

## NESTING BEHAVIOR OF THE RUFIOUS-SIDED TOWHEE IN COASTAL CALIFORNIA

By JOHN DAVIS

Despite the relative abundance and wide distribution of the Rufous-sided Towhee (*Pipilo erythrophthalmus*) in the western United States, the only major study of its breeding cycle in that area is the one recently published by Baumann (1959). Baumann described the entire cycle of a population of towhees at San Francisco, California, from the establishment of territory to the final independence of juveniles. The present study is restricted to the actual nesting behavior of a few pairs of towhees at the Hastings Reservation, northern Monterey County, California. Information on the singing behavior and gonad cycle of this population has been given in a previous paper (Davis, 1958).

### MATERIALS AND METHODS

Observations were made on a few nests for long periods of time; this procedure resulted in a lack of information on certain aspects of the nesting program, but it allowed a quantitative approach to other aspects of nesting behavior which would otherwise not have been possible. Most of the observations are mine, but in addition the field notes of other workers at the Hastings Reservation have been used. Of special value was a long, careful series of notes taken by John A. Gray, Jr., on a towhee nest in 1939. This nest was elevated and could be seen by the observer; all the nests that I watched were placed on the ground and screened by surrounding vegetation.

Information on incubation and on the brooding and feeding of nestlings was derived from the following nests, which will be referred to subsequently by the numbers given here: Nest 1—observed by John A. Gray, Jr., for 70½ hours on 11 days between June 21 and July 8, 1939; Nest 2—observed by me for 232½ hours on 19 days between May 6 and 26, 1954; Nest 3—observed by me for 71½ hours on 10 days between May 26 and June 9, 1955; Nest 4—observed by me for 11½ hours on May 16, 17, and 19, 1956.

A total of 386 hours was spent observing these four nests. In addition, brief observations were made on the building of two nests. Since no nest went to completion, it was not possible to obtain information on the behavior of the young after departure. All references to time are Pacific standard time.

I take this opportunity to acknowledge gratefully the long-continued support of the program at the Hastings Reservation by Mrs. Russell P. Hastings which made possible both Gray's and my field work.

### NESTING DATES

Nesting at the Hastings Reservation ordinarily starts in the last ten days of April. The earliest nest was found near the beginning of the incubation period on April 10, 1960; it contained a definitive clutch of three eggs. Building must have started in the first week of April. The next earliest evidence of nesting was recorded on April 27, 1939, when a nest containing four eggs was found. Building of this nest must have started prior to April 20. In the same year, a towhee was seen carrying nest material on April 21, and a female was seen carrying material on April 24. In 1946 one was noted carrying material on April 24, and in 1955 a female was seen with her bill full of coarse, dry grass on April 28. Additional information on the start of breeding was derived from specimens collected near the Reservation. Of four females collected on April 15, 1955, none was in breeding condition; two of three collected on April 27 had defeathered incubation patches and although they had not yet laid, indications were that laying would have

started within a few days. In 1956, a single female collected on April 12 had not yet reached breeding condition; of two collected on April 27 one had not yet reached full breeding condition and the other had already laid one egg.

The latest nest at the Reservation was found on June 28, 1941, at which time it contained three eggs. Thus, the major part of the breeding season is confined to a period of about two and one-half months. It is not possible to state whether nests found in June represented second nests or renesting by pairs which had attempted unsuccessfully to nest earlier in the season. The failure of all nests actually observed for long periods of time suggests that many, if not most, of the June nests represented renestings. Further, most of the juveniles observed during the summer months appeared to be at about the same stage of development, suggesting that most pairs raise only one brood at this locality. That some pairs may raise two broods is suggested by the collecting of a bob-tailed juvenile, perhaps two days out of the nest, on August 2, 1955. The situation is similar to that described by Baumann (1959:190) for towhees at San Francisco; of four pairs studied by him, three raised one brood, and one raised two broods.

#### NEST SITES AND MATERIALS

Of 25 nests found by various observers at the Hastings Reservation, 23 were placed in depressions in the ground so that the upper surface of the nest was either flush with the ground surface or projected slightly above it. It is not known whether the depressions in which nests were placed were natural or made by the towhees. Two nests were surrounded by unbroken oak leaf litter, suggesting that the nest depressions had been scratched out. Cohen (1899:62), describing the nesting of this species at Alameda, California, stated that "in all these ground-nesting cases the bird scratches a hollow in the sandy soil or leaf mould about an inch deep before bringing building material," but since the statement was not supported by any specific observation, it is difficult to know whether it was based on observation or assumption. Only two of the 25 nests at the Reservation were placed above the ground; one was 3 feet up in a tangle of coffeeberry (*Rhamnus californica*) and Nuttall bedstraw (*Galium nuttallii*) and the other was 18 inches up in California sagebrush (*Artemisia californica*).

Although most nests of the Rufous-sided Towhee throughout its western range have been found on the ground, there may be some variation among local populations in the location of the nest. Egg data slips in the Museum of Vertebrate Zoology for 12 California and one Nevada nest of this species from a total of 12 localities show that eight nests were placed from 2 to 6 feet above ground and only five were placed on the ground. On the other hand, data slips for a series of 11 nests collected near Fyffe, Eldorado County, California, show that ten were placed on the ground and one 2½ feet above ground, and of 11 nests found by Baumann (1959:184), ten were placed on the ground and one was 32 inches up in a bush.

It would seem that long series of nests from restricted localities show a great preponderance of ground nests; the data slips for 12 localities, previously referred to, may have shown a preponderance of elevated nests because such nests might be more easily found by casual collectors not concentrating on this one species. Of considerable interest is the statement of Cohen (1899:61) that in Alameda, from 1886 to 1892, he found "annually an average of eight sets and a few nests containing young. There were then approximately nine pairs of birds. . . . At that time the nests were placed on the ground with very rare exceptions, but owing to an army of cats that had become self supporting there were in 1898 only seven pairs . . . on the premises and nearly all the nests for the last five or six years were placed off the ground. . . . Having freed the premises from the cats by late spring, the Oregon Towhees began to build more on the ground. . . ." This

suggests that the Rufous-sided Towhee is primarily a ground nester but that a local population may change its nesting habits in response to abnormally high pressure from nest predators.

Nests at the Reservation were characteristically placed in relatively exposed situations and never deep within tangles or heavy thickets of brush. Most were found in grassy and/or leaf-littered areas at the edges of thickets or near isolated shrubs or trees so that overhanging branches might afford some shelter from above. Several nests were placed on the ground between the branches of fallen oak limbs. Since nests were flush with the ground, or nearly so, surrounding vegetation such as bracken (*Pteridium aquilinum*), tarweed (*Madea* sp.), common vervain (*Verbena lasiostachys*), or various grasses provided sufficient lateral screening.

Despite the relatively exposed situations in which nests were found, they were impossible to discover unless one followed a bird to the nest or accidentally flushed an incubating or brooding female. The relatively exposed sites of most nests had both advantages and disadvantages. Trips to and from the nest were made easily by the parents without their having to work through heavy vegetation; on the other hand, nests were frequently exposed to the sun and this entailed protection of the eggs or young by extensive incubating or brooding.

Nests showed a surprising uniformity of construction despite the variety of locations in which they were found. Of 12 for which some description has been set down, the outer supporting structure of 11 was composed of strips of bark, usually in combination with a few dead leaves and pieces of coarse, dry grass. Only one nest lacked bark strips in its outer portion. Nests that were examined closely were made of strips of inner bark, with only a few scraps or short strips of outer bark present. In one nest strips of the inner bark of willow (*Salix* sp.) were used and in another strips of the inner bark of poison oak (*Rhus diversiloba*). In both instances the materials were obtained nearby. The longest bark strip noted in any nest measured 11½ inches; most strips were about one-half inch wide.

The inner cups of all nests were composed of fine, dry grass stems. In one nest most of the stems had been nipped off at or near the base, and some of the stems bore roots. In this instance most of the stems contained dry seed heads, identified as soft chess (*Bromus mollis*), which were available near the nest. The largest stem was 13 inches long from root to seed head and had been neatly coiled into the walls of the compact lining. The materials used by the towhees at the Reservation were apparently identical to those used by the towhees studied at San Francisco by Baumann (1959:185).

Measurements of nests varied surprisingly little. The inner cups of three nests measured  $3\frac{3}{8} \times 3\frac{1}{4}$ ,  $3\frac{1}{4} \times 3\frac{1}{4}$ , and  $3 \times 3$  inches, the birds achieving a nearly, or seemingly perfectly, circular cup in each instance. The inner cups of four nests were  $2\frac{7}{8}$ ,  $2\frac{3}{4}$ ,  $2\frac{1}{4}$ , and  $2\frac{1}{2}$  inches deep. Outside diameters of three nests were  $4\frac{1}{4} \times 4\frac{3}{4}$ ,  $4\frac{1}{4} \times 4\frac{1}{2}$ , and  $4\frac{1}{2} \times 4\frac{1}{2}$  inches. The very narrow limits of variation of placement, materials, and size of nests at the Reservation suggest that the behavior patterns associated with nest construction have been selected for rather rigidly in this population.

#### NEST BUILDING

Nest building was observed in only two pairs, and in each the female gathered and placed all the material. One female was watched building a nest on the ground on May 5 and 6, 1955. On May 5, between 6:03 and 6:36 a.m., she made 12 trips to the nest, averaging one every 2.8 minutes. On these trips she carried large pieces of nest material, twice identified as bark, apparently for the outer supporting structure. She gathered this material about 25 feet from the nest. From 6:36 to 7:07 she remained away from

the nest; at 7:07 she resumed building. On May 6, she made 14 trips between 5:32 and 6:26 a.m., one every 3.9 minutes. On three trips the material that she carried was identified as coarse, dry grass. Observations were resumed at 6:54, and in the next 32 minutes she made seven trips, one every 4.6 minutes. From 7:28 to 7:32 she foraged, resuming work on the nest at 7:33, but after only one trip she joined her mate to scold a weasel passing through their territory between 7:36 and 7:46.

Resuming her building activity at 7:46, she spent two minutes gathering fine, dry grass stems 10 to 15 inches long, holding them by the middle so that when she flew to the nest at 7:48 they trailed back along the sides of her body. Between 7:48 and 7:59 she made four trips; twice she carried fine, dry grass, and once, two pieces of limp, gray, weathered grass. The change in the nature of the materials being used since 7:46 suggested that she was now working on the inner lining. Between 7:59 and 8:25 she did no building, and at 8:25 I searched for the nest. Although I had seen her make a number of trips, it took me five minutes to locate the nest, so well was it hidden. It seemed complete save for the bottom of the inner cup, which had just been started. Between 5:15 and 6:00 p.m., she made two trips, carrying fine, dry grass on one, and a mixture of fine and coarse dry grass on the other.

On May 7, no trip was made between 8:53 and 9:45 a.m., and when I visited the nest neither member of the pair was in sight. The nest at this time appeared to be complete; it had been soaked by intermittent rain falling earlier in the morning. I placed a small twig in the cup; on the following day, May 8, it had been removed, indicating that the nest had at least been visited, if not worked on. The nest was completely dry at this time. On May 10 no bird visited the nest between 4:00 and 6:00 p.m., and on May 11, the first egg was laid. Construction of this nest took at least two days.

Another nest under construction (Nest 3) was located on May 21, 1955. At 8:45 a.m. I found the female carrying coarse, dry grass. From 8:55 to 9:34 she made three trips, carrying long, fairly fine dry grass; this was held in the middle in the same fashion as the female at the first nest. The nature of the material being carried suggested that work had just started on the inner cup. No further trip was noted between 9:34 and 11:05 a.m., or between 3:06 and 5:15 p.m. When the nest was next examined at 7:17 a.m. on May 23, two eggs were present, so that the nest must have been completed on May 21 or early on the 22nd at the latest.

The males of both pairs took no part whatsoever in gathering materials or in building. The male of the pair watched on May 5 and 6 never accompanied his mate while she gathered material and carried it to the nest, nor did he come close to the nest at any time. He spent a great deal of time singing, often out of sight of his mate. Occasionally, when the female left the nest, she would join him, sometimes after he had called but more often while he was singing. Infrequently the male flew to the female after she had left the nest, but when she then left him to gather material, he did not follow her. The male of the pair watched at Nest 3 on May 21 behaved in the same manner. Thus, at the two nests where brief observations were made, the males not only took no part in nest building, but they made no effort to stay near their mates or nests.

#### CLUTCH SIZE AND EGG LAYING

Clutch size over the western part of the range of the species ranges from two (Baumann, 1959:190) to six (Cooper, 1870:242), with the great majority of clutches being of three or four eggs. Fifteen nests found at the Hastings Reservation either contained young or had been watched over a period long enough to determine the end of egg laying. Of these 15, one contained two, six contained three, seven contained four, and one contained five eggs or young. The pitfalls present in accurately determining clutch

size are exemplified by Nest 3, in which the female laid the last of five eggs on May 26. Between the evening of June 2 and the early morning of June 4 one of the eggs disappeared and no trace of it was ever found. An observer discovering this nest on June 4 would have assumed a four-egg clutch. In the light of this experience, reports of two-egg clutches should be viewed with suspicion. It is not possible to state how often errors of this nature have influenced reported clutch size in this or other species. In the present instance, one can say only that 13 of the 15 nests found at the Hastings Reservation contained either three (6 nests) or four (7 nests) eggs or young, and that the population agrees in clutch size with the figures reported over the western range of the species.

In two nests in which egg laying was followed, eggs were laid one a day on successive days until the clutch was complete. Eggs appeared to be laid in the morning. In one nest, the first egg was laid between 5:30 p.m., May 10, and 12:46 p.m., May 11. The third egg was laid between 4:35 p.m., May 12, and 11:35 a.m., May 13, and the fourth and last egg was laid between 6:20 and 9:48 a.m., May 14. In Nest 3, the third egg was laid between 5:45 p.m., May 23, and 9:40 a.m., May 24, the fourth between 5:25 p.m., May 24, and 11:30 a.m., May 25, and the fifth between 7:27 and 10:16 a.m., May 26.

The length of time elapsing between the completion of the nest and the laying of the first egg was determined in two cases. One nest was completed on May 7, and the first egg was laid four days later, on May 11. At Nest 3, the female was still building on May 21. When the nest was next visited, early on the morning of May 23, it contained two eggs, one apparently laid on May 22 and one on May 23. It appeared as though the nest had been completed on one day and that laying had started on the next. The late date of completion of this nest may have accounted for the lack of a waiting period prior to the start of egg laying.

Copulation was seen only once, on May 6, when the female involved was still building her nest. In this instance, copulation preceded the laying of the first egg by five days. Baumann (1959:186-187) reported copulation involving a nest-building female.

During the laying period, females apparently visit the nest and manipulate the eggs. This was suggested by the shifting in position of marked eggs in one nest before the clutch had been completed and incubation started.

#### INCUBATION

*Length of period.*—The exact incubation period was established only at Nest 3, in which all eggs were marked. On May 23, 1955, this nest contained two eggs; both were marked "1." Eggs were laid, one each day, until the clutch of five was complete on May 26, the last egg having been laid between 7:27 and 10:16 a.m. on that date. One of the first two eggs later disappeared and no trace of it was found. At 10:19 a.m., June 7, the remaining egg "1" and eggs "3" and "4" had hatched; the last egg laid, "5," hatched between 11:55 a.m. and 3:22 p.m. The incubation period at this nest, from the laying of the last egg to hatching of same, was between 12.07 and 12.33 days.

Linsdale (MS) found a nest containing two eggs on June 2, 1941. On June 3, three eggs were present. At the next visit, on June 7, the female was incubating four eggs. Assuming a laying rate of one egg a day, the clutch would have been complete on June 4, and incubation would have started on that date. On June 15, three of the eggs had hatched. If the last egg had hatched later in the day, the incubation period would have been about 12 days. Baumann (1959:196) reported incubation periods of 14 and 13 days for two nests at San Francisco, although the date of April 12 given for the beginning of incubation for the 14-day nest should have been April 20 (*op. cit.*: 186). Although the samples of two nests at each locality are far too small to support any con-

clusions, there is a suggestion that the incubation period is somewhat shorter at the Hastings Reservation.

*Sessions on nest.*—At every nest, incubation was performed only by the female. The only possible exception to this was at Nest 2, to which the male made a visit of 15 minutes at a time when it was not known whether the female was present or not. If the male actually incubated during this period, and this seems very doubtful, his attendance during 120.5 hours of observation would have been 0.21 per cent.

Incubation apparently starts with the completion of the clutch. At Nest 3, in which five eggs were laid, the female was absent between 5:08 and 7:27 a.m., May 26, at which time four eggs were present. Between 7:27 and 11:48 she was on the nest 74.5 per cent of the time, and when the nest was checked during her absence at 10:15, five eggs were present. Heavy incubation continued until hatching.

At Nest 2, eliminating partial off and on periods, the mean attendance during 92.5 hours of observation on nine days between May 5 and 15, the day before hatching, was 76.8 per cent. At Nest 3, attendance based on similar data for 30.5 hours of observation on seven days during the entire incubation period, May 28 to June 6, was 81.4 per cent. At Nest 1, at which hatching occurred on June 30, attendance for entire on-off cycles aggregating 485 minutes on June 21, 24, and 26, was 77.8 per cent. At no nest was any particular trend in attendance noted as the incubation period progressed.

Table 1  
Attendance of Incubating Female in Relation to Temperature

Date	♀ Attendance (per cent)	Obs. period (minutes)	Max. temp. (°F.)	Min. temp. (°F.)	Av. temp. (°F.)
Nest 2					
May 6, 1954	66.1	636	87	51	69.0
7	76.5	729	81	43	62.0
8	75.4	898	76	47	61.5
10	81.1	851	63	46	54.5
11	78.4	660	74	37	55.5
12	74.0	856	71	35	53.0
13	73.7	686	77	40	58.5
14	80.6	841	80	35	57.5
15	78.2	904	70	46	58.0
Nest 3					
May 28, 1955	81.2	493	80	48	64.0
30	82.8	552	83	38	60.5
June 1	75.6	265	59	29	44.0
2	78.4	451	68	39	53.5
4	82.6	567	87	53	70.0
6	83.0	542	91	55	73.0

Daily attendance figures show no consistent correlation with temperature (table 1). At Nest 2, there was an inverse correlation between attendance and temperature on the days of highest and lowest maxima, attendance being lowest on the day of highest maximum (May 6) and highest on the day of lowest maximum (May 10). Between these extremes, no correlation is apparent. The only correlation with minimum and average temperatures occurred on May 6, when lowest attendance coincided with highest minimum and average temperatures. Exactly the reverse is shown at Nest 3. Here, the three days of highest attendance occurred on the three days of highest maximum tempera-

tures, and the three days of lowest attendance coincided with the lowest daily maxima. The days of lowest and highest minima coincided with the days of lowest and highest attendance. The two days of lowest attendance coincided with the two days of lowest average temperature, and the day of highest attendance coincided with the day of highest average temperature. It is obvious that nests 2 and 3 were diametrically opposed with regard to correlation between attendance and temperature, and no conclusions can be drawn on the basis of this small sample.

At Nest 2, 115 on periods and 115 off periods averaged 37.0 and 11.2 minutes, respectively. At Nest 3, 32 on and off periods averaged 46.5 and 10.6 minutes, and at Nest 1, ten on and off periods averaged 36.4 and 12.0 minutes. The overall averages for these 157 periods are 38.9 and 11.1 minutes. It will be noted that on periods were nearly identical for nests 1 and 2, and considerably longer for nest 3. However, the average off periods for all nests were nearly similar. As can be seen (table 2), the length of 147 off periods was not correlated with the length of the preceding on periods. Regardless of length of the preceding on period, off periods averaged between 10.5 and 11.8 minutes. The ranges and coefficients of variation for the three different classes of off periods are remarkably similar.

Table 2

Relation of Off Period to Preceding On Period during Incubation<sup>1</sup>

Range of On Period	0-20	21-40	41 and over
Number	24	65	58
Mean On Period	14.9	29.6	58.0
Off Period			
Mean	11.0	10.5	11.8
Standard error	0.87	0.51	0.59
Range	3.0-20.0	3.5-24.0	4.0-26.0
Coefficient of variability	38.9	39.1	37.8

<sup>1</sup> Combined data from nests 1, 2, and 3, expressed in minutes.

On and off periods showed no regularity or rhythm. Very long or very short periods could occur at any time of day. In view of the greater consistency of off periods as compared to on periods, it seems probable that desire to return to the nest, probably increasing as time passes during an off period, constitutes a stronger stimulus than hunger or whatever factor or factors impel the female to leave the nest.

*Behavior.*—At nests 1, 2, and 3 the females showed a definite tendency to use a particular approach when returning to the nest after an absence. At Nest 1, which was three feet above ground, the female usually flew to a point about six feet up in an adjacent live oak, thence to the nest shrub at a point above the nest, and then she dropped down to a point below the nest and worked up to it. She usually entered the nest from the south side. The habit of perching above and then below the nest, and then working up to it, was invariable. At Nest 2, the female nearly always flew to the thicket immediately west of the nest; if approaching from the east, she would pass beyond the nest to the thicket. In either case, she would then work back through the thicket to a takeoff point near the nest from which she would fly down to resume incubation. She used two takeoff points indiscriminately, one on a strand of barbed wire and the other on a branch of a poison oak paralleling the wire and nearly touching it. Both points were 35 inches from the nest. Examination of the branch of the poison oak after the nestlings had disappeared revealed an area 3 inches long on which the outer bark had been worn away by the female's repeated takeoffs. At Nest 3, the female showed somewhat greater variety in the early stages of her approach to the nest. She would

invariably fly to a large live oak near the nest, landing from five to 20 feet up on the side of the tree away from the nest. She would then work down and around until she was on a branch or an intertwining poison oak vine from one to five feet up on the side of the tree nearest the nest. From here she would always fly down to a fallen limb immediately adjacent to the nest, hop down, and resume incubation.

The only observations of the female on the nest were made by Gray at Nest 1. This female seemed alert at all times, turning her head to peer toward Scrub Jays (*Aphelocoma coerulescens*) calling nearby and occasionally looking toward her mate when he sang or called near her. Infrequently she would stand up and lower her head, apparently working on the nest or moving the eggs, sometimes stretching her wings and ruffling her plumage as she rose. She was almost entirely silent when incubating, calling from the nest only four times in 13½ hours of observation.

At Nest 3, in which all eggs were marked, I visited the nest several times during absences of the female. It was apparent that the eggs had been shifted in position in the course of the preceding incubating period, but such shifting was purely random and there was no evidence of any regular rotation.

When leaving the nest, females showed considerable variation in the direction of their departure. Sometimes this was determined by the location of the male. Females would sometimes fly toward the male if he were singing or calling, or if the male were silent when the female left the nest, she would sometimes fly toward the area in which he had last sung or called. There were many cases, however, in which the female would fly in some other direction. At Nest 2, regardless of the whereabouts of the male, the female many times flew to the crown of a large live oak upslope from the nest, stretching her wings and ruffling her plumage on alighting. She would then forage through the dense crown of the oak, moving through the crown toward the upslope side, where I would lose sight of her. She took this route frequently even though the male might be calling or singing from some other direction. After leaving the nest the female usually called several times, apparently informing the male of her whereabouts. Usually, the male was either calling or singing when the female left the nest, so that she was aware of his location. Thus, within a short time after the departure of the female, each member of the pair had located the other.

The reactions of the male to the departure of the female from the nest may be judged in part by the nature of his behavior immediately before and after her departure. This was noted for 108 flights from the nest by the incubating female at Nest 2 (table 3). In 39 instances the male's behavior changed, and it seems likely that these changes resulted from his seeing the female leave the nest. In 69 instances no change in behavior was noted, with one qualification. A few times when the male sang both before and after the female left the nest, he broke his steady singing, which normally was at intervals from 4 to 7 seconds, with an interval of 15 to 20 seconds just after the female flew; he then resumed steady singing. It seemed likely that he had seen his mate leave the nest in these instances. But usually he gave no evidence that he was aware that the female had left the nest. He showed no tendency to join her, nor did she show any particular tendency to join him. A few times the male joined his mate shortly after she had left the nest, but such behavior was rare. Baumann (1959:193) stated that the male remained near enough to the nest in the absence of the female so that he could keep it under surveillance, but this was not true of the male at Nest 2. I visited this nest a number of times in the absence of the female without drawing the attention of either member of the pair.

In only 37 of 108 cases was the male silent immediately after the female flew from the nest (table 3), but sooner or later he would call or sing before she resumed incuba-



Table 3  
Behavior of Male Before and After Incubating Female Left Nest 2

Behavior before	Behavior after	Number
Calls	Silent	5
Calls	Sings	4
Sings	Silent	15
Sings	Calls	1
Silent	Calls	3
Silent	Sings	11
		—
		39
Calls	Calls	4
Sings	Sings	48
Silent	Silent	17
		—
		69

tion. In the other 71 instances the female knew the whereabouts of her mate at the time she left the nest. Thus, each member of the pair was usually aware of the location of the other member, although there appeared to be no well-marked tendency for them to stay near each other when the female was not sitting. The impression that I received was of a rather casual relationship with the members of the pair keeping in touch with each other without frequent contact, a situation similar to what has been previously described for nest building.

When the female returned to the nest, in nests 1 and 3 as well as in Nest 2, she almost invariably called on her return flight, apparently informing her mate that she was returning to the eggs. Sometimes such calling was confined to the beginning of the return flight, but often the female would call a few times from the takeoff point just before dropping down to the nest. At Nest 2, the male rarely accompanied his mate on her return trip. Indeed, on several occasions, the returning female was attacked by a Brown Towhee (*Pipilo fuscus*) which apparently had a nest nearby. Despite the loud alarm calls of the female when attacked, and the loud sounds of the chase as it proceeded through the thicket adjacent to the nest, the male never appeared to aid his mate.

Only twice did the male at Nest 2 seem to lose track of the female; this occurred when he made single trips to the nest with food in the absence of the incubating female, on May 12 and 14. However, Nolan (1958:264) found that male Prairie Warblers (*Dendroica discolor*) brought food to the nest during the incubation period, "largely or wholly without regard to whether the female happens to be on her nest at the time," and the same may be true of the Rufous-sided Towhee.

It is difficult to determine whether or not the female left the nest in response to the singing or calling of the male. Unlike the Song Sparrow (*Melospiza melodia*), which has a special "signal song" to which the incubating female responds (Nice, 1937:126), the Rufous-sided Towhee lacks such a special song. There were a few cases of the female leaving the nest immediately after the male had called or sung, and in these one might say that the male had called the female from the nest. In the great majority of cases, however, there was no such immediate response by the female and it was impossible to decide whether she had left the nest independently or not. For example, if the male started to sing after a silence of 15 minutes, and the female left the nest after he had been singing for five minutes, did this represent a response of the female to the male, or not?

While the female was incubating at Nest 2, the male either sang, or called, or was silent. Most of his time was spent in silence; the next greatest percentage of his time

was spent in singing; and only a small fraction of his time was spent in calling. Table 4 shows the number and duration of periods of calling, singing, or silence that preceded 122 departures of the female during incubation at Nest 2.

She left the nest most quickly in response to the calling of the male. In 14 of the 16 instances recorded, the male called between 0.5 and 1.0 minute before the female re-

Table 4

Duration of Male Behavior Preceding Departure of Incubating Female from Nest 2

	Number	Range	Mean	Standard error
Calling	16	0.5-3	1.44	0.22
Singing	68	0.5-20	4.43	0.46
Silence	38	0.5-42	11.07	1.47

sponded; twice, he called for three minutes before she left the nest. It seems likely that in 14 instances, and possibly in all 16, the male actually called the female from the nest. The small percentage of cases in which calling immediately preceded the female's departure from the nest is a reflection of the slight amount of calling that this male did. However, the short time that elapsed between the inception of calling and the departure of the female suggests that the male actually summoned the female, although infrequently, by calling. This agrees with the observation of Baumann (1959:193), that the male occasionally called the female from the nest by use of the call note.

The effectiveness of singing as a signal to the female is far more difficult to assess. Here the lag in response of the female to the singing of the male ranged from 0.5 to 20 minutes. For the minimum value it appeared as though the female had responded to the male's singing; for the maximum lag, she definitely did not. Between these two extremes every lag in response between 1 and 9 minutes occurred, as well as lags of 11, 12, 14, and 16 minutes. It is impossible to establish a point below which it may be said that the female responded to the singing of the male and above which she did not.

Although it is not possible to determine this point, it can be said that if the female does leave the nest in response to the singing of her mate, song is a far less effective signal than calling, as the mean time lapse between the beginning of song and the departure of the female from the nest was over three times as long as the mean time lapse in calling. The difference between these means is significant (table 4), and the mean incubation period preceding the departure of the female in response to the calling of the male (31.3 minutes for 15 periods) was shorter than the mean incubation period preceding her "response" to his singing (39.2 minutes for 65 periods).

Finally, we may consider silence as a stimulus to the female to leave the nest. Silence on the part of the male would result in the inability of the female to locate her mate unless she could see him from the nest. Indeed, if the male were silent and out of sight, the female would not know if he were still on territory, or even alive. Since the male at Nest 2 called or sang frequently enough so that prolonged silences did not occur often, one might assume that only a relatively prolonged silence would be effective in causing the female to leave the nest, her tension presumably mounting over a period of time until it had reached a point at which she would fly in search of her mate. The mean time elapsing between the male's becoming silent and the female's leaving the nest was 11.07 minutes, almost eight times as long as the mean male calling period preceding her departure and about two and one-half times as long as the mean singing period (table 4). Silent periods preceding the departure of the incubating female ranged as low as 0.5 minute (1 case), 1 minute (3 cases), and 2 minutes (3 cases). It is possible that in these instances the female left the nest independently or in response to the calling or

singing that had immediately preceded these brief silent periods. Nonetheless, these short intervals of silence are included with the longer silent periods as they represented the behavior of the male immediately prior to the departure of the female from the nest. However, it is obvious that the same difficulties are inherent in evaluating the efficacy of silence as a stimulus inducing the female to leave the nest as are inherent in singing. The periods of silence of the male preceding the departure of the female from the nest ranged from 0.5 to 42 minutes, with all gradations between, and it is not possible to designate a particular interval of silence above which the female will respond.

When a female returns to the nest after an absence, she is probably influenced by conflicting stimuli. First, psychological attachment to the nest would tend to insure her presence there. Other factors, such as inclement weather or the presence of a predator near the nest, would tend to intensify this stimulus. Second, opposing stimuli arising from discomfort such as hunger, thirst, or cramped position, or from anxiety over the whereabouts of the male, would tend to make the female leave the nest. Assuming mild climatic conditions and the absence of an enemy near the nest, attachment to the nest must be strong when the female resumes incubation after an absence. The discomfort and anxiety factors must be low; certainly they would have been low in the case of the female at Nest 2, as she always foraged and communicated with her mate during her absences from the nest.

As time passed after her return, however, we might expect a decreased intensity of the nest attachment stimulus and increased intensity of the discomfort stimulus, and if the male were silent, increased intensity of the anxiety stimulus as well. At some point in time, the discomfort and/or anxiety stimuli must equal the intensity of the nest attachment stimulus. From this point on, the female would presumably be ready to leave the nest. If the male began to call or sing at this point or shortly thereafter, the female would probably leave the nest. If the female had not reached the point at which the opposing stimuli were roughly equal in intensity, calling or singing would probably be ineffective.

There were many more instances of calling and singing which were ignored by the female than instances in which she responded. Even in the case of the Song Sparrow, the female frequently does not respond to the "signal song" of the male but leaves the nest independently. Nice (1937:126) states that, in response to the "signal song" of the male, "the female often comes off the nest at once, but sometimes she merely answers with *ee-ee-ee* and remains; she may come off within a few minutes or stay until a second signal song some time later; or she may come off with no reference to her mate." One may wonder how effective this signal really is. The point at which calling or singing comes in relation to the intensities of the stimuli impinging on the female is obviously of paramount importance.

With regard to silence, since it must operate over a rather prolonged period of time to be effective, its inception may occur at a point of time shortly after the female had returned to the nest. There would be considerable opportunity for the male to break his silence, however briefly he might sing or call, before the discomfort and/or anxiety stimuli overrode the nest attachment stimulus. If the male's silence is sufficiently prolonged, it is conceivable that it will augment the anxiety stimulus to the point at which the female would leave the nest earlier than if the male had been vocalizing. The necessity for a period of silence to be prolonged to be effective may explain why silent periods preceded the departure of the female from the nest in only 38 cases as compared to 68 cases in which singing preceded her departure, although the male spent a greater part of his time in silence than in singing.

*Anticipatory food bringing.*—In 120.5 hours of observation at Nest 2 during the

incubation period, the male made a total of 15 trips to the nest. These aggregated 21.6 minutes and included one visit of 15 minutes during which it was not known whether or not the female was at the nest. The remaining 14 visits averaged 28.2 seconds long, ranging from 10 seconds to two minutes. On nine of these, the male carried food to the nest while the female was present; after eight visits he left the nest with his bill empty, and after one it could not be seen whether or not his bill was empty. On three visits the male came to the incubating female but it could not be seen whether or not he carried food. On one of these trips he wiped his bill after leaving the nest, behavior which suggested that he had been carrying food. Twice he brought food to the nest in the absence of the female, once leaving empty-billed and once still carrying the food with him.

At Nest 3, the male made only three trips to the nest in 54 hours of observation during the incubation period from May 26 to June 6. On May 30, he brought food to the female and remained at the nest for 35 seconds; on June 4, he brought food to the nest while the female was absent, and he remained for two minutes; and on June 6, the day before hatching, he came to the female on the nest and remained for 45 seconds, but it could not be determined whether or not he brought food.

Table 5  
Anticipatory Food Bringing by Male at Nest 2

Date	Female	Male arrives	Male stays	Male leaves
May 8, 1954	on	with food	120 sec.	no food
10	on	with food	30 sec.	no food
11	on	?	20 sec.	no food
	on	with food	30 sec.	no food
	on	with food	30 sec.	no food
12	on	with food	20 sec.	no food
	on	with food	20 sec.	no food
	off	with food	10 sec.	with food
	( ?	no food	15 min.	no food)
13	on	with food	15 sec.	?
14	off	with food	15 sec.	no food
	on	with food	30 sec.	no food
	on	?	15 sec.	no food
15	on	with food	20 sec.	no food
	on	?	20 sec.	no food

The incidence of the male's 15 trips to Nest 2 is summarized in table 5. There was an absence or low incidence of such trips between May 5 and 10 and a noticeably increased incidence in the last six days of the incubation period, from May 11 to 16. At Nest 3, two of the male's three trips occurred in the last three days of incubation. Nolan (1958:269-270), discussing anticipatory food bringing by male Prairie Warblers, presented considerable evidence that it is through this activity that the male learns of the hatching of the young, and anticipatory food bringing may serve the same function in the Rufous-sided Towhee.

#### BROODING

Brooding was performed at every nest by the female only. At all nests, the male sometimes spent several minutes at the nest when delivering food to the young in the absence of the female. At nests 2 and 3 it was not possible to see whether or not the male brooded at such times. At Nest 1, which was visible to the observer, the male occasionally spent periods up to eight minutes long at the nest in the absence of the female, perching on the rim for several minutes after delivering food to the young, but he never actually settled to brood them.

There was a decided difference in the amount of brooding that was undertaken at nests 1, 2, and 3. Because of the trend toward decreasing attendance as the nestling period progressed, average figures mean little and it is necessary to compare the nests on a day to day basis relative to the day of hatching. It can be seen (table 6) that attendance was far higher at Nest 2 than at Nest 1 when equivalent days are compared, for the first eight days after hatching day. Nest 3, for which data are available only for hatching day and the second day after hatching, appears to be more nearly similar to Nest 2 than to Nest 1 as regards attendance.

Table 6

## Female Brooding Attendance

Date	Obs. period (minutes)	Attendance (per cent)	Max. temp. (°F.)	Min. temp. (°F.)	Average temp. (°F.)
Nest 1					
Hatching, June 30					
July 1	360	51.1	85.0	40.0	62.5
2	540	48.9	76.0	45.0	60.5
3	480	46.4	70.0	42.0	56.0
4	540	30.0	75.0	50.0	62.5
5	120	30.8	75.0	50.0	62.5
6	480	24.0	69.0	40.0	54.5
7	420	11.0	82.0	46.0	64.0
8	318	3.8	88.0	52.0	70.0
Nest 2					
Hatching, May 16					
May 17	861	80.6	88.0	52.0	70.0
18	687	88.6	93.0	52.0	72.5
19	867	68.0	87.0	42.0	64.5
20	698	70.4	78.0	37.0	57.5
21	854	63.1	76.0	36.0	56.0
22	898	54.9	78.0	42.0	60.0
24	855	21.1	76.0	47.0	61.5
25	669	11.6	76.0	39.0	57.5
26	246	0.0	65.0	35.0	50.0
Nest 3					
Hatching, June 7					
June 7	247	72.3	86.0	52.0	69.0
9	475	75.7	92.0	50.0	71.0

At nests 1 and 2, the amount of daily attendance by the females showed an almost steady decrease as the nestling period progressed. This trend was more even at Nest 1. The noticeable drop in attendance between the third and fourth days after the hatching day at Nest 1 was not evident at Nest 2. The only point of similarity between the two nests was the general decrease in attendance as the nestling period progressed.

The difference in attendance at nests 1 and 2 during the first six days after hatching day is not correlated with differences in the daily temperatures prevailing at each nest during this period (table 6). Part of the difference undoubtedly lies in the fact that Nest 1 was shaded at all times, whereas Nest 2 was in full sun from about 11:30 a.m. to about 1:30 p.m. This led to lengthy periods of attendance at Nest 2 during the middle part of the day, whereas such lengthy periods were not evident at Nest 1. Further, Nest 1 contained four nestlings and Nest 2 only two, so that there was much greater pressure on the female at Nest 1 to do less brooding and more feeding. The nearly similar

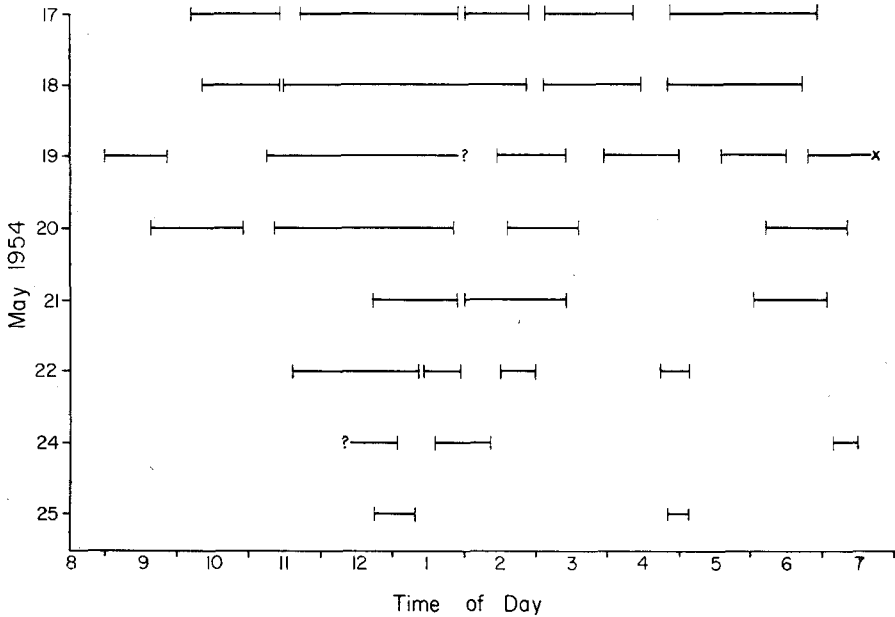


Fig. 1. Brooding periods of 15 minutes or more from 8:30 a.m. to the end of the daily observation period at Nest 2, May 17 to 25, 1954. Question mark (?) indicates that the exact beginning or end of a brooding period was not known; the symbol "X" indicates that the female was still brooding when observations ended.

attendance figures at Nest 1 during the seventh and eighth days after hatching day as compared to Nest 2 on the eighth and ninth days after hatching day undoubtedly reflect the decreased attendance at Nest 2 during the middle portions of those days.

As opposed to incubation, during which periods on and off the nest showed no regularity or rhythm, certain trends were evident in the brooding program at Nest 2 (fig. 1). During the first five days after the hatching day there was a definite tendency for the female to brood heavily from late morning to early afternoon, when the nest was in full sun, and again in the late afternoon. On the sixth, eighth, and ninth days the tendency to brood heavily during the middle of the day continued, and on those three days it was only during this period that any appreciable amount of brooding was done. The only period during which the nestlings were brooded on all days of observation was from 12:16 to 12:34 p.m. (fig. 1), another suggestion that the young were in special need of protection from the sun at about midday. Since there was no particular tendency during incubation to cover the eggs at that time of day, it would appear as though the nestlings were more endangered by direct sun than were the eggs. The obvious decrease in brooding during the middle part of the eighth and ninth days after the hatching day suggests that direct sun was not as dangerous to the nestlings during those days, when some degree of thermoregulation had apparently been achieved.

Because of the steady decrease in brooding as the nestling period progressed, it is not feasible to calculate average on and off periods. It is also difficult to determine whether there was any correlation between length of an on period and the length of the following off period. Using the first six days of the nestling period at Nest 2, when attendance figures were comparable to the attendance figures recorded during incubation, and considering only complete on and off cycles, 16 on periods averaging 30.9

minutes were followed by off periods averaging 13.9 minutes, and 18 on periods averaging 92.3 minutes were followed by off periods averaging 22.4 minutes. Unlike incubation, there appeared to be a tendency for the length of off periods to be influenced by the length of the immediately preceding on periods, but the average difference between off periods just noted is not statistically significant.

At Nest 1, when the male came to the nest with food while the female was brooding, she sometimes left the nest, thus exchanging with the male. At other times she would merely back off the young or move to one side, allowing the male to feed the nestlings, and she would resume brooding after he had left. In most instances when the male arrived at the nest shortly after the female had resumed brooding following an absence, the female would remain at the nest rather than exchange with the male. At Nest 2, during the first five days of the nestling period, when attendance by the female ranged from 63.1 to 88.6 per cent, the female exchanged with the male only after mean daily brooding periods ranging from 50.2 to 104.0 minutes, regardless of how many visits the male might make to the nest during such brooding periods. Between the sixth and ninth days, when her attendance ranged from 54.9 to 11.6 per cent, the mean daily brooding periods preceding exchange with the male ranged from 11.3 to 7.1 minutes. In other words, as the nestling period progressed, the attachment of the female to the nest decreased considerably, and her threshold of response for exchange with the male became noticeably lower.

#### TEMPERATURES IN NEST

At Nest 4, in which two nestlings hatched on May 15 and two on May 16, temperature readings were made on May 16, 17, and 19, by means of a constantan-copper thermocouple inserted through the bottom of the nest so that it was in contact with the undersides of the lowest nestlings. While the female brooded, the temperature at the bottom of the nest cup ranged from 73.4° to 77.9°F., although ambient air temperature two feet above the nest ranged from 42.8° to 60.8°F. When the young were unattended and the air temperature was 72.5°, the nest temperature was 75.2°; when the air temperature was 42.8°, the nest temperature fell to 60.8°. Thus, the brooding of the female kept the temperature at the bottom of the nest cup within narrow limits, but in the absence of the female, the nest temperature fluctuated in relation to the air temperature.

#### FEEDING

Observations on feeding were difficult to make except at Nest 1, as on many occasions it was not possible to see whether or not an adult actually carried food in its bill as it went to the nest. Even at Nest 1 it was not possible to note each time whether an incoming adult carried food, but even when no food was seen by the observer, the adult would make feeding motions after it had come to the young. Therefore, it is assumed that each time an adult came to any nest, feeding took place.

At Nest 2, the eggs hatched between 7:01 p.m., May 15, and 12:30 p.m., May 16, when the nest contents were checked briefly. Between 2:30 and 5:15 p.m. the male made seven brief trips to the nest, on three of which he was definitely seen to carry food. Following two of these trips, when the female was at the nest, he left with his bill empty, but after the third, made in the absence of the female, he left with the food still in his bill. In the same period, the female came to the nest five times between brooding periods, but it was not possible to see whether she carried food on these trips. In Nest 3 the four eggs were intact at 6:38 a.m. on June 7. At 9:17 a.m. the male visited the nest for 30 seconds; when the nest was inspected at 10:19, three eggs had hatched. Between 10:19 and 11:58 a.m., he made no further trips to the nest; the female left and returned six

times in this period. On one return trip her bill was definitely empty, and on two trips she carried insect larvae. Between 3:22 and 5:50 p.m., the male came to the nest nine times. On five trips he carried insect larvae, and on two of these trips his bill was crammed with food. In this period the female came to the nest five times; on three trips no food was seen in her bill, but on two trips her bill was crammed with larvae. From these observations, it appears as though both adults feed the young on the day of hatching. Baumann (1959:196-198) found that the newly hatched young at one nest were fed almost entirely by the male, with only one definite feeding by the female in 7 hours and 40 minutes of observation.

Table 7

## Rates of Feeding of Nestlings by Adults

Date	Female attendance (per cent)	Total trips by male	Total trips by female	Male's hourly rate	Female's hourly rate	Total hourly rate
Nest 1						
July 1	51.1	15	16	2.5	2.67	5.17
2	48.9	27	29	3.0	3.22	6.22
3	46.4	27	24	3.4	3.00	6.40
4	30.0	38	31	4.2	3.44	7.64
5	30.8	9	10	4.5	5.00	9.50
6	24.0	40	43	5.0	5.37	10.37
7	11.0	34	47	4.9	6.71	11.61
8	3.8	26	43	4.9	8.11	13.01
Nest 2						
May 17	80.6	53	14	3.7	0.98	4.68
18	88.6	39	7	3.5	0.61	4.11
19	68.0	49	11	3.4	0.76	4.16
20	70.4	33	8	2.8	0.95	3.75
21	63.1	48	14	3.4	0.98	4.38
22	54.9	51	26	3.4	1.74	5.14
24	21.1	57	51	4.0	3.58	7.58
25	11.6	37	53	3.3	4.75	8.05
26	0.0	7	18	2.0	5.27	7.27

The daily rates of feeding nestlings by the males and females at nests 1 and 2 are summarized in table 7. The amount of feeding done by the female was almost entirely dependent on the amount of brooding which she performed. At Nest 2, where brooding was very heavy during the first five days after hatching day, the female did relatively little feeding, and the male fed much more frequently. On the sixth day, the female's feeding rate began to rise; on the eighth day it nearly equaled the male's, and it definitely surpassed the male's on the ninth and tenth days. The male's feeding rate varied within narrow limits until the tenth day, when it fell off sharply, so that on that day the female made about two and one-half times as many trips as the male.

At Nest 1, at which the female's attendance was far lower, she made about the same number of trips as the male during the first six days after hatching day. During the seventh and eighth days her feeding rate rose sharply, and on the eighth day she made 62 per cent of all trips to the nest. As at Nest 2, the female's feeding rate rose more or less steadily as her attendance fell off. On the other hand, the male, unlike the male at Nest 2, showed a steady rise in feeding rate during the first six days and then remained constant during the seventh and eighth days.

Since Nest 1 contained four young, and Nest 2 only two, it may well be that the



decreased attendance at Nest 1, and the higher feeding rates at that nest resulted from greater demands on the adults by the larger number of young. At Nest 2, the combined feeding rates varied irregularly between fairly narrow limits during the first five days after hatching day, rose steadily and sharply on the sixth, eighth, and ninth days, and fell off sharply on the tenth day, reflecting the great decrease in the male's feeding rate on that day. In contrast, the combined feeding rate at Nest 1 rose steadily throughout the nestling period, and it was considerably higher throughout than the combined rate at Nest 2.

When the male came to Nest 2 in the absence of the female, he tended to stay for longer periods than when the female was present. This tendency was specially well-marked during the first five days after hatching day (table 8); after the sixth day the male's visits rarely coincided with the presence of the female, and aside from occasional brooding by her, neither adult stayed at the nest longer than was presumed necessary

Table 8

Mean Duration of Male's Visits to Nest 2 in Presence and Absence of Female<sup>1</sup>

Date	Female on	Female off
May 17	54.0 (28)	104.7 (15)
18	46.7 (30)	102.2 (5)
19	41.3 (32)	146.0 (12)
20	34.3 (20)	86.8 (8)
21	45.2 (20)	99.7 (15)
22	33.4 (11)	39.4 (29)

<sup>1</sup> In seconds; number in parentheses.

to feed the young. At Nest 1, with its far lower rate of attendance by the female, the visits of the male did not often coincide with the presence of the female and they tended to be brief whether the female was on the nest or not. However, the six longest visits to the nest by the male on the second, third, and fourth days after hatching day, ranging from 1.5 to 8.0 minutes, were all made in the absence of the female. On these visits the male, after feeding, stood on the nest rim and watched the young. Gray (MS) noted that at Nest 1 the "♂ stays a shorter time when ♀ is at nest."

At Nest 1, it was possible to see that if the male brought food when the female was present, she would either back up or move to one side to permit the male to feed the young directly; the food brought by the male was never transferred to the female for delivery to the young. Twice, while the male was feeding the nestlings, the female reached up and took insects from the side of his bill and fed them to the young, but these were the only instances in which the male did not deliver all of his food directly.

The average frequency of feeding by hour of the day is given for Nest 1 in table 9

Table 9

Average Number of Feeding Trips per Hour at Nest 1 from July 1 to 7

Hour	5-6 a.m.	6-7	9-10	10-11	2-3 p.m.	3-4	4-5
♂	4.5	3.5	3.5	4.0	3.5	4.0	3.3
♀	4.5	3.8	3.7	3.7	4.7	4.0	5.0
Both	9.0	7.3	7.2	7.7	8.2	8.0	8.3

and for Nest 2 in figure 2. At Nest 2 it may be seen that the male fed more frequently in the early morning than in the late afternoon. The female fed at a rather even rate from 5:00 to 11:00 a.m. She fed at a much reduced rate between 11:00 a.m. and 2:00 p.m., reflecting the lengthy periods of brooding in this period during the first six days

after hatching day. She then fed at a somewhat higher rate during the remainder of the afternoon, but less frequently than she had during the morning. At Nest 1, the greatest frequency of feeding occurred between 5:00 and 6:00 a.m. As opposed to Nest 2, feeding was generally more frequent in the afternoon at Nest 1. On the basis of the frequencies recorded at these two nests, there appears to be no well-marked daily trend, except that the highest rate of each nest occurred in either the first or second hour of the day.

When the frequency of feeding at Nest 2 is plotted hourly for all of the days of observation combined (fig. 2), it will be seen that the frequency for male and female combined and for the male alone accord rather closely, especially from 5:00 to 10:00

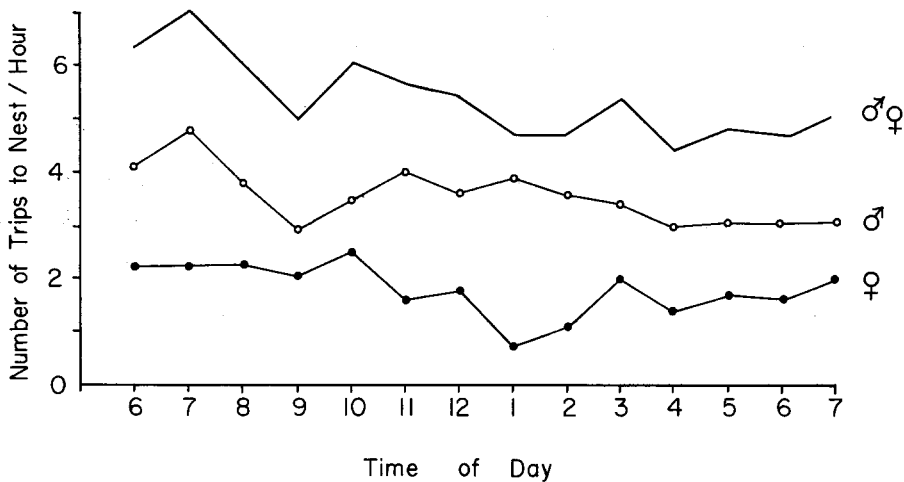


Fig. 2. Mean hourly feeding rates at Nest 2 for male and female together, male alone, and female alone, for all days of observation combined, May 17 to 25, 1954. Time of day on abscissa; number of trips to the nest per hour on ordinate.

a.m. In this period, the hourly frequency of feeding by the female varied very little. In other words, hourly variation in the frequency of feeding up to 10:00 a.m. was established by hourly variation in the male's feeding rate superimposed on the nearly constant feeding rate of the female. Between 10:00 a.m. and 2:00 p.m. both adults fed the young less frequently than during the early morning. The decline in the female's feeding rate is especially well-marked, reflecting the heavy brooding which she accomplished in this period on the first six days after hatching day. From 3:00 to 7:00 p.m. both adults fed less frequently than from 5:00 to 10:00 a.m. For the female this undoubtedly reflects the heavy brooding which she did between about 4:30 and 6:30 p.m. on the first three days of the nestling period.

There appeared to be a seasonal shift in the nature of the food brought to nests 1, 2, 3, and 4. At Nest 2, between May 16 and 26, the food brought to the nest on 143 trips was identified as insect larvae, and on five trips as imagos. The first imago, a moth, was brought on the sixth day after hatching day. At Nest 4, on May 16, 17, and 19, larvae were brought 14 times and only one imago, a moth, was noted. At Nest 3, on June 7 and 9, larvae were brought on 40 trips and imagos on none. In sharp contrast, food items specifically noted as brought on 20 trips to Nest 1 consisted of larvae on seven trips, grasshoppers on nine, and imagos on four. One of the imagos was a moth. On July 6, Gray (MS), noted that "food consists mainly of grasshoppers this p.m.," and in his summary of activities at Nest 1, he noted that "food consisted mainly of

grasshoppers, ranging in size from  $\frac{3}{4}\pm''$  long to  $\frac{1}{4}\pm''$  long. Other insects . . . and some larvae were also brought to the nest." From these data, it appears possible that nestlings in early nests are fed mainly larvae, whereas nestlings in later nests are fed mainly grasshoppers, the shift coinciding with the relatively greater abundance of larvae in the spring and the relatively greater abundance of grasshoppers in the early summer.

#### BEHAVIOR DURING NESTLING PERIOD

At Nest 2, as we have seen, the female's attendance from May 17 to 22 ranged from 54.9 to 88.6 per cent; from May 24 to 26 it ranged from 0.0 to 21.1 per cent, and during this latter period her rate of feeding the young rose sharply. The amount of time spent singing by the male from May 17 to 21 ranged from 13.3 to 21.5 per cent, and from May 22 to 25 from 34.8 to 50.1 per cent (Davis, 1958:322). Although the periods of high female attendance and decreased male singing do not coincide perfectly, the nestling period can be divided into two general parts, one from May 17 to 21 characterized by close attendance of the female and frequent and prolonged silences of the male, and one from May 22 to 26, characterized by the decreasing attendance of the female and the resumption of frequent singing by the male. Although the male was noticeably more silent during the first five days after hatching day than he had been during the incubation period, his trips to the nest with food, in combination with his occasional periods of calling or singing, served to break up effectively his long periods of silence and reveal his whereabouts to the sitting female. His activity immediately preceding 48 departures of the female from the nest was noted between May 17 and 21. Only three times did the female leave while the male was singing, a marked contrast to the situation that prevailed during the incubation period. Three times she left while the male called; twenty-five of her departures were preceded by the male's silence. In the remaining 17 instances she left the nest as the male came in with food, thus exchanging with him; she did not always wait for him to come close to the nest but several times flew when he was 10 to 20 feet away.

When coming to the nest, the male used a variety of approaches, sometimes using one or the other of the female's two takeoff points but more frequently flying down from some other point on the fence west of the nest. Often he approached at such a low level that I lost sight of him in the thicket west of the nest. Apparently when using the low approach he hopped through the grass between the fence and the nest; after following the early stages of his approach I would lose sight of him until he suddenly flew up from the nest after delivering food. In general his approach was less conspicuous than that of the female, who continued to use the same takeoff points that she had used during the incubation period. As then, she nearly always called briefly on her way to the nest, sometimes from her takeoff point, whereas the male usually came in silently. In general, the most striking feature of the first five days of the nestling period lay in the silent and stealthy behavior of the male.

By May 24, the male again sang at a rate comparable to that of the incubation period; the female's attendance had decreased sharply and her rate of feeding the young had increased to nearly equal that of her mate. At this time, and on through May 26, the last day of observation, the activities of the pair made them more conspicuous than at any time in the nesting period. In terms of concealing the whereabouts of the nest from possible enemies, these last three days were the most critical, as the frequency of visits to the nest was highest and the male, with his steadily increasing frequency of singing, was much more conspicuous than he had been. He frequently sang while foraging just prior to bringing food to the young, behavior that might easily attract a potential enemy's attention to him just before he flew to the nest.

During these last three days the parents used the same approaches to the nest that they had been using, with one exception. In the midafternoon of May 24, the female, who had been doing all of her foraging upslope from the nest, started to forage occasionally in the extreme north end of the thicket west of the nest. When leaving this area to bring food to the young, she worked her way through the thicket at such a low level that I could follow her only a short distance. Apparently, she went the whole way on the ground. After following the early stages of her approach, I would next see her as she flew up from the nest. On May 25 she did about half of her foraging in the thicket, but on May 26 she was again using the upslope foraging area and her usual approach to the nest. The temporary switch to the thicket may have been an attempt to find a new foraging area; perhaps this spot was abandoned because of the laborious approach to the nest through the length of the thicket.

At Nest 1, Gray noted the side of the nest to which the adults came in 475 of their trips with food for the young between July 1 and 8. There was a noticeable difference between the parents, the male coming to the west side of the nest 211 times and to the south side 28, the female coming to the south side 223 times and to the west side only 13.

At Nest 1, both sexes were faithful in disposing of the fecal sacs of the young. During the first few days of the nestling period the adults usually ate the sacs, but later they almost invariably carried them away. All nests that were found were remarkably clean and showed no evidence of fouling. The female at Nest 1 often worked on the bottom of the nest before settling to brood. Toward the end of Gray's observations the nest became badly stretched, at first because of the movements of the young, but in part because on July 7 a king snake (*Lampropeltis getulus*) crawled onto the nest before being removed by the observer.

#### NEST ENEMIES

Most enemies can be divided into three categories: predators on eggs and young, non-predatory animals that may accidentally damage the nest by trampling, and brood parasites. The most important predators, as judged by their abundance and by the reactions of nesting towhees to them, were the Scrub Jay, the king snake, and the California ground squirrel (*Citellus beecheyi*). The appearance of a jay near Nest 2 always evoked loud and steady calling by the male. If the female were not on the nest, she would join her mate, both birds calling loudly and rapidly as they moved about, keeping near the jay until it left the area. At Nest 1, Gray noted several times that the sitting female would peer alertly toward jays screaming nearby.

At Nest 3, on the morning of June 9, the female was absent when the male returned at 8:59 with food for the young. He perched in an oak near the nest and was about to fly down to the young when a jay landed on a fallen branch a few inches from the nest. The male at once flew downslope, calling loudly; the jay peered down, almost certainly at the nest, and seemed about to fly down to it, when the female flew in rapidly, uttering loud, squealing notes unlike any I had ever heard given by a Rufous-sided Towhee. She hovered in front of the jay, her wings beating and tail fanned, literally screening the nest from the intruder. At this point the male flew rapidly upslope toward the nest and the jay screamed once and flew. The female at once went down to the nest. It was obvious that the jay would have destroyed the nestlings had not the female intervened, and it was equally obvious that the male was completely ineffective in defending the nest and returned to it only after the female had appeared. Following this episode the male's singing rate rose appreciably and remained high for the rest of the morning (Davis, 1958:323). Despite this successful defense the young, which had hatched on June 7, had disappeared by the morning of June 11.

King snakes were noted endangering nests twice. At Nest 1, on July 7, Gray noted the two adults calling loudly near the nest for about two minutes, and then a king snake about four feet long came into view, crawling up to the nest from below. After the snake had reached the nest, both parents dived at it and struck it with their wings, but not with their bills. As Gray watched, the snake probed at the nestlings with its tongue; by the time the observer reached the nest, the snake was actually lying on top of the four young. The snake was removed and the nestlings, although appearing stunned and crushed, recovered, and appeared to have suffered no harm, although they would have been destroyed had not the snake been removed.

At Nest 2, on May 22, the male, in an oak near the nest, flew down to the thicket just west of the nest and called loudly several times; he then started toward the nest but suddenly flew down to the grass between it and the dirt road to the east and rushed at something, his wings outstretched and his tail fanned, as he called loudly and steadily. The female left the nest but remained near it, also calling loudly. The male made several rushes, his impetus carrying him several feet past the grass and out into the adjacent roadway. The female moved about calling loudly but remaining near the nest. I moved until I could see the object of their concern, a small king snake approximately 15 inches long and about 5 feet from the nest. I then returned to my original station. The male continued to make rushes at the snake, his neck bent, head down, wings outstretched, and tail fanned and nearly touching the ground. He attacked the snake for a total of eight minutes, and for the next four minutes the parents continued to call loudly. Forty-three minutes after the male's first attack I checked the nest and found both nestlings unharmed and the nest intact. In the meantime the male had started to forage and the female had returned to the nest, leaving a few minutes later to forage. Both adults made several trips with food, but they would go only as far as their takeoff points, refusing to go down to the nest and swallowing the food that they had brought. It was obvious that the birds had become so wary after their experience with the snake that they would not go down to the nest in my presence, and I left the area.

Ground squirrels were not established near Nest 2 but they frequently wandered near it. Any squirrel moving about near the nest invariably evoked loud calling by the male, or by both parents if the female were off the nest. As when Scrub Jays threatened, the female absolutely refused to go to the nest if a ground squirrel were nearby. Thus, in addition to the direct threat that predators present to eggs and young, they also present an indirect threat. The steadfast refusal of the female to return to the nest in the presence of a predator makes it seem possible that the mere presence of a predator near a nest on a very hot or cold day, or during a period when the nestlings might be in direct sun, could, if sufficiently prolonged, keep the female from eggs or young long enough to result in their death from exposure.

Other predators noted near nests were striped skunks (*Mephitis mephitis*), western gray squirrels (*Sciurus griseus*), and a longtail weasel (*Mustela frenata*). A wood rat (*Neotoma fuscipes*) with a house in the thicket adjacent to Nest 2 was ignored by the towhees although it was active several times in the daytime. Once the female at Nest 2 left the nest to pursue a large western whiptail (*Cnemidophorus tigris*) which had come near. The pursuit consisted of a slow herding of the lizard and the female returned to the nest after the whiptail had retreated about 15 feet.

None of the nests followed by Gray or myself went to completion. Nest 2 came the closest; the young, hatched on May 16, were still being fed on the morning of May 26. Their fledging period, according to the figures presented by Baumann (1959:199), was about over. Yet the parents suddenly broke off their steady feeding of the young and after some time had passed, I checked the nest and found it empty. If the young had

left the nest, some predator must have captured them almost immediately, as I never saw them again. The nests of Rufous-sided Towhees, built on or near the ground, are perhaps in so much danger at all times that any interference by an observer may tip the balance in favor of the predator. A few visits to the nest to mark eggs or examine young may flatten surrounding vegetation enough to form a path which will be investigated by a squirrel or snake, or even lead the eye of a jay perched above to the nest. At any rate, the ultimate failure of all the nests observed in this study may well have resulted from revealing the whereabouts of each nest to predators through the disturbance caused by observers.

Baumann (*op. cit.*:191) mentions only Scrub Jays and Brown-headed Cowbirds (*Molothrus ater*) as causing concern to nesting towhees, and the nests studied by him were apparently not destroyed by predators, despite his frequent visits to them, although he notes that each pair "lost, or abandoned" at least one nest (*op. cit.*:190). Perhaps the absence of terrestrial predators such as snakes and ground squirrels in his study area accounted for the higher nesting success of the pairs watched by him.

The second category of potential nest enemies, those which might accidentally damage nests by trampling, includes rabbits, deer, and quail. Nest 3 was almost trampled by a doe; she was standing 10 feet from it and suddenly became aware of my presence and bolted. Only the fallen branches adjacent to the nest kept her from running over it. Nest 2 was protected on the west by a dense thicket 35 inches away, but a dirt road and bordering strip of grass on the east provided no protection. However, the nest had been placed at the west base of a small California wild rose (*Rosa californica*) which had been browsed down, probably by deer, to a small, stout stub about six inches high. Twice, a pair of California Quail (*Lophortyx californicus*) dashed across the road and passed within two feet of the nest. The protective value of the small rose stub became apparent, as it would serve to turn aside running birds or small mammals which might have accidentally stepped on eggs or young.

Brood parasitism of Californian races of the Rufous-sided Towhee is rare. The worst offender appears to be the California Quail; a number of towhee nests have been found containing eggs of this species (Nidiologist, 2:85, 1895; Atkins, 1916:201-202; Bleitz, 1956:77-78; Cohen, 1899:63; Taylor, 1885:142). Parasitism by the Brown-headed Cowbird has been reported rarely for coastal races of the Rufous-sided Towhee in California. However, the continuing increase of cowbirds in the coastal regions of California may result in more frequent parasitism by this species. At the Hastings Reservation breeding of the Brown-headed Cowbird was recorded for the first time in the summer of 1959, with the Blue-gray Gnatcatcher (*Polioptila caerulea*) as the host species (R. B. Root, MS).

#### SUMMARY

Nesting of the Rufous-sided Towhee at the Hastings Reservation in coastal California occurs between about April 20 and June 20. Extreme dates for the discovery of nests containing eggs are April 10, 1960, and June 28, 1941. Most pairs apparently raise one brood.

Nests are built solely by the female. Most nests are placed on the ground, and the choice of nest materials and the placement and size of nests varies between very narrow limits.

Incubation is performed solely by the female. During the incubation period, which fell between 12.07 and 12.33 days for one nest, the male visits the nest and brings food to the incubating female. Attendance during incubation is not significantly correlated with temperature and does not change with stage in incubation.

Brooding is performed solely by the female. During the first half of the nestling period, when the female's brooding attendance is high, the male does most of the feeding of the young. As the female's attendance decreases, her rate of feeding the young rises steadily and near the end of the nestling period it surpasses that of the male.

The most serious nest predators of this species at the Hastings Reservation appear to be the king snake, Scrub Jay, and California ground squirrel.

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*Hastings Reservation, University of California, Carmel Valley, California, June 5, 1960.*