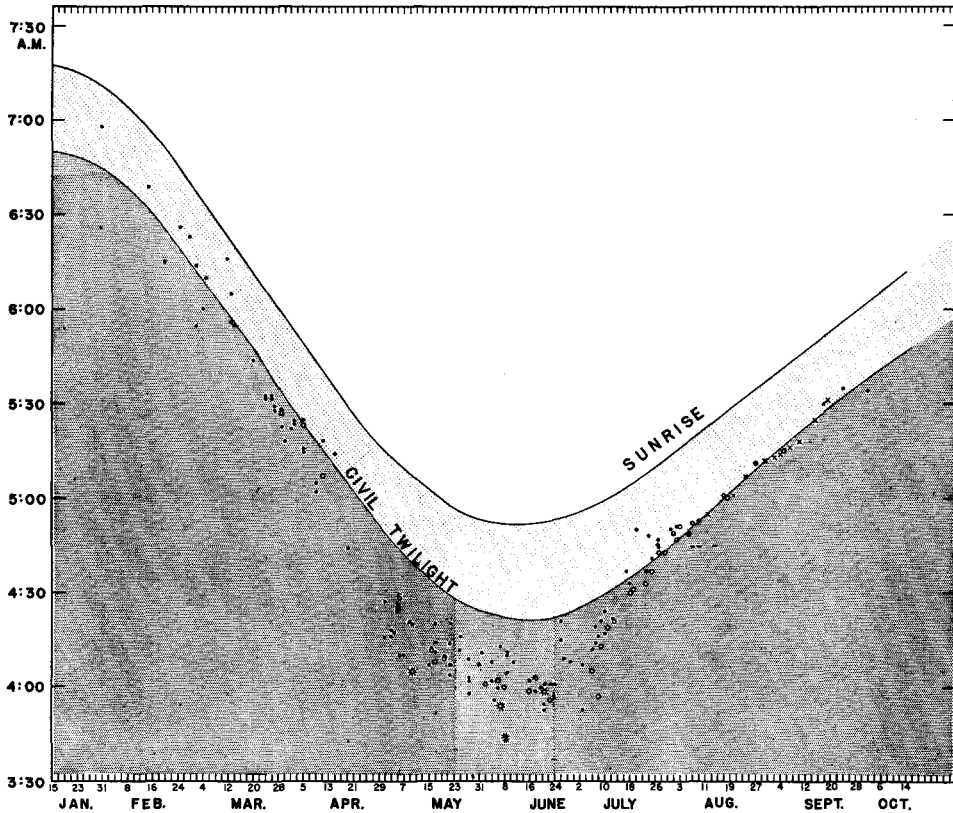


Fig. 4. Times of first songs of the day of *Pipilo erythrophthalmus* relative to morning civil twilight and sunrise on clear mornings only. Dots represent males of unknown status; circles represent a single unmated male. Rayed dots represent males already singing when observations began. The symbol X represents mornings in 1955 when observations were made but no song was heard; dashes represent similar data for 1956. Records were made in 1955 and 1956 at the Hastings Reservation.

Awakening song.—The term "awakening song" is something of a misnomer, as there is no evidence that a bird sings immediately upon awakening (Allard, 1930:455; Nice, 1943:99). Awakening song is used here as synonymous with first song (of the day), without any implication as to the actual awakening times of the individuals involved.

The awakening song of the Rufous-sided Towhee consists of a series of trills, coming between five minutes after and 25 minutes before the beginning of morning civil twilight. I have never heard night singing by this species, and there is no problem as to what constitutes true awakening song, as there is, for example, in the Song Sparrow (Nice,

1943:102). In January and February, uninterrupted periods of first singing averaged 5.33 minutes long for six males. On six mornings in May and June, nesting males sang awakening songs averaging 26.9 minutes long, interrupted only by occasional changes of singing perch. From July 24 to October 2, uninterrupted first singing was confined to very brief periods; in 12 instances it averaged 2.5 minutes long, and in ten instances it averaged 4.6 trills.

A total of 206 awakening songs was recorded between January 31 and October 2, 1954 to 1956. Of these, 152 occurred on clear mornings and 54 occurred on overcast mornings. The relation of songs heard on clear mornings to both morning civil twilight and sunrise is shown in figure 4. Between January and August, five general periods can be distinguished. In January and February, when song is becoming established in the male population, first song is relatively late. It comes noticeably earlier in March and in the first half of April, when mated males are seen on territory. From the middle of April, about two weeks before the onset of the breeding season, to the end of June, which is for most birds the end of the nesting season, awakening song is noticeably early. Of the nine songs recorded between April 16 and 30, eight were heard on overcast mornings, and they are not comparable to the other songs considered thus far. A single song heard on the clear morning of April 19 came 21 minutes before civil twilight, a figure somewhat below the average for May 1 to 15, but within the range of variation for the 18 songs recorded during that period. The eight songs recorded on overcast mornings averaged 13.9 minutes before civil twilight, considerably earlier than the average of 4.3 minutes for 10 songs occurring on overcast mornings between March 3 and April 12, and exactly the same as the average of seven songs recorded on overcast mornings from May 1 to 15. This suggests that the great increase in earliness, first evident on clear mornings from May 1 to 15, actually started about the middle of April.

	No. calls prior to first song	N	No. sang without calling	No. minutes from 1st call to 1st song	N
MAR.-APRIL	23.2	8	0	4.34	14
MAY 1-15	1.75	4	3	0.40 ⁺	5
MAY 17-31	2.36	11	6	0.85 ⁺	13
JUNE 4-11	3.7	9	4	0.17 ⁺	9
JUNE 16-29	4.2	16	6	0.75 ⁺	16
JULY 3-13	6.2	13	5	1.1	12
JULY 17-31	35.4	9	0	5.6	13
AUG. 1-18	37.5	2	0	3.5	9

Fig. 5. Seasonal variation in numbers of calls preceding the first song of the day of *Pipilo erythrophthalmus*, and variation in time elapsing between first call and first song of the day, on clear mornings only. Records were made in 1955 and 1956 at the Hastings Reservation. Those figures with superscript + - signs in the second column from the right are approximations only.

The period July 3 to 14, when song came about five minutes later than during the period May 16 to June 29, may represent a transition toward the abrupt shift to lateness occurring in the last half of July and persisting throughout August, as indicated by the songs of one aberrant, unmated male in 1955. Records between September 18 and October 2 average slightly later than those for August, but they are too few to be significant.

Another well-marked trend was noted in the amount of calling that males did prior to their first song of the day, as indicated by the average number of calls preceding first song and the average time elapsing from first call to first song (fig. 5). The most pronounced breaks occur between the end of April and the middle of May, and between the middle and the end of July. Here, the evidence indicates that, although earliness of first song might have been similar in the last half of April and the first half of May, the amount of calling prior to first song was not. On the clear morning of April 19, a male called 40 times before he sang; on clear mornings between May 1 and 15, four males for which calls were counted called 0, 7, 0, and 0 times (average, 1.75). Six males for which calls prior to first song were recorded on overcast mornings between April 16 and 28 averaged 37 calls; three males on the overcast mornings of May 7 and 12 averaged 2.33 calls (0, 0, and 7), and nine males on overcast mornings during the entire month of May averaged only 11.6 calls. The virtual elimination of calling prior to first song apparently occurred between May 1 and 15, starting with the onset of the nesting season.

The gradual increase in the amount of calling between May 1 and June 29 may have been coincidental, as the differences between successive two-week periods are slight. The slight increase in calling in the period from July 3 to 13, paralleling the slight decrease in earliness of first song in that period, may have been a transition toward the precipitous increase in calling noted between July 17 and 31, which paralleled the great increase in lateness of song in that period.

The Rufous-sided Towhee was not the only species to show a seasonal decrease in the amount of calling prior to first song, followed by a gradual increase later in the season. The Western Flycatcher and the Western Wood Pewee also showed such seasonal variation in their singing program, although on a different monthly schedule than that of the towhee.

Songs on overcast mornings averaged later than those heard on clear mornings. Since overcast days were, for the most part, interspersed in irregular fashion with clear days, the average time of first song on overcast mornings was compared to the average time of first song heard on clear mornings within two days, before and after, of each overcast morning. The overall averages are: clear mornings, 16.4 minutes before civil twilight, and cloudy mornings, 10.3 minutes before civil twilight. The average difference of 6.1 minutes is rather close to the 4.5 minutes difference found in the Song Sparrow by Nice (1943:106). Males called more before singing on overcast mornings. In March and April, eight males averaged 23.2 calls on clear mornings, and nine males averaged 34.6 calls on cloudy mornings. The corresponding figures for May are 2.2 calls for 15 males and 11.6 calls for nine males.

Discussion.—A number of features of the singing of the Rufous-sided Towhee show seasonal variation. The appearance and disappearance of song, height of singing perch, complexity of song, amount of singing, time of awakening song, and times of first and last vocalizing of the day relative to sunrise and sunset all show variation which correlates either with the onset and progression of the gonad cycle, or with a given individual's status in the breeding season. Initially, the question is, what effect, if any, does the gonad cycle have on singing, and what is the effect on the singing of an individual of his status as a breeding bird.

In 1955, song was first heard on January 31. At about this time (February 2) Leydig

cells ranged from fairly common to common in the testes of three males, and a definite increase in the average numbers of Leydig cells had been noted between January 5 and February 2. In 1956, singing appeared on February 1; again, Leydig cells in the testes of males taken at about this time (February 4) ranged from fairly common to common. Thus, singing did not appear in any male until there had been an increase in the Leydig cells in the male population generally. In 1955, singing was considered widespread in the male population by February 16. Between February 2 and 16, 1955, there was a further increase in the numbers of Leydig cells; a similar increase was noted between February 4 and 15, 1956. The spread of singing through the male population thus appeared to correlate with an increasing level of Leydig cells in the first half of February.

Nice (1937:63-65), with 15 records of the date of first singing of the Song Sparrow at Columbus, Ohio, found a high degree of correlation between the date of first singing and the mean temperatures on that date and on the two days previous. She noted some singing on January 7 and 8 following two warm days, and from January 13 to 21 following one warm day. She also noted that as singing appeared on later dates, it appeared at progressively lower temperatures, and the appearance of song followed a curve which indicated that the temperature threshold decreased about 0.75°F . per day. For the Rufous-sided Towhee, temperatures are available for eight dates for the start of singing. No well-marked correlations or trends are discernible. At the Hastings Reservation, the maximum deviation of mean temperature from normal, either positive or negative, was at the most 5.8 degrees on any date, and the proportional divergence from normal was even less than at Columbus, since the mean temperature there in January was 29°F . (*op. cit.*: 224), and the 18-year mean for this month at the Reservation is 47.2°F . The apparent lack of correlation with temperature in the Rufous-sided Towhees is very probably a result of the milder and more even climate in which they live. The amount of excess temperature (summed daily excess above normal after December 31) also shows no correlation with the appearance of song.

At the Reservation, the dates of first appearance of song refer to only a few individuals which were apparently advanced in their readiness to sing, and there was no correlation between the first singing of such individuals and the minor fluctuations in mean environmental temperature that preceded singing. But the dates were not those on which singing was widespread in the male population. It is not possible to tell from Nice's account what proportion of the total population was singing on any given starting date. Hence, my limited data, although showing no correlation, serve to stress the point that no correlation need necessarily occur and that any test of significant correlation between first song and temperature requires populational samples.

Since there is some evidence that low temperatures may retard the gonad cycle (Blanchard, 1941; Burger, 1948; Davis and Davis, 1954; Engels and Jenner, 1956; Marshall, 1951), it seems possible that the correlation found by Nice between environmental temperatures and the starting dates of song may be secondary, and that the primary correlation may be between temperature and the gonad cycle, with the start of singing merely an indication of the degree of an individual's gonadal development on a given date. This might explain the lowering of the temperature threshold by 0.75°F . per day; in other words, this might be another way of saying that the degree of gonadal development necessary for the appearance of song takes one day longer to come about for every drop in temperature of 0.75°F . One must assume that if the temperature threshold for the appearance of song drops steadily with the passage of time, either some physiologic change must be occurring in the individual, or some change in the social structure of the population must provide the stimulus for song. The latter does not seem

likely, as "hostile behavior towards territorial rivals *begins at the time that singing is well established*" (Nice, 1937:67, italics mine). Further evidence for temperature-gonadal control rather than for direct temperature control over the start of singing is found in the fact that singing in the Song Sparrow ceases in November and "no matter what warm and pleasant weather may occur in December, only occasional snatches of song are heard" (*op. cit.*: 63).

The lack of correlation found by Nice (*op. cit.*:66-67) between the amount of total daily sunshine and the amount of singing by Song Sparrows in January and February cannot be considered as evidence against the gonadal control of early season singing. Bartholomew (1949:462-6) investigated the effect of variation in natural light intensity on the testis cycle of the House Sparrow. Except near sunrise and sunset, the lowest light intensity recorded, during a violent snow squall, was far above the threshold necessary to bring about maximal gonadal development. Since figures for total daily sunshine do not indicate light values near sunrise and sunset, the former statistic is not significant in this regard.

In the Rufous-sided Towhee, the noticeable shift toward the earliness of awakening song that starts at about mid-April correlates with the attainment of breeding condition in the males. Although Leydig cells were classed as "very common" by mid-March, studies on other passerines, using special histological techniques (*Corvus monedula*, Threadgold, 1956a, 1956b) or very detailed methods of estimating the amount of the glandular components of the intertubular tissue (*Zonotrichia leucophrys gambelii*, Blanchard and Erickson, 1949) indicate that the interstitial cells increase up to the time that breeding condition is achieved. If the Rufous-sided Towhee follows this pattern, as seems likely, then the maximum development of the interstitial cells would have occurred in mid-April, when the males came into breeding condition. The shift in the time of awakening song that occurred in mid-April apparently coincided with maximum gonadal development. The shift in the time of awakening song from a relatively late time in January and February to an earlier time in March and the first half of April occurred at a time when the testes were still undergoing development, both inter- and intratubularly. This shift may thus be a response to the increasing level of interstitial cells.

Nice (1943:103-104) noted a shift toward earliness of awakening song in the Song Sparrow from a "basic" period in January and February to an "intermediate" period in February and March. She correlated this shift with the excess temperature occurring during the two weeks preceding the shift in each year. She also found evidence of a decreasing temperature threshold, the shift occurring after a smaller amount of excess temperature the later it was noted. Again, it seems probable that the primary correlation was between temperature and gonadal development, and she states that "[the intermediate period] was never reached in January no matter how warm the weather" (*op. cit.*:104).

If singing were controlled solely by the gonadal development of the individual, we would expect a steady increase in the singing of the Rufous-sided Towhee from about the beginning of February through the middle of April. However, this was not the case, as there was a noticeable decrease in singing during the first half of April, just as the males were coming into breeding condition. Further, during the breeding season, unmated male towhees sing considerably more than mated males. This was true of unmated males heard in April, May, and June. This phenomenon has been reported for a number of species (see, for example, Nice, 1943:172-174), and in some cases the arrival of a mate suppresses song instantaneously and completely (for example, in the Snow Bunting, *Plectrophenax nivalis*, Tinbergen, 1939:77). The difference in the amount of sing-

ing between mated and unmated males appears to exist independently of gonadal development, and certainly the instantaneous, or nearly instantaneous suppression of song in an unmated male when a mate appears cannot be thought of as under gonadal control. Nice (1943:119) lists a number of changes in the amount of singing by Song Sparrows which correlate with the progression of events in the nesting cycle. She found that song was inhibited just prior to nesting, but that it was uninhibited during building, laying, and incubating. Male passerines usually reach breeding condition before the females do; in the Song Sparrow in the San Francisco Bay region of California, males reach breeding condition from four to six weeks ahead of the females (Johnston, 1956:32). Surely the males studied by Nice had reached maximal gonadal development well before nest building got under way. Yet, singing was noticeably inhibited prior to building and uninhibited later. Such changes in the amount of singing do not correlate with gonadal changes, but they appear to depend on the events in the nesting cycle taking place at a particular time.

Nice (*loc. cit.*) noted that song was inhibited after the appearance of young in the nest. In the Rufous-sided Towhee, a similar decrease in the amount of singing was noted in males which had young in the nest. It may be that the appearance of young evokes other hormonal activity and that this, in turn, may cause a regression of the gonads with a concomitant decrease in the amount of singing. The hormone involved would probably be prolactin, which evokes parental behavior. Lofts and Marshall (1956:105) state, "It has been known for many years that the artificial administration of prolactin leads to testis collapse in birds (Riddle and Bates, 1933). This is now shown [in *Passer domesticus*, *Fringilla coelebs*, and *Chloris chloris*] probably to be identical with the tubular steatogenesis, involving also the production of cholesterol, that occurs naturally in wild seasonal birds when the young hatch and are being fed by the parents." Bailey (1950:249) noted that prolactin, in addition to blocking the response of the testes of *Zonotrichia leucophrys pugetensis* to light treatment, also inhibited the singing of treated birds, as opposed to the controls, which sang loudly and frequently. It seems possible that the suppression of song in male Song Sparrows and towhees after their young have hatched is under hormonal control. However, the testes of male towhees throughout June and the first week of July contained greatly expanded tubules, an abundance of grouped spermatozoa, and a minimum of interstitial tissue per section, this narrowly compressed between adjacent tubules. All these features are typical of testes in full breeding condition. That some decrease in testis volume had occurred in June is indicated by the fact that the volume of five testes of adults in breeding condition in April and May (longest and shortest diameters measured to the nearest 0.5 mm.) averaged 315.9 mm.³, whereas seven testes of breeding adults taken between June 8 and July 6 averaged 267.1 mm.³. However, this difference in volume is hardly indicative of any pronounced tubular collapse.

The whole problem of testis regression possibly induced by prolactin following the appearance of young in the nest is further complicated by the fact that many passerines commonly raise two or more broods in a single season. In the period from 1954 to 1956 at the Hastings Reservation, most pairs of the Rufous-sided Towhee raised only one brood, as indicated by the size of juveniles noted during the spring and summer months. That some pairs raised two broods is indicated by the collecting of a very small, bob-tailed juvenile, probably two days out of the nest, on August 2, 1955. In other parts of the range, such as at Berkeley, California, where conditions are more humid, Rufous-sided Towhees commonly raise two broods, and the potential to breed twice in a season is undoubtedly inherent in the species. In species, or populations, which normally raise two or more broods a year, it must be assumed that if prolactin secretion in the male,

following the appearance of the young in the nest, depresses the gonads with a concomitant depression of song, such gonadal suppression cannot be final, or similar to the eventual collapse of the gonads at the end of the breeding season, as the male would not be sexually competent when it came time to start a second nesting. Further, in any species, the first nest may be destroyed after the young have hatched but before they have fledged. If prolactin had caused an irreversible gonadal regression by the time of nest destruction, a renesting would be impossible.

Although it is possible in the laboratory to bring about a pronounced collapse of the gonads by the administration of prolactin, it seems likely that in nature a very delicate balance is achieved between gonadal function and other hormonal activity. This would insure the participation of the male in rearing the young in those species in which both sexes participate in this activity, yet it would allow the male to maintain, or recover, sexual competence so that renesting or second nesting is possible. At least some recovery of male breeding behavior following the fledging of first brood young in the Song Sparrow is indicated by Nice's statement (1943:175) that pouncing, the courtship display of the male, "is confined typically to the early stages of the nesting cycle . . . It may reappear, however, the day that the young leave the nest, if another brood is to be started immediately."

The disappearance of singing in the Rufous-sided Towhee in late summer correlates with both gonadal regression and molt. The most pronounced decline in singing, as indicated by census records (table 6), the noticeable shift toward lateness of awakening song (fig. 4), and the increase in calling prior to awakening song (fig. 5), all appeared on about July 20. This was also the first date on which the testes of all males showed signs of regression, and it was the first date on which molting males were collected. It seems likely that both factors play a part in bringing about the cessation of song. However, it seems unlikely that molt, although it is a severe drain on the energy resources of the individual, would alone be sufficient to inhibit the singing of a few trills, at least early in the morning. Yet, such inhibition occurs. Actually, molt and gonadal regression should not be thought of as completely separate, unrelated processes. In many species, both passerine and non-passerine, molt is preceded by a period of thyroid activity, and the suggestion has been made that increased thyroid function may interfere with gonadal development (Davis and Davis, 1954:342). It is futile to speculate on which factor, molt or gonadal regression, has the most profound effect on singing, as we are by no means justified in assuming that these are entirely independent processes, at least in north temperate birds.

In the fall, the slight but regular appearance of song in a few male Rufous-sided Towhees may be evidence of a slight rise in gonadal activity in such individuals. There was no evidence of gonadal recrudescence in any adult, but one first-year male had gonads which were in Stage 3, spermatogenically, and the gonads of this male and two others of a total of seven first-year males collected between September 14 and October 12, 1955, contained occasional Leydig cells, whereas these cells were classed as either "rare" or "small and rare" in the testes of seven adults collected during the same period. Further, several songs heard in September were noticeably aberrant, suggesting that they might have been the songs of first-year males. It may be, then, that the gonads become slightly active in a few first-year males, perhaps individuals hatched unusually early in the breeding season, and that such birds are responsible for the few brief periods of singing heard each fall.

It should be noted that song is heard in the fall and winter in several species of territorial birds, but in at least one instance, there was no sign of gonadal activity at that time. In *Zonotrichia leucophrys nuttalli*, which remains on its breeding territory through-

out the year, Blanchard (1941:13) had many records of fall and winter song, but she found that the gonads of this race were completely inactive from early or mid-October at least to middle or late December (*op. cit.*:52). *Zonotrichia leucophrys pugetensis*, which is a winter resident at Berkeley, arrives there in late September and early October in large flocks, and it is therefore not territorial at that time. Yet, these birds are singing on their arrival at Berkeley (*op. cit.*:39), although the males start to undergo gonadal regression in late July and early August, and "by the time they arrive on their wintering grounds their testes, if we may judge from volume alone, have already reached the inactive condition" (*op. cit.*:87). In the winter resident Golden-crowned Sparrow (*Zonotrichia atricapilla*), which is not territorial on its wintering grounds, considerable singing is heard in September and October when it arrives in California, but the gonads at that time "are at winter size and condition" (Miller, 1948:3). It is possible that such singing in non-territorial winter residents has to do with the establishment of dominance relationships in winter flocks, but even so, it is apparently not under gonadal control. The problem involving fall and winter song, and its cause and control, are very complex for those species in which there is no well marked autumnal gonadal activity, and such singing apparently depends on behavioral factors which are not understood at present.

In the Rufous-sided Towhee, there were individual instances of singing that could not be explained on the basis of gonadal control, temperature factors, or the position of the male in the breeding cycle. Song heard on August 10, 12, 13, 26, and 30 occurred at a time when males are far into the molt and gonadal regression. One male sang on November 26, at a time when the gonads are at the winter minimum. This date is about three and one-half months after the normal cessation of summer song, about six weeks after the cessation of fall song, and about two months before the first appearance of song near the beginning of the next reproductive cycle. In 1955, a male sang on January 5, and the next singing was not heard until January 31. The most aberrant bird was an unmated male whose awakening song had been heard over a long period of time in 1955. Another male in the same area sang his last awakening song on July 27, but the unmated male sang an awakening song on every morning on which observations were made up to and including August 9, and subsequently on five of 11 mornings (four clear, one overcast) of observation up to and including September 5, when his last awakening song was heard. In 1955, the last song heard from any male other than this one was noted on August 7. On August 11, the unmated male sang 8 to 10 loud basic trills at 8:35 a.m. and on August 16, he sang 11 basic trills, about two-thirds normal volume, at 7:04 p.m. The persistence of this bird in singing an awakening song almost throughout the period of molt and gonadal regression could not be explained.

SUMMARY

The gonad cycles of the Rufous-sided Towhee near the Hastings Reservation were determined for the breeding seasons of 1955 and 1956. Males reached breeding condition at about mid-April and females about two weeks later. The testes of all males were regressing by July 20. The interstitial tissue showed an initial increase in the numbers of Leydig cells between mid-January and the beginning of February and a further increase from the beginning of February to at least mid-March.

The singing behavior of the Rufous-sided Towhee at the Hastings Reservation is described. Singing usually starts between mid-January and the first week of February, and it comes to an end in early August. In September and October, there is a slight but regular appearance of singing, involving only a few males.

Singing is widespread by mid-March, but in early April there is a noticeable decrease in the amount of song. By the last week in April, at the time that nesting gets under

way, singing is again at a high level. Nesting males sing a higher percentage of the time during incubation than after the young have been hatched. Unmated males are the most persistent singers of all.

Awakening song comes earliest in relation to sunrise and morning civil twilight from mid-April to the end of June. During the first two weeks in July it comes somewhat later, and by July 20 it comes at a much later time.

The beginning of singing correlates with the initial increase in the number of Leydig cells in the interstitial tissue, and the establishment of song in the male population correlates with the further increase in Leydig cells during the first half of February. The pronounced increase in the earliness of awakening song starting in mid-April occurs when males have reached full breeding condition. The great decrease in the amount of singing and the lateness in the time of awakening song in the latter part of July correlate with the onset of molt and gonadal regression. The limited but regular appearance of singing in September and October may correlate with the slight increase in the number of Leydig cells that occur in those months in the testes of a few first-year birds.

The decrease in singing during the first half of April and the apparent decrease in singing by an unmated male after he had become paired do not appear to correlate with any gonadal changes.

LITERATURE CITED

- Allard, H. A.
1930. The first morning song of some birds of Washington, D. C.: its relation to light. *Amer. Nat.*, 64:436-469.
- Armstrong, E. A.
1955. *The wren* (Collins, London).
- Bailey, R. E.
1950. Inhibition with prolactin of light-induced gonad increase in white-crowned sparrows. *Condor*, 52:247-251.
1952. The incubation patch of passerine birds. *Condor*, 54:121-136.
- Bartholomew, G. A., Jr.
1949. The effect of light intensity and day length on reproduction in the English sparrow. *Bull. Mus. Comp. Zool.*, 101:431-476.
- Blanchard, B. D.
1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.*, 46:1-178.
- Blanchard, B. D., and Erickson, M. M.
1949. The cycle in the Gambel sparrow. *Univ. Calif. Publ. Zool.*, 47:255-318.
- Burger, J. W.
1948. The relation of external temperature to spermatogenesis in the male starling. *Jour. Exp. Zool.*, 109:259-266.
1949. A review of experimental investigations on seasonal reproduction in birds. *Wilson Bull.*, 61:211-230.
- Davis, J.
1957. Determination of age in the spotted towhee. *Condor*, 59:185-202.
- Davis, J., and Davis, B. S.
1954. The annual gonad and thyroid cycles of the English sparrow in southern California. *Condor*, 56:328-345.
- Dawson, W. L.
1923. *The birds of California*. Vol. I (South Moulton Co., San Diego, etc.).
- Engels, W. L., and Jenner, C. E.
1956. The effect of temperature on testicular recrudescence in juncos at different photoperiods. *Biol. Bull.*, 110:129-137.

- Grinnell, J., and Storer, T. I.
1924. Animal life in the Yosemite (Univ. Calif. Press, Berkeley).
- Hartshorne, C.
1956. The montony-threshold in singing birds. *Auk*, 73:176-192.
- Hoffmann, R.
1927. Birds of the Pacific states (Houghton Mifflin Co., Boston).
- Howard, L.
1952. Birds as individuals (Collins, London).
- Johnston, R. F.
1956. Population structure in salt marsh song sparrows. Part I. Environment and annual cycle. *Condor*, 58:24-44.
- Linsdale, J. M.
1947. A ten-year record of bird occurrence on the Hastings Reservation. *Condor*, 49:236-241.
- Lofts, B., and Marshall, A. J.
1956. The effects of prolactin administration on the internal rhythm of reproduction in male birds. *Jour. Endocrin.*, 13:101-106.
- Marshall, A. J.
1951. The refractory period of testis rhythm in birds and its possible bearing on breeding and migration. *Wilson Bull.*, 63:238-261.
- Marshall, J. T., Jr.
1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. *Pac. Coast Avif. No. 32*:1-125.
- McCabe, T. T.
1943. An aspect of collectors' technique. *Auk*, 60:550-558.
- Miller, A. H.
1948. The refractory period in light-induced reproductive development of golden-crowned sparrows. *Jour. Exp. Zool.*, 109:1-11.
1954. The occurrence and maintenance of the refractory period in crowned sparrows. *Condor*, 56:13-20.
- Nice, M. M.
1937. Studies in the life history of the song sparrow. I. A population study of the song sparrow. *Trans. Linn. Soc. N. Y.*, 4:1-247.
1943. Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerines. *Trans. Linn. Soc. N. Y.*, 6:1-328.
- Peterson, R. T.
1941. A field guide to western birds (Houghton Mifflin Co., Boston).
- Threadgold, L. T.
1956a. The annual gonad cycle of the male jackdaw *Corvus monedula*. Qualitative aspects. *La Cellule*, 58:19-42.
1956b. The annual gonad cycle of the male jackdaw *Corvus monedula*. Quantitative aspects. *La Cellule*, 58:45-54.
- Tinbergen, N.
1939. The behavior of the snow bunting in spring. *Trans. Linn. Soc. N. Y.*, 5:1-94.
- Weydemeyer, W.
1934. Singing of the mountain bluebird and the western bluebird. *Condor*, 36:249-251.
- Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F., and Tucker, B. W.
1948. The handbook of British birds. Vol. 2. Fifth impr. (H. F. and G. Witherby Ltd., London).
- Wright, P. L., and Wright, M. H.
1944. The reproductive cycle of the male red-winged blackbird. *Condor*, 46:46-59.

Hastings Reservation, University of California, Carmel Valley, California, December 6, 1957.