

NOTES ON PARENTAL BEHAVIOR AND DEVELOPMENT OF THE YOUNG IN THE WOOD THRUSH

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This paper is based on observations of a pair of Wood Thrushes (*Hylocichla mustelina*) during a single season. It details parental behavior and nestling development and compares this information with previously published data on Wood Thrushes, in particular that of Brackbill (1943, 1958), Kendeigh (1952), and Weaver (1939; in Bent, 1949). In general, the literature is cited without comment where information is consistent with my findings, with discussion reserved for inconsistencies or points of special interest. This is contribution No. 946 from the Department of Zoology, Indiana University.

The pair observed by me built two nests in dry upland woods near Bloomington, Indiana, in 1964. The first of these, which I refer to as the principal nest, produced fledgling young. It was built on a horizontal branch of a large spruce (*Picea abies*), about one m from the trunk and two m above the ground. This nest was two m from a window in my house, and from there my family and I made frequent observations of it. The second nest was located 92 m from the principal nest, and an effort to raise a second brood in it failed. During our observations the weather was mild with little rain; times given are all Eastern Standard.

I netted and color-banded the adults on the day after the nestlings hatched in the principal nest. Only one of the pair had an incubation patch, as reported by Weaver (in Bent, 1949:108) and Brackbill (1958:79) in color-banded birds. This indicates that only the female incubates in this species, contrary to Roberts (1936:121-122) and Todd (1940:442), whose evidence of males' incubating is unsupported and unconvincing. In addition, in my study when the bird that incubated left the nest the other frequently came to the rim and sang but never incubated. I consider the singer to have been the male; hence some observations are ascribed either to the male or the female even before I color-banded the pair.

ARRIVAL TO ONSET OF INCUBATION

The first Wood Thrush was heard in my yard on 18 April 1964, and the principal nest was found on 29 April. Although the nest seemed complete when discovered, a thrush brought material to it several times between 07:30 and 08:00 on 30 April. No further activity was seen until 3 May, when a Brown-headed Cowbird (*Molothrus ater*) laid in the nest before 07:30 and the thrush laid its first egg between 12:30 and 16:30. A thrush, presumably the female, spent the night of 3 May on the nest (see Brackbill, 1958:80), leaving it sometime before 05:30 on 4 May but returning at 06:15, 06:45, and 10:20 and sitting for about five minutes each time. The second thrush egg was laid between 10:25 and 13:50. The assumed female was on the nest continuously from 11:30 until 13:50, and again for a few minutes at 13:55

and 14:45; during 15 other observations prior to 19:53 the nest was unoccupied. A bird was present at 19:53 and on into the night (evening civil twilight was at about 20:11).

On 5 May at 05:25 the nest was unoccupied. I made 15 approximately evenly distributed observations between 05:35 and 10:30, and a bird was present on six. Egg 3 was laid between 10:30 and 13:50, when I observed almost continuously and never saw the nest unoccupied. The female was on the nest on four of my 12 observations between 15:10 and 19:42, all four times after 17:00. At 19:48 she went to the nest and was present into the night. Egg 4 was laid between 11:45 and 16:50 on 6 May. Full-scale incubation attentiveness appeared to begin on that day, as described below.

I obtained additional information about the length of the interval between building and laying and about the hour of laying in 1966, when a nest was apparently completed on 14 May and received its first egg on 18 May. Four eggs were laid, on consecutive days at the following times: egg 1 between 07:30 and 12:00, egg 2 between 11:05 and 12:30, egg 3 between 08:00 and 14:15, and egg 4 between 09:30 and 16:30. Beginning no later than the day egg 2 was laid the nest was occupied by a thrush during the night.

Brackbill (1958:78-79) observed that eggs of this species usually are laid between 09:00 and 12:00 but at times in the early afternoon. He found laying to be earlier on cool days.

FEMALE BEHAVIOR AT THE NEST DURING THE INCUBATION PERIOD

Attentiveness.—On 6 May, the day on which the last egg was laid, the female was on the principal nest on 16 of 26 observations (61.5 percent) prior to 12:00 and on 14 of 19 observations (73.7 percent) between 12:00 and darkness.

From 7 May through 18 May, the day before hatching began, but exclusive of 15 May when the nest was watched all day, I made 284 nest inspections, rather evenly distributed between about 05:30 and nightfall. The female was incubating on 182 of these, or 64.1 percent (see Davis, 1954). This percentage is lower than any of those obtained by Brackbill (1958:81) by pooling periods of continuous observation at each of seven nests; but Kendeigh (1952:135) recorded on a potentiometer that a female Wood Thrush spent only 66.1 percent of three full days (i.e., during daylight) on her nest. The female of the principal nest was present on about 69 percent of 133 inspections made before 12:00 and only 60 percent of 151 inspections made after 12:00, but the difference, tested by chi square, is not significant. There is no significant difference in attentiveness when the data from the first half of the incubation period are compared with those from the second half.

TABLE 1
LENGTHS¹ OF ATTENTIVE AND INATTENTIVE PERIODS² OF FEMALE WOOD THRUSH,
ACCORDING TO TIME OF DAY

Time of day	Attentive periods			Inattentive periods		
	n	\bar{x}	extremes	n	\bar{x}	extremes
05:17-07:59	7	18.2	27.5-11.5	8	4.4	8.0-1.5
07:59-11:02	7	19.1	26.0-14.5	7	7.0	10.0-5.0
11:02-14:08	4	36.3	115.5-6.0	4	7.5	9.5-5.0
14:08-16:59	6	19.0	35.0-4.0	6	11.3	17.0-6.0
16:59-19:45	6	17.7	25.5-12.0	6	10.0	13.0-4.0

¹ Lengths are in minutes, rounded to the half-minute.

² Data were obtained by a continuous observation from the beginning of the first attentive period to the end of the last inattentive period on 15 May, the tenth day of the incubation period.

A continuous watch was carried out on 15 May, which was fair with extreme temperatures of 79° and 45° F. On the preceding evening, the female had retired to the nest at 19:25, about 55 minutes before civil twilight (compare Kendeigh, 1952:Table 32). She left it for the first time on 15 May at 05:17, about 14 minutes after civil twilight (compare Kendeigh, loc. cit.). Her attentive period during the night had lasted 9 hours and 52 minutes (see Brackbill, 1943:75). She returned to the nest for the night at 19:45 on 15 May; the interval between the beginning of her first attentive period and the end of her last inattentive period was 14 hours and 47 minutes long.

The number of attentive periods on 15 May was 30 and of inattentive periods 31, which represents a more frequent alternation of attentiveness and inattentiveness than those of two females monitored by Kendeigh (1952:loc. cit.) with a potentiometer. Some of Brackbill's (1958:81) data are more consistent with mine but were not obtained by day-long observation. The mean length of the 30 attentive periods was 20.9 minutes, with a standard deviation of 19.2 minutes. (Lengths of attentive periods were not normally distributed; the median length was 17 minutes.) The mean length of the inattentive periods was 7.8 minutes, with a standard deviation of 2.4 minutes. The female was sitting on or standing over the nest during 626.5 minutes of the 868 minutes between 05:17 and 19:45, or 72.2 percent of the time (see Kendeigh, 1952:134-137). Assuming that she was continuously attentive at night, she was on the nest 1198.5 minutes of the 1440 minutes making up the calendar day of 15 May, or 83.2 percent of the 24 hours. However, on 115 occasions while I watched her, she rose to turn eggs, to shift position, to preen, to pick at the nest, or to stand over the eggs (Brackbill, 1953:82). These movements, during which no heat was applied to the eggs, consumed about 90 minutes.

Attentiveness on 15 May varied according to the time of day. To show this, I have divided the daylight period into five intervals, each approximately three hours long. The intervals begin and end a few minutes before or after, rather than exactly on, the hour because this permits me to start and end intervals with the onset of an attentive or an inattentive period. Table 1 shows for each interval the number, mean duration in minutes, and extreme lengths of attentive and inattentive periods, rounded to the half-minute.

The long attentive period and the high percentage (83 percent) of attentive

time in interval 3 was doubtless associated with the fact that the sun shone directly on the nest from 11:00 to 13:30. During the other intervals the attentive periods were much shorter and showed considerable similarity. Inattentiveness was greatest during the afternoon and evening (37.4 percent in interval 4, 35.9 percent in interval 5); this decline in attentiveness was produced by increasing the length of the inattentive periods while holding the length of the attentive periods roughly constant. These results differ from those of Kendeigh (1952:136-137), who found that two females incubated least between 08:00 and 16:00.

Behavior other than incubation.—Other behavior of the female at the nest on 15 May consisted of dozing, preening, egg turning, examining and picking at objects (perhaps parasites), tugging vigorously and persistently at something in the cavity, and changing the direction in which she faced. Dozing, which usually began shortly after inattentive periods ended, was not noted after 09:20. It ordinarily lasted about 30 seconds, but at 08:00 the female appeared to doze for about seven minutes. Preening was recorded 18 times between 07:51 and 20:00, most frequently during the long mid-day attentive period. The mean duration of bouts of preening was about one minute, the longest about four minutes. Egg turning behavior consisted of thrusting the head and bill beyond the eggs and then drawing the bill backward in a raking motion (see Weaver, in Bent, 1949:108); doubtless there was also some moving of the eggs whenever the female changed positions. I counted about 115 movements that probably caused some shifting of the eggs.

During the long period on the nest in the middle of the day the female appeared to be in considerable discomfort. Much of the time her bill was open about ten mm at the tip, and she seemed to pant (see Weaver, in Bent, 1949:114). She frequently raised the feathers of the crown, which occasionally remained erect for several seconds but at other times rose and fell in a slow rhythm.

The direction in which the female faced while sitting on the nest was recorded after each return to it as well as after nearly all occasions on which she rose to turn or inspect the eggs, pick at the nest, etc. There was a significant ($P = <0.01$) preference for facing away from the house, two walls of which joined to form a right-angled sheltered space in which the nest tree stood. Routes in leaving the nest and returning to it varied little and probably were dictated by the position of the house.

On 15 May the female arrived with a caterpillar at 10:35, looked into the nest, ate the caterpillar, and settled on the eggs.

In addition to the observation that her last inattentive period ended at 19:25 on 14 May and 19:45 on 15 May, I recorded four other times of re-

tirement during incubation, viz., 19:44, 19:39, 19:36, and 19:35. On another evening the female was on the nest when I looked at 19:15 and was still present when I quit watching after dark.

MALE BEHAVIOR AT THE NEST DURING INCUBATION

Increasingly as the incubation period advanced, the male perched on or near the nest when the female was absent. During the first two days of the period I did not see this behavior on 21 inspections made when the female was absent; the next two days the male was at the nest in three of the 18 inattentive periods of the female that I observed; in the last half of the incubation period he guarded the nest during about 60 percent of the observed inattentive periods. Brackbill (1943:75-76; 1953:83) witnessed males guarding nests with considerably greater regularity than this, but Weaver (in Bent, 1949:111) found much variation among males.

The day-long watch on 15 May provided details of the male's guarding behavior. He went to the nest during 18 of the 31 inattentive periods (standing on the rim for 123 minutes of the 241.5 total minutes that the female was away), perched within a few meters of it on two others, and foraged on the ground just below it on yet another. His earliest visit began at 07:07, his latest at 19:36; the shortest lasted one minute, the longest 17 minutes. Except twice when the female's departure and male's arrival were simultaneous, he appeared at the nest from 15 seconds to several minutes after his mate had left. He remained until she returned, occasionally leaving a second or two before she alit. Six times he stayed within a meter or so for from 30 seconds to two minutes after the female had resumed incubating, and once he stood on the rim for five seconds after she had entered the nest.

The male sang during all but five of his visits to the nest on 15 May (see Brackbill, 1943:76); four of the silent episodes occurred in the afternoon. The number of songs per visit varied from one to 111, the latter number during a visit lasting slightly over seven minutes. The total number of songs at the nest that day was 352, most sung at normal volume but some quite faintly. Singing invariably stopped when a potential intruder appeared.

Other behavior of the male consisted of occasional picking at objects in the nest and, once, persistent nervous flirting of his wings. On 6 May he brought food and offered it to the female. She rose and perched on the rim; the object seemed to fall into the nest, whereupon the female poked into the cavity and may have eaten it. On 15 May, the male brought food and passed it to the female (see Weaver, in Bent, 1949:108-109). She ate it, and he left immediately. Bent (1949:147) reports that the male Hermit Thrush (*Catharus guttatus*) brings much food to his incubating mate. This feeding of the female may account for Bent's observation (op. cit.:149) that an incubating female Hermit Thrush left the nest at no other times except early morning and just before sunset.

REACTIONS TO OTHER ANIMALS

With rare exceptions the many birds that approached the nest were completely ignored. Most notably, a pair of Robins (*Turdus migratorius*) built a nest five m from the principal nest and at about the same level. Between 1 May, when the Robins' building began, and 17 May, when a predator took their eggs, the two pairs of turdids were often close to each other; but I saw no agonistic behavior or any other interaction. Brackbill (1943:83) found that a pair of Wood Thrushes were tolerant of Robins nesting about 16 m from the nest of the former. These observations contrast with Weaver's (in Bent, 1949:104) report that Wood Thrushes usually fight Robins and actually exclude them from the territory (1939:19). Also ignored were House Wrens (*Troglodytes aedon*), Gray-cheeked Thrushes (*Catharus minimus*), House Sparrows (*Passer domesticus*), Cardinals (*Cardinalis cardinalis*), and White-throated Sparrows (*Zonotrichia albicollis*). House Sparrows, foraging within 0.3 m of the Wood Thrush nest, caused the branch on which it rested to jiggle without eliciting the slightest response. The female's crown feathers rose (see Weaver, in Bent, 1949:114; Dilger, 1956:326-331) and she occasionally looked down alertly when a bird made a sudden noise on the ground beneath her, and once the male appeared to look around cautiously when a Blue Jay (*Cyanocitta cristata*) called several times nearby. A day or two later when a Blue Jay called about 17 m from the nest, a Wood Thrush, probably the male, flew directly at the jay and chased it away.

Cottontails (*Sylvilagus floridanus*) and frequent chipmunks (*Tamias striatus*) passing under the nest were watched alertly, as were chipmunks that climbed into the nest tree. When a house cat (*Felis catus*) walked below her nest, the female rose slightly and sat with neck extended, tail and bill pointed about 45° above the horizontal (see Weaver, in Bent, 1949:105). Similarly, when a fox squirrel (*Sciurus niger*) jumped from the house into the nest tree while the male was on the nest rim, the thrush pointed his bill straight upward and became motionless. He maintained this pose even after the squirrel had moved away and apparently out of his line of vision; his head returned gradually to its usual position a minute or so later. A squirrel jumped into the tree while the female was standing in the nest, and she immediately settled on the eggs. Passing children caused the female to raise her bill to a 45° angle and to erect her crown feathers. My occasional visits to the nest led both birds to attack me, flying close to my head and calling both the familiar *quit* note and a plaintive descending note resembling *whew*. The male and perhaps the female snapped the bill loudly when passing my head (see Weaver, in Bent, 1949:115; Dilger, 1956:326-331).

HATCHING; DURATION OF INCUBATION

Eggs 1 and 2 disappeared during incubation. Egg 1 was on the ground below the nest, broken and dried, when a chipmunk ate it shell and all on 15 May. The cowbird egg never hatched and disappeared on 25 May.

Egg 3 revealed a small projecting bump with a discolored (dried) area around it at 12:48 on 18 May, and pipping of egg 4 began to be evident at about 16:00 the same day. Neither egg had hatched at darkness. I frightened the female off at 05:16 on 19 May and found that egg 3 had hatched. The shell was present, the nestling still in half of it (compare Brackbill, 1958:81); an adult removed one of the halves at 05:20 and the other was carried away one minute later, possibly by the same bird. Brackbill (1948:76; 1958:81) and Weaver (in Bent, 1949:109) noted the carrying away of egg shells; Weaver saw a female eat a shell.

Egg 4 hatched at about 05:35, about 14.5 hours after it pipped. Weaver (1949:109) reports a similar and also a somewhat longer interval. The male, the only adult present when egg 4 hatched, poked at the nest's contents for five minutes, then carried half the shell away. In ten seconds one of the pair landed on the rim and in two minutes flew away with the remainder of the shell.

The incubation period of egg 4 was 304 hours and 18 minutes, i.e., about 12.7 days, plus or minus a maximum error of 2 hours and 32 minutes (half the length of the interval between the two inspections during which egg 4 was laid). Weaver (in Bent, 1949:107-108) states that the incubation period of two nests was 13-14 days long, but details that she presents indicate that the last egg took only about 13 days to hatch. Brackbill (1958:81-82) reports incubation periods almost identical in length to that of the principal nest.

CARE OF THE NESTLINGS

On the day the eggs hatched the female returned to the nest without food at 05:21, left after 12 minutes, returned without food after nine minutes, left after five minutes, and came back six minutes later at 05:53 with a green caterpillar too large for the nestling to eat (see Brackbill, 1958:83). Between 05:21 and 05:53 the male came to the nest three times without food and probed silently into the cavity. At 05:54 he returned with a caterpillar, which the female accepted and ate. The male then removed from the nest the large green caterpillar that his mate had brought earlier, and she took this from him too and ate it. The older nestling ate first at 06:24, over one hour after I discovered it, and again at 06:41. The female brought these items; the male had visited the nest four more times by 06:41 but had brought no additional food.

Between the day when the young hatched and 31 May, when they left the nest, I made approximately 150 observations as I passed the window. On about 145 of these there was an adult present; most of the exceptions were between 19:00 and 20:00. After I had color-banded the pair, I noted the sex

of the bird in attendance; among 82 cases, the female was present 58 times and the male 24 times.

On the fourth day of life of the young, I watched the nest from 07:15 to 11:34. The female was present 75.8 percent of the 264 minutes but spent a considerable part of this time standing, looking at and poking the nestlings, delivering food, eating feces, and preening. Her attentive rhythm was much slower than it had been on the day-long watch during incubation, although the weather was very similar. Her full periods at the nest lasted 30, 50, and 64 minutes; two incompletely observed periods lasted more than 19 and 37 minutes. Inattentive periods during this observation were 6, 13, 21, and 17 minutes long. The male visited the nest ten times and was on the rim for 53.5 minutes of the female's 57 minutes of absence (see Brackbill, 1958:84; Harbaum, 1921). He provided most of the food (see Brackbill, 1943:77), at least eight loads as compared with the female's three, and the amount brought per load appeared to be much larger than the female's. Sometimes the items were single large caterpillars or moths, but on at least three visits he brought three or four items at a time, appearing to regurgitate those carried in the back of his mouth. Regurgitation of food for the nestlings has been attributed to the Hermit Thrush (McClintock, 1910:411) and to Swainson's Thrush (Stanwood, 1913:131). At times the male Wood Thrush passed his food to the female to be delivered; occasionally he divided it with her. Both adults ate occasional surplus items.

All fecal sacs were eaten, at least four by the female and two by the male; evidently Wood Thrushes carry few sacs away, at least until the nestlings are well grown (see Weaver, in Bent, 1949:110-111; Brackbill, 1943:79-80; 1958:83-84). The young did not always defecate immediately after feeding. Once the female ate a sac 12 minutes after the most recent delivery of food.

The female spent every night on the nest while the young were present. Until they were large, I weighed a nestling just before dark each evening. This disturbance precluded obtaining information about the female's normal retirement time, but it probably would have been later than it had been during incubation. One night she fed the young at 20:10; and on the last three days of the nestling interval, when I did not weigh the young, she retired at 19:57, 20:11, and 20:11 (this last was about 25 minutes before civil twilight).

NEST LEAVING; DURATION OF NESTLING INTERVAL

The older nestling left the nest at about 13:15 on 31 May, the younger at 13:35. The latter perched on the nest rim at 13:30 and was fed there at 13:34. One minute later it hopped a few cm out on the nest branch. After a further minute it moved another 15 cm away; its sibling was then two m from the nest. The younger bird weighed 36.0 g at nest leaving, the older only 30.1 g. The two were able to hop along the ground very quickly; occasionally, however, one tottered and fell in its haste. They appeared to be able to fly only about 0.3 m. Brackbill (1943:80) observed flights of about 16 m by young just out of the nest.

TABLE 2

WEIGHTS OF WOOD THRUSH NESTLINGS,¹ ACCORDING TO 24-HOUR INCREMENTS IN AGE²

Approximate age in hours	Weights per nestling, in grams		
	1	2	3
0.5	3.8	—	4.2
24	5.0	—	5.8
48	7.9	6.7	—
72	11.3	—	14.3
96	15.6	14.1	17.0
120	20.3	17.6	21.2
144	24.3	21.1	24.9
168	25.6	25.0	28.5
192	29.3	26.8	31.5
216	31.7	29.5 ³	—

¹ Bird 1 was the younger nestling from the principal nest, in which there was one other nestling. Birds 2 and 3 were nest mates from a brood of three.

² Weighing stopped when the birds reached the age at which they could no longer be handled without causing premature nest-leaving.

³ The third member of this brood, not otherwise dealt with in this table, weighed 28.6 g at this age.

The older bird spent about 296 hours and 5 minutes, i.e., about 12.3 days, in the nest after hatching, the younger exactly 294 hours and 55 minutes. In 1965, I recorded the approximate length of nest life of one young Wood Thrush from a brood of three. It left the nest 299 hours and 45 minutes, plus or minus about 10 hours, after hatching. These intervals in the nest accord with those reported as typical by Weaver (in Bent, 1949:109). Brackbill states (1943:80) that young fledged prematurely after ten days, but in his later paper (1959:84) he gives 12 to 14 days as the normal age at which he observed nestlings depart.

WEIGHT OF EGGS AND NESTLINGS

The last egg laid in the principal nest weighed 4.8 g no longer than four hours after it was laid. At 07:00 on the day before it hatched, before pipping began, it weighed 4.1 g, having lost 15.5 percent of its original weight. Slightly more than an hour before it hatched, when the cracks in the shell had certainly caused some drying of fluids and consequent weight loss, it weighed 3.9 g.

Table 2 shows the weights of three nestling Wood Thrushes at approximately 24-hour intervals during that part of their nest life in which I could handle them. Bird 1 in the table was the younger nestling in the principal nest. Birds 2 and 3 were two members of the 1965 brood referred to in the

preceding subsection. Weights were taken at about 07:00 and 19:00; they changed very little overnight. Weaver (in Bent, 1949:110) reports that a newly hatched Wood Thrush weighed about 5.1 g, relatively much heavier than the young birds I examined.

DEVELOPMENT OF PLUMAGE

The neossoptiles of a nestling from the principal nest were dark gray at hatching; this description is not based on a color chart. I counted six over one eye, seven over the other. The occipital pteryla bore two neossoptiles on each side of the head, the spinal pteryla 15, the humeral two on one side and one on the other. This pattern differs greatly from the pterylosis described by Wetherbee (1957:414-416) as the basic pattern for the Turdidae.

At the age of 48 hours the femoral, humeral, spinal (excluding the cervical region), and alar tracts of the nestlings were visible beneath the skin. Twelve hours later the capital tract was becoming visible, and the tips of the primaries projected very slightly. At 72 hours the tracts and regions previously visible had become more conspicuous. The ventral and crural tracts still could not be seen, but 12 hours later both were discernible.

At 96 hours the primary sheaths projected about 2 mm, the secondary sheaths 1 mm, and some secondary coverts were just emerging. The interramal, malar, sternal, axillar, and abdominal regions were becoming visible beneath the skin. Sheaths of tracts that had been visible earlier were now about to emerge from the skin.

At 120 hours the primaries were about 5 mm long, the secondaries slightly shorter; the greater coverts of these two regions and the alula feathers were about 3 mm long. Femoral, humeral, spinal, and some anterior ventral quills projected beyond the surface of the skin. Twelve hours later feathers of the capital and crural tracts and the middle secondary coverts had just begun to project. Some primaries and secondaries were 10 mm long.

At 144 hours feather tips showed beyond the sheaths of the greater and middle secondary coverts. Twelve hours later the tips of feathers showed from all sheaths but those of the capital and crural tracts, the primaries and secondaries, and the interramal and malar regions.

At 168 hours the primaries and secondaries were 17 to 20 mm long, still fully sheathed. Twelve hours later the primary sheaths were about 21 mm long, with feather tips projecting. The spinal feathers were growing, and the dorsal surface of the birds no longer looked bare; the color was fuscous. Colors referred to in this and the next paragraph were obtained by placing the bird next to a color chart (Palmer, 1962:chart following 4) and judging accordingly. The anal circlet was noticed for the first time; it consisted of well-developed quills.

At 192 hours the dorsal surface of the body and wings was brownish olive, except that the scapulars were sepia. The secondary coverts were brownish olive with tawny tips. The capital feathers, now rapidly emerging, were brownish olive on the frontal and anterior coronal regions, rufous posteriorly. The belly was light cream. The primaries and secondaries were about 25 mm long, about 4 mm of this consisting of feather tips. Twenty-four hours later these alar feathers were about 31 mm long, half sheath and half feather tip. The plumage changed little in appearance thereafter. The gape was

orange on the lower mandible, orange yellow on the upper. The darkening mandibles were largely fuscous, the tip sepia; the rictal flanges were buffy yellow to cream; flesh tones still showed around the nares.

When the young left the nest the primaries were about 45 mm long, and the bent wing, flattened and measured in the usual way, was 67 mm.

DEVELOPMENT OF BEHAVIOR

At age 96 hours the eyes had not yet opened, but at about 108 hours they opened slightly when the young gaped (see Weaver, in Bent, 1949:110).

At 144 hours the young clung to the nest lining when handled. At 168 hours they uttered faint calls during weighing. A few hours later they gave a rapid series of calls whenever handled. At about 200 hours, however, nestlings still showed no fear of me and gaped at my hand when I placed them on a balance.

Not till age 240 hours did the young move about much in the nest (see Weaver, in Bent, 1949:111). They then became exceedingly active, preening, scratching (the foot over the wing), fanning the wings, stretching, and getting to the nest rim for a few seconds. These activities were especially frequent when the sun shone on the nest.

SECOND-BROOD AND REPLACEMENT NESTING

On 16 June the pair from the principal nest apparently were no longer caring for their fledglings, which on that day were about 28 days old (see Brackbill, 1958:85). On 3 July I discovered the female sitting on a new nest, about three m above the ground. When I first examined it closely late on 4 July, the nest held only two cowbird eggs; by 19:00 on 5 July these had hatched. The nest failed on 9 or 10 July and I saw no subsequent evidence of breeding, although I have found Wood Thrushes about six days old and still in the nest at Bloomington as late as 22 August. Production of second broods has been reported for pairs of color-banded Wood Thrushes (Brackbill, 1943:74, 81; 1958:85; Weaver, in Bent, 1949:112).

The incubation of the cowbird eggs that hatched on 5 July probably began on about 24 June. If the female thrush built this nest in three or four days, waited two or three days, and then laid two or three eggs, she must have begun to build the second-brood nest approximately in the period 17–19 June, i.e., some 17 to 19 days after her first brood left the nest. Brackbill (1958:79) observed several cases in which the interval between these events apparently was no longer than four or five days, and Harbaum (1921) saw an unbanded female building within three days of a first brood's nest-leaving (but see Brackbill, 1943:74, and Weaver, 1939:22).

SUMMARY

A Wood Thrush nest appeared to be complete when found, 12 days after the male first sang on the territory. Three days then passed before laying began. Four eggs were laid on consecutive days, probably all of them at about noon. Only the female appeared to incubate; she spent every night on the nest after the first egg was laid. According to one method of sampling, the female spent about 64 percent of the daylight hours on the nest during the incubation period; on a day when the nest was watched continuously she was present 72 percent of the time and left the nest 31 times. The male often perched on or near the nest and sang when the female was absent. Behavior of the pair toward birds and other animals is described. The incubation period was about 12.7 days, and the two young that hatched left the nest when slightly over 12 days old. The weights of the nestlings at various ages are presented, and the development of the plumage and certain nestling behavior are described. The female began a second-brood nest about 17 to 19 days after the nestlings left the first nest, but this effort was unsuccessful.

LITERATURE CITED

- BENT, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Nat. Mus. Bull., 196.
- BRACKBILL, H. 1943. A nesting study of the Wood Thrush. Wilson Bull., 55:73-87.
- BRACKBILL, H. 1958. Nesting behavior of the Wood Thrush. Wilson Bull., 70:70-89.
- DAVIS, D. E. 1954. A simple method for obtaining attentive data. Auk, 71:331-332.
- DILGER, W. C. 1956. Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. Auk, 73:313-353.
- HARBAUM, F. 1921. A family of Wood Thrushes. Bird-Lore, 23:140-141.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biolog. Monog., 22.
- McCLINTOCK, N. 1910. A Hermit Thrush study. Auk, 27:409-418.
- PALMER, R. S. (ed.). 1962. Handbook of North American birds, vol. 1. Yale University Press, New Haven.
- ROBERTS, T. S. 1936. The birds of Minnesota, vol. 2. Univ. of Minn. Press, Minneapolis.
- STANWOOD, C. J. 1913. The Olive-backed Thrush (*Hylocichla ustulata swainsoni*) at his summer home. Wilson Bull., 25:118-137.
- TODD, W. E. C. 1940. The birds of western Pennsylvania. Univ. of Pittsburgh Press, Pittsburgh.
- WEAVER, F. G. 1939. Studies in the life history of the Wood Thrush. Bird-banding, 10: 16-23.
- WETHERBEE, D. K. 1957. Natal plumages and downy pteryloses of passerine birds of North America. Amer. Mus. Nat. Hist. Bull., 113:339-436.

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