

NESTING BEHAVIOR OF THE WOOD THRUSH

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FROM 1942 to 1954 I watched, sketchily to intensively as my circumstances permitted, 37 nestings of the Wood Thrush (*Hylocichla mustelina*) in suburban Baltimore, Maryland, concentrating on the early stages that I had missed in a previous study (Brackbill, 1943). Many of the birds studied were color-banded.

ARRIVAL AND PAIRING

Arrival of breeding males.—Breeding males sometimes were and sometimes were not the first Wood Thrushes in their territories in spring. My best example was a male that I color-banded in 1942 on April 29, the day of the species' arrival; in 1943 Wood Thrushes arrived April 28, but this male not until May 8, when he had to oust another male from his old territory; in 1944 the species arrived April 26 and the marked male April 27.

Returns.—Four of 10 color-banded breeding males returned, three in the year following their banding, and one in each of the two years following; three of these birds may have returned oftener, but at that point I moved from their neighborhood. Of 10 color-banded breeding females, one returned, the year after its banding. From 26 color-banded nestlings I obtained no returns.

Time of pairing.—Two males obtained mates one and three days, respectively, after their own arrival. Weaver (1949:103, 104) reported three males obtaining mates two, three and six days after arrival. I have never seen the manner of pair formation.

Retention of mates.—Both members of three pairs of multiple-brooded birds were color-banded; these pairs stayed together throughout the season. In none of five possible cases did both members of a color-banded pair return, and so there were no rematings from year to year.

THE NEST

Tolerance for human habitation.—The increasing neighborliness of the Wood Thrush has been noted by Weaver (1939:16) at Ithaca, New York, Todd (1940:441) in western Pennsylvania, and Griscom (1945:59) in the New York City and Boston areas. Such a change in behavior of Wood Thrushes has occurred in the Maryland region, too, in the first quarter of the century. Writing of the Baltimore area, Resler (1891:106) said this bird "appears to be not so well known as the majority of our other songsters, in consequence of being more solitary and shy." Maynard (1902:44) said that in the District of Columbia area it is "an inhabitant of most woods about Washington," but Cooke (1929:65) stated that "they now nest freely about

lawns in the suburbs as well as in the woods." And from 1942 through 1954 they have been common in the wooded residential parts of Baltimore, with a pair often to be found every few blocks, or even every block for a little distance.

Twenty-five of my nests were on the grounds of occupied houses, three on vacant lots between houses, three in trees growing at curbs, two in the edges of a park opposite houses, and only three in wild land and one appreciably inside a park. As for proximity to dwellings, two nests were in bushes against the walls of houses, one was two yards from the back of a house and only a little farther from the steps, and five were in bushes marking property lines, with houses only three and four yards away on two sides.

Nest-site selection—A few observations show that the male Wood Thrush can influence the choice of a nest-site, but they suggest that the choice is actually made by the female—the nest-builder. The male, by means of calls or song, sometimes brings potential sites to his mate's attention, and he may even initiate building. However, the female may or may not adopt sites thus indicated, and so it seems that she must be regarded as the true site-selector.

Observations of a pair in 1949 were most illuminating; these birds were not banded. One evening I found the male singing at a horizontal fork low in a tree. Soon the female flew beside him and in some seconds he left, and then the female began a period of "nest molding" at the fork. While she was still there, the male flew well up into a different tree with a piece of white paper. The female shortly left the fork and I lost sight of both birds, but a little later one or the other of them took paper into a third tree—to a point at which I could see no other material—and it was there that building continued, the builder being the female all of five times that I could make an identification (the male was singing elsewhere).

In 1943 the first nest of a color-banded male was on the same branch as his first nest of 1942, and on almost the same spot, although he had different mates in the two years. Since his territory contained a variety of suitable nest-sites (proved by the fact that he and three mates also used four others there during three years that he was under observation), necessity did not cause this duplication, and it is inconceivable that chance did. Certainly this male influenced his 1943 mate to build at the old site. Two incidents suggest how this was accomplished. An hour and a quarter after I first found him with his 1943 mate I saw him at the old site, giving bursts of very loud *quit* calls. The next day the nest was begun there. The day after that, I thought, but in dim light could not be sure, that the banded male made the second building trip of the day. Thus it may be that the male's calls attracted the female's attention to the spot, and it is also possible that the male carried a little material during the earliest building—although from then on the working bird whenever identified (10 out of 14 trips) was the female.

In 1944 I made a somewhat similar observation on this same male. On the evening of May 4, the day he obtained a mate, I came upon him in an oak that in the previous two years had been one of his principal singing trees giving extremely muffled and unmusical song trills and calls; his mate was on the ground about 13 yards away. On May 9 I first saw the female tentatively pick up nest material; on May 13 I found the nearly-completed nest in the oak mentioned.

Weaver (1949:103) describes a female testing a site in much the manner

of my 1949 female, and (1949:106) reports that "in one case a pair built in the identical spot it had used the year before."

Height.—I believe the 37 nests I located comprised all but two of the entire number built in my study areas. In this suburban environment the height range, 4 to 35 feet, was typical of that generally reported for the Wood Thrush, but there was a much greater proportion of moderately high nests than Preston and Norris (1947:256) found in natural woodland. Almost half of my suburban nests were at 13 to 22 feet, whereas two-thirds of those in natural woodland were at 5 to 10 feet. This seems attributable to the fact that trees of sapling size are uncommon in residential areas; from the upper branches of shrubs to the lower branches of large trees there is a stratum in which few building sites are available. Of my nests, 12 were in bushes, 6 in saplings, 19 in large trees.

Placement, materials.—I have little to add to Weaver's account (1949:105-106) of nest sites and materials, except as regards the statement that "the nest is usually fixed in a fork . . . but some were found saddled on horizontal branches."

In my experience, nests are often set on the base of a horizontal fork, a spot that provides broader support than a single stem. Similarly, nests on straight horizontal branches are generally placed at a spot where one or more twigs grow out, or where the branch is crossed by another stem of the bush or tree or by a vine. The thickness of branches at nest-sites has varied from $\frac{1}{2}$ inch to 3 inches. I have never seen a nest set in a two-pronged vertical fork, but have found some inside multiple forks, or "baskets," of upward-growing stems. The branch chosen for a tree nest is usually the lowest on its side of the tree, if not the lowest on the tree; of 15 nests on which I have notes, 9 were on the lowest branch on at least their side, and three on the next-to-lowest; the others were as high as the fourth tier of branches. Tree nests as a rule have been one-third to three-fourths of the way—three to 11 feet—out branches; one exception, in a sapling, was built against the main stem, its base resting on thin twigs that formed a slight crotch. Like Weaver (1939:16), I have never found a nest in a conifer, though many were available and one was used as a song perch. Neither have I ever found a nest in the thorny bushes—rose, barberry, pyracantha—that are commonly used by some species in the same suburban areas. Nests in other bushes may be either in the heavily-foliaged crowns or among the lower, leafless stems.

Concealment, shade.—With both tree and bush nests, the degree of concealment varied greatly. In trees, the lateral twigs that gave secondary support occasionally bore leaves that almost entirely hid the nests. More often, the nests' similarity in color to their supporting branches, and their tendency to melt into the mottled background of light and shade created by foliage, made them hard to locate. Nests in the crowns of bushes were sometimes

practically invisible, but those down among scantily leaved stems were fairly conspicuous.

The customary use of sites low in trees insured shade from the foliage above. Thick crown foliage or overhanging trees shaded all but one of the nests in saplings, too—that one was considerably exposed to the afternoon sun but was completely successful. The bushes used for nesting were with one exception well shaded by trees.

Size.—Not counting the materials that occasionally hung down as much as 14 inches below the base proper, seven nests (six bush, one tree) had outside heights of 2 to 5¾ inches and widths of 4 to 5½ inches. One was 4½ inches wide at the base but only 4 at the rim. One built on a slanting branch was made level by being ¾ inches deep on the lower side and only 2 inches deep on the upper side.

The inside depths of the seven nests ranged from 1¼ to, usually, 2 inches, and the inside width from 2¾ to 3¼, or occasionally, 3⅝. Two nests were not quite round: 3 by 3¼ inches and 3¼ by 3½ inches in inside diameters. One nest measured only after its two young had left was 4 by 4¼ inches, indicating that use had widened it about an inch.

Successive nests of the same birds.—I have already (1950:8) shown that successive nests of the same pair of Wood Thrushes may be at heights as similar as 17 and 13 feet or as dissimilar as 18 and 8 feet, and that they may be dissimilar in their placement. An additional observation is: a color-banded pair of birds in one year had successive nests 9 feet up in a lilac, set in a "basket" of four stems; 6 feet 6 inches up in a silky cornel, set on a fork that slanted upward at 45 degrees, with another branch supporting its lower side; 5 feet 10 inches up in the top of an unidentified bush, set on a horizontal fork, from one arm of which two twigs grew out.

With five out of six pairs of marked birds, successive nests have been progressively lower; the sixth pair nested at 7 feet 3 inches, 13 feet 9 inches, 10 feet 9 inches.

I have never seen a nest used twice in the same year, and have never seen one survive weathering from one year to the next.

Sex of the builder.—Observations at 12 nests, ranging up to 9½ and 19 hours' watching of color-banded birds, showed building to be a female activity. Aside from the uncertain 1943 occasion, and that of 1949 during nest-site selection, both described above, I only three times saw males work, and those birds did not add material but merely molded during absences of their mates.

On June 27, 1948, the third nest of a pair was being lined. When the female left on what became a 20-minute absence, the male flew to the nest-rim. He occasionally pecked in the nest, then after 11 minutes entered it and began molding, just like a female but less vigorously. He worked sporadically until just before his mate returned, his halts being made to mark the doings of other birds in the neighborhood, and once to sing for half a minute in response to a neighboring thrush.

On May 15, 1954, the first day of work on a first nest, a male twice, during absences of his mate, went to the nest without material and worked in it, once for two minutes

and once intermittently for nine, both times leaving only when his mate returned. He, too, worked just like a female, in molding, in moving material from one spot to another, and in lapping straws from the outside up over the rim into the inside.

Building hours.—I saw building done as early as 5:00 a.m., E.S.T. (10 minutes after sunrise), as late as 7:32 p.m. (two minutes after sunset), and at all hours between except for the period from 3:00 to 4:50 p.m.; however, usually only on the days of intensive building was there work in the afternoon. Nests are often begun in the evening. On the second and third days, which are generally the days of most intensive work, building may be done in the evening as well as the morning and early afternoon. I once saw work done on the evening of a fourth day. Later than that, when the nest is generally getting mere touches, these seem to be given it only in the early morning.

Time required.—The time taken to build five nests was determined: two first-brood nests, five days; one first-brood and one second-brood nest, six days; one first-brood nest, seven days. In each case, only slight touches were given on the mornings of the last two (once three) days. I did not obtain precise data on successive nests of any bird.

Source of materials.—Materials at times were gathered as much as 70 and 85 yards from the nest-site, but I believe most were obtained within 25 or 35 yards. Besides loose-lying materials, rooted grass—both dead and living—is pulled at and sometimes obtained.

Manner of building.—At no single nest was I able to watch building procedure throughout, but at one nest or another I saw all stages of work, and I saw most stages more than once. The following account is a composite.

Soft white paper, cellophane, string, or long stems of dead grass—usually some combination of those things—are first draped across the nest-site; they commonly hang down a number of inches below the branch. Dead grass, rootlets and dead leaves are then placed atop this; as she adds each billful the female squats on it and squirms about, packing it down.

When a substantial foundation has been achieved in that way, the nest wall is begun. Arriving with more material, the bird drops this in front of her or to one side, then reaches to the edge of the nest-mass and pulls some of the outer material upward and inward and tucks it into the bottom; this lapping-over may be done several times in succession. Then the bird “molds”—squats and, with wings, rump and tail all more or less raised, apparently presses forward with her breast while also using her feet behind her. Rises, turns a varying distance to one side or the other, perhaps does more lapping-over, and molds again. As many as 30 molds, taking the bird around in the nest for three full circles and occupying as much as six minutes, may be made on a single visit to the nest. In this way the material about the outside of the mass is gradually pushed and built upward and compacted into the nest wall. In the later stages of this work, lapping-over from the outside is sometimes omitted, but loose ends of material that project into the nest-cup are frequently tucked back into the wall.

Only one bird was watched while putting in the mud layer of her nest. She did this by means of typical molding, and sometimes held an appreciable amount of mud on her bill during a number of molds, apparently distributing it in the course of her work. The lining of rootlets is also worked into place by molding, but molding in which the

feet seem to be used much more than the breast. At the nest I was able to watch most lengthily, the number of molds made on one visit increased, as building progressed, to a maximum when mud was being used, then decreased somewhat as the nest was being lined.

Generally, the nest is really complete after three days' work. On two or three more mornings, however—as late as her first egg-laying day—the female may still give it a few touches. During this period, one bird sometimes added material, and sometimes went to the nest empty-billed, stood in it idly during the greater part of her visit, and only occasionally made an adjustment. Another bird, on the morning of her first laying day, sometimes seemed to take a bit of material from one spot and put it as much as 90 degrees farther around the rim; she also seemed occasionally to move something from the rim to the bottom of the nest, and she still sometimes lapped material slightly over the rim.

This is the same method of building that Herrick (1935:174-175) has recorded for the American Robin (*Turdus migratorius*).

Reversals of direction in molding.—Herrick noted (1935:174, 193-196) that when making a number of molds during the same working visit to its nest, a Robin normally keeps turning in the same direction—to its right, say—and then on its next visit makes its turns to the left, and so on alternately. However, if it makes an extreme number of molds during one visit, the direction of its turns may be reversed once or oftener in the course of that visit; the reversal is “related rather to the number of molds than to that of the visits.”

At a nest at which I paid particular attention to this point, the Wood Thrush behaved similarly. During the first 185 minutes of one working day, for example, this bird made 42 visits to her nest. With L meaning left and R right, and spaces merely setting off the series of visits during which reversals were made with complete regularity, the direction of her turns throughout each visit was:

RLRLRLRL LRLR RLRLR RLRLRLRL RLRLRL LRLRLRL LRL ... (series
74 36 44 74 76 72 36 ... unfinished)

The figures below each series are the closely approximate number of molds made during that series. It may be noted that the second failure to reverse occurred after an interval of only one minute between trips; this suggests that the third series should be regarded as a continuation of the second, and if that is done it is apparent that a true failure to reverse occurred with great regularity after about every 75 molds. In contrast to that failure to reverse direction after a one-minute absence, the first two trips of the day show a reversal although 30 minutes elapsed between them; Herrick (1935:193) similarly records a reversal by a Robin after a 24-minute absence.

Rhythm.—When building intensively the working female showed an attentive-inattentive rhythm like that of incubation. Examples from three nests are:

Second nest of year, second day of work, 9:41-10:45 a.m.:

Attentive (minutes)	+ 17.5	1	14.5
Inattentive (minutes)		11.5	8.5 11

Third nest of year, same bird, third day of work, 9:28-11:08 a.m.:

Attentive	43.5	5
Inattentive	+ 12.5	20 19 +

First nest of year, third day of work, 5:10-8:15 a.m.:

Attentive	+ 5	1.5	12	14	83.5	6.5
Inattentive		30	6.5	6	10	7.5 2.5 +

During the last series of attentive periods listed, the number of building visits made to the nest was 1, 1, 6, 6, 25 and 3, respectively.

A building drive.— Once a long strip of crepe paper that a female was taking to her nest caught in the bush 2½ feet away. She tried to dislodge it and failed, but then instead of going for other material went on to the nest and worked just as if she had added something. I have seen a male House Wren (*Troglodytes aëdon*) act similarly. One that was carrying twigs into a nest-box often had difficulty maneuvering them into the hole, and five times I saw him knock them out of his bill. Once this happened as soon as he alighted at the box, and that time he went to the ground and recovered the twig, but the other four times it happened only after he had been struggling with the twig for some time, and on all of those occasions he then went into the box empty-billed and stayed as long as if he had added material. It appears that, once started on a building action, both of these birds had to carry it through, even though the original motivation no longer existed.

Male's activities during building.—At seven nests, of five pairs of birds, I obtained more than casual observations on the male's activities during the building period. Different birds acted somewhat differently, but it is possible to summarize as follows: the male sings, but usually not very much, throughout this period; he defends the territory, but very imperfectly; he begins to stand guard at or near the nest during some of the female's inattentive periods—two males entered the nest and molded, as related above; during the later stages of work he sometimes accompanies the female to and from the nest and stays nearby while she builds; at this time he also engages in sexual flights with her; and he feeds the young of the preceding brood, if there are any.

COPULATION

I did not see copulation, but during the building and laying periods at several nests saw sexual flights and other possibly stimulatory acts, and saw one male attempt copulation and fail—apparently because the female, which had begun to incubate, had passed that stage of her sexual cycle.

Early on the morning of May 9, 1943, only a few hours after the female's arrival in one territory, I found her with the already-color-banded male on the lawn. Twice within three minutes she toyed with pieces of cloth and cellophane, and between times once ran at the male and seemed to peck him. Nothing further occurred during the few minutes more the birds stayed there. Nest-building began the next day about 12 yards from that spot, and the first egg was laid May 14. A similar incident occurred on May 28, 1949, five days after a storm had destroyed the nest and eggs of a color-banded pair. At noon, while the birds were feeding on a lawn, the female once ran at the male and apparently pecked him; some squeaky calls were given by

one bird or the other during the incident. Again, nothing further occurred. I think the first egg of a new set was laid the next day. Both of these incidents looked like attacks, but as copulation must have been occurring at the time, or about to occur, perhaps they were stimulatory.

Sexual flights were seen at various nests, as early as the third day of building and as late as early morning on the second of three laying days, when incubation had begun. The birds flew at a moderate speed over winding courses, often only three or four feet above the ground. Eight out of nine flights were made in silence; during the other, long *eee*'s were frequently given, but I could not tell whether by one bird or both. Some males were singing just before the flights began; song was sometimes resumed afterward. The flights were seen oftenest in the early morning, but also in the evening and once around noon. One pair of birds made two within four minutes; another pair made four within 45 minutes. One female made a building trip to the nest between two flights that were 11 minutes apart. Weaver (1949:104-105) describes similar flights.

On June 2, 1943, the first egg was laid in the nest of a color-banded male and an unbanded female. At 5:45 a.m. on June 3 the female was incubating and the male singing nearby. After 20 minutes the female flew about 50 yards away, and almost at once the male disappeared. Some minutes later, from my place near the nest, I saw two thrushes flitting about perhaps 10 feet up in a tree in the area to which the female had gone; there were wing-flutterings and apparent attempts at mounting, then the birds went out of sight on a sexual flight. Shortly after this the pair alighted 25 feet up in a tree near the nest, and there, with neck stretched high and crest raised, the male began persistently running along a branch at his mate and bumping her on the side or shoulder with his breast; often he fluttered his wings a trifle. Sometimes, too, he flew hoveringly at her as if to mount, and once he did drop his feet to her back and then opened one wing horizontally and fluttered it briefly; the female, however, moved from under him. After a minute the birds went into a tree still nearer the nest; there the male continued his actions, but now sometimes when he approached the female she pecked at him and drove him back. Two and a half minutes after these performances had begun, the birds again flew out of sight, and during the few minutes more that I could watch they did not return. According to Howard (1929:52) this was typical behavior for a male that is still sexually eager and a female whose copulation period had just been ended by the beginning of incubation. The attempts at copulation in trees contrast with Weaver's belief (1939:21) that she once saw it take place in the air, and with her statement that A. A. Allen believes it normally takes place on the ground.

THE EGGS

Interval between building and laying.—At 10 nests, the first egg was laid from one to three days after building had been essentially completed. Three of these nests were among those seen to be given slight touches on the later mornings, as related under "Manner of building." Because there was indication of this at a fourth nest also, and because such working trips were so few that only prolonged watching disclosed them, I believe this behavior probably is the rule.

Laying rate.—Eggs are laid one a day on successive days.

Clutch size.—Sixteen clutches observed as laid or (two of them) found during the first few days of incubation ranged from 1 to 5, with 3 and 4 most common. The division was: 1 c/1; 2 c/2; 6 c/3; 6 c/4; 1 c/5.

Clutches tended strongly to be largest at the beginning of the season. The c/5 was a first clutch. Five of the c/4's were first clutches and one a third clutch. Two of the c/3's were first clutches, three were known second clutches, and the other was indicated by its date to be a second clutch. Both c/2's were second clutches, and the c/1 a third clutch.

Clutches smaller than 3 eggs all followed some disturbance of the breeding cycle. One c/2 was laid after a storm destroyed the first nest during incubation. The other c/2 followed a nesting in which only a Brown-headed Cowbird (*Molothrus ater*) was raised, and the c/1 was a third laying of this same female after a storm destroyed her second nest and eggs.

Successive clutches of same females.—Successive sets of three color-banded females showed no fixed relationship in size. One bird whose nestings were undisturbed laid clutches of 3 and 3; another, 4 and 3. One whose first nesting was unsuccessful laid three clutches of 4, 2 and 4; in the following year this female's first clutch numbered 5—this is the only bird on which I have data for more than one year.

Laying dates.—The earliest observed laying date was May 12; the latest, July 6. Eight first clutches were laid in the period, May 12 to 21. Three second clutches of birds that had undisturbed first nestings were laid June 16 to 26. Two third clutches of birds that had had one previous failure were laid July 1 to 6. Cooke (1929:65) reports eggs as early as May 1 in the Washington, D.C., region, and Kirkwood (1895:370) gives a late date of July 28 for Maryland.

Laying hour; effect of temperature.—Data on 18 eggs, representing nine nests, show that laying is usually done between 9:00 a.m. and noon, E.S.T., but sometimes not until early afternoon. At least 12 of the eggs were laid after 9:00 a.m., and at least 11 were laid before 12:15 p.m. The earliest-found egg was laid between 7:55 and 9:34 a.m., and the next-earliest between 9:11 and 10:14 a.m. The latest was laid between 1:30 and 4:48 p.m.; two

others were laid between 11:42 a.m. and 1:35 p.m., and 12:57 and 2:20 p.m. Weaver (1949:107) reported two eggs laid at about 10:30 a.m.

It appears that laying is done earlier on cool days than on warm ones. All of nine eggs known to have been laid before noon (by six different birds) were laid on days when the temperature at 6:00 a.m. was 52 to 58° F.; the mean temperatures for those days ranged from 11° below normal to 4° above normal. All three of the eggs that were laid after 11:42 a.m. (by two different birds) were laid on days when the temperature at 6:00 a.m. was 70° and 71°; the means for those days ranged from 6° to 16° above normal. The earliest-found egg was laid on a day that was 4° below normal, and the latest-laid egg on a day that was 6° above normal. (The temperatures given are the official ones for Baltimore city, not those in the nesting territories, and so are relative rather than exact.)

Fledging-to-egg and egg-replacement times.—At four second-brood nests the first eggs were laid 9, 9, 11 and 12 days, respectively, after the young had left the previous nests. Weaver (1939:22) reported one interval of "16 days," but the dates given show 17, and her statements there and those reported later (1949:112) conflict.

Laying was resumed more quickly—on the seventh day, and not later than the eighth day—after the destruction of two nests by storms on the third and eighth days of incubation, respectively. The bird that had begun her second clutch on the eleventh day after fledging her first brood was the one that now laid in a third nest on the seventh day.

Nice (1937:111, 133) found that with the Song Sparrow (*Melospiza melodia*) the fledging-to-egg interval is longer and more variable than the egg-replacement time after destruction of a nest. Blanchard (1941:34) also found this true with the White-crowned Sparrow (*Zonotrichia leucophrys*), and Walkinshaw (1945:12–13) with the Field Sparrow (*Spizella pusilla*). Lack (1953:201), however, reports great variation under both circumstances with the British Robin (*Erithacus rubecula*).

INCUBATION

Sex.—Observations at 17 nests, ranging from one to 68 identifications of the sitting bird—more than 10 identifications were made at each of nine nests—confirmed my previous finding (1943:75) that the female alone incubates. Weaver (1949:108) also found this to be true.

Brood patch.—The brood patch begins to develop within the week before laying starts. Three females had the abdomen still feathered when banded six, seven, and six to eight days before they laid their first eggs; at least two of these birds had begun their nests at the time they were trapped. A fourth female, trapped when her nest was near completion, had only a few downy feathers on the abdomen; I do not know when she began to lay.

Time and manner of start.—Observations at 14 nests show that daytime incubation usually begins on the second laying day, but sometimes on the first and sometimes as late as the fourth. It most often begins on the penultimate laying day, but may begin as early as the first of four. Night roosting on the nest sometimes begins with the first egg, sometimes with the second. I can demonstrate no clear difference in behavior as between first and second broods; two of three nests at which daytime sittings began with the first egg were second-brood nests, but the two nests at which roosting began with the first egg were first-brood nests.

Close observations on the start of daytime incubation were made at 10 nests. At three there were some sittings from the first laying day, at five from the second laying day (at three of these, at least, beginning some hours before the second egg was actually laid), and at one each from the third and fourth laying days. At five out of the 10 nests the sittings began on the day of the penultimate egg, but two birds began with the first of four eggs, and three on the second of four laying days. Except at an eleventh nest, in which only one egg was laid, no bird completed her clutch before beginning to sit.

Another bird, which laid three eggs, was already incubating early on the morning of the second laying day, when her nest was found. At a nest in which a Cowbird egg, and then a thrush egg, were laid on successive days, incubation began early on the morning of the second day, before the thrush laid. And at a nest in which two thrush eggs were laid, and then a Cowbird's, there was some incubation from at least the second of the three days.

The way in which incubating behavior develops can be illustrated through one female and her two nests. My observations were fullest at the first nest, in which four eggs were laid. With the laying of the first egg the bird began to spend brief periods, very occasionally, standing on the rim of the nest. With the laying of the second egg, periods of such attentiveness became much more frequent, and finally changed into some covering of the eggs. With the laying of the third egg incubation became typical and steady. At the second nest, in which three eggs were laid, the same behavior apparently developed one day faster, for during an hour's watching early on the morning of the second laying day I saw not only one period of simple attendance on the nest-rim but part of an appreciable sitting.

Amount and rhythm.—Some figures on the attentiveness of females during incubation of full clutches (*i.e.*, laying and hatching periods excluded) are given in Table 1. For the sake of completeness two earlier ones (Brackbill, 1943:75) are repeated on the first two lines of the table. The females usually ended their sittings of their own accord, but sometimes ended them (and sometimes did not) when their mates came near the nest or began singing in the vicinity.

Hatching hour.—Hatching may occur during either the day or the night. Data were obtained on 24 eggs in 11 nests, as follows: 18 hatched during daylight—four of these between 5:00 and 7:00 a.m., E.S.T., one between 9:30 a.m. and 1:40 p.m., one at 3:35 p.m., one between 5:00 and 6:00 p.m., the other 11 at unknown hours; six hatched during darkness.

The 24 eggs included eight final eggs of clutches; of these, four hatched

TABLE 1
ATTENTIVENESS OF INCUBATING FEMALE WOOD THRUSHES

	Hours Watched	Eggs Covered	No. Seen	Attentive Periods		Inattentive Periods		
				Range in Min.	Average	No. Seen	Range in Min.	Average
First-brood nest	15¾	78.0%	11	11-47	31.0	22	6-16	8.5
Second brood, same bird	17	80.3	12	7-58	27.0	18	1-12	6.1
First-brood nest	5	88.0	5	11-42	25.0	8	6-13	8.0
Second brood, same bird	4	60.0*	1	45		6	2- 9	5.0
First-brood nest	9¼	69.2	23	2-28	13.6	25	2-23	6.1
Renesting after failure	7½	75.6	8	17-37	26.0	13	4-11	6.0
First-brood nest	29	71.2	37	6-49**	24.4	47	4-21	9.8

*Time spent at the nest without covering the eggs would raise total attentiveness to 94 per cent.

**Another attentive period, on a hot day (78° to 82°F.) was still unfinished after 80 minutes. However, during it the bird frequently stood up and picked in the nest for periods of one to five minutes; the eggs were covered for only 45 of the 80 minutes. With this one exception, incidentally, all of that bird's attentive periods during incubation were much shorter than the sittings during which she laid her eggs; those were:

Egg 1 laid sometime between 9:11-10:14 a.m.;	sitting less than 63 minutes
Egg 2 sitting	9:55-11:00 a.m. 65 minutes
Egg 3 sitting	9:32-10:55 a.m. 83 minutes
Egg 4 sitting	10:13-11:40 a.m. 87 minutes

during daylight, three at unknown hours between 6:00 p.m. and 7:00 a.m., and one definitely during darkness.

At one nest I flushed a bird at 4:26 a.m., 17 minutes before sunrise, and found an egg hatched, the shell still present and both it and the nestling dry, indicating that this night hatching had occurred sometime earlier but the parent was waiting until a normal time to leave the nest.

Hatching order.—All of the eggs in four marked sets, and at least the final two eggs of four more sets, hatched in the order of laying. In one of the latter sets, however, Egg No. 2 hatched at least half an hour before Egg 1; there had been some incubation at this nest from the second laying day.

Spread of hatching.—Precise observations at one nest showed that hatching was spread over 39 hours. At five other nests I learned only that the spreads were greater than 25, 27½, 31¼, 34 and 39 hours, respectively.

Egg shell disposal.—The female carried away both halves of one shell, but not until an hour after the nestling had freed itself from at least one half; in the meanwhile the female had made three more sittings, and both parents had made or attempted to make some feedings. I had once before seen a shell carried away (1943:76), and Ivor (1952:286) has reported this method of disposal.

Incubation period.—Incubation period here means the time between the

laying and hatching of the last egg of a set. The time of hatching was counted as that when a bird severed its shell so that one half fell away, when the bird was found still within one half of the shell, or when it was found with down wet and part or all of the shell still in the nest.

Observations at eight nests show the incubation period to be about $12\frac{3}{4}$ days. My closest timing was of a marked egg that took 12 days, 19 hours, 39 minutes \pm 44 minutes to hatch. Another took 12 days, 21 hours, 11 minutes \pm 6 hours 32 minutes. All of six other eggs (five of them marked) took more than 12 full days to hatch; at least two of the six took more than 12 days, 12 hours. The maximum possible time for one egg was 12 days, 18 hours, 5 minutes, and for another 12 days, 20 hours, 55 minutes. Weaver (1949:108) gives 13 days for marked final eggs in two nests at Ithaca.

Overtime incubation.—An egg that was the only one laid in one nest, and that never hatched, was incubated for 25 days—from July 1, the laying day, until sometime on July 26.

Female's incubating behavior.—Most females sat very patiently, at least during the early days of incubation, merely rising occasionally to turn the eggs with their bills, or to change their position somewhat; sometimes they squirmed around to face a different direction without rising perceptibly. One bird whose rises and resettlings were recorded through 13 sittings showed no regular alternation of direction in her turns, either within or between sittings. Now and then the birds may preen, or may doze a bit. One once left her eggs for a moment to pick an insect off a nearby branch. In the later stages of incubation, especially, birds commonly rise frequently and use their bill in the nest with a motion like the drumming of woodpeckers; although this suggests a probing for mites, my fingers held briefly in the nests on these days have not always produced any.

Observations at two nests when the official temperature was 76° F. and higher showed much attentive time being spent standing above the eggs instead of covering them. One female, watched for 71 minutes when the temperature was 76 to 78° F., spent $25\frac{3}{4}$ of 62 attentive minutes standing above the eggs. Watched for 104 minutes when the temperature was 85 to 89° , this bird spent $54\frac{1}{2}$ of 101 attentive minutes so. The dates were four and one days, respectively, before hatching began.

Another female, watched for 123 minutes while the temperature was 79° , 78° , 82° and the sun was continuously splashing her or the side of her nest, spent 40 of 113 attentive minutes standing above the eggs, and, while sitting, occasionally held her bill open. On the other hand, 115 minutes of watching two days earlier, when the temperature was 82° to 78° , showed no such actions. These dates were five and seven days before hatching began. Like the brooding female of my earlier paper (1943:77) this bird often stood on the nest-rim, but not on the sunward side.

Male's activities during incubation.—Observations of appreciable length at five more nests confirmed my earlier findings (1943:75-76). During their mates' attentive periods, males generally sang considerably, often from nearby perches that enabled them to defend the immediate area of the nest; they foraged, sometimes far from the nest; and with varying frequency they paid brief visits to the nest-bush or tree, sometimes going within a few inches of the nest; these visits occasionally led the females to end a sitting.

During their mates' inattentive periods the males almost always stood guard over the nest; at second nests they did this with much regularity even though they still had first-brood fledglings in their care. The guard perch was often the rim of the nest, but sometimes was elsewhere in the nest-bush or in some nearby tree. It was not uncommon for some singing to be done during this guarding, even from the nest-rim.

NESTLING PERIOD

How male learns of hatching.—I was present during hatching of the first egg at only one nest; there the male learned of hatching by seeing the nestling and seeing his mate feed it. Twenty minutes later he also began making feedings.

I began watching this nest at 2:42 p.m.; the female was sitting. At 3:35 she left and I found the first nestling out of one-half of its shell. There had been no sign of the male so far, and he did not come now to guard the nest. At 3:43 the female returned and went on the nest without making a feeding. At 3:48 the male arrived at the nest-rim and the female left; the male had no food, and merely stood looking into the nest until at 3:52 the female returned; he then moved aside but stayed close while she seemed to make a feeding, after which he left. At 4:09 he returned with food and gave it to the nestling.

Ivor (1952:286) believed that at a nest he watched, the male learned of the hatching in some other way.

Feedings.—Both parents feed the nestlings.

At one nest the first bird to hatch was first fed by the female, perhaps only 17 minutes after it hatched, and was first fed by the male 17 minutes after that, as described just above. During its first hour this nestling was fed at least three times, and probably five, then it once refused food.

One pair of observations showed the feeding day to be 15 hours (4:31 a.m., E.S.T., sky partly cloudy, to 7:35 p.m., sky clear). The first feeding was made 10 minutes before sunrise and the last seven minutes after sunset. On a clear morning the first feeding at this nest was made 19 minutes before sunrise.

Once while a male was standing on the nest-rim after making a feeding and eating a dropping, the two newly-hatched young shortly resumed gaping. After they had gaped for some time the male thrust his empty bill into each mouth a few times. Schantz (1939:164) has reported such behavior by American Robins.

Nest sanitation.—Although at two previous nests I had seen feces carried away a few times (1943:79) and I later saw this at two more nests, during

13 and 18 hours of watching feedings at two others all excreta were eaten, even on nest-leaving day. As I had found before, when the female remained at the nest through feedings by the male he did not wait for excreta to appear.

Brooding.—Observations at seven nests showed this to be done by the female alone, and at three nests I again found it to be done throughout the young birds' nest life (*cf.* 1943:77).

At one nest, brooding was done for 45.6 per cent of 6½ hours that I watched. There was no decrease in amount as the young grew, but there was some inverse correlation with temperature.

The male, during the nestling period, not only helps with feeding and sanitation, but continues to guard at or near the nest during many of the female's inattentive periods. At the nest I watched most closely, he regularly guarded while the young were small, and for decreasing portions of the female's absences, and at varying distances from the nest, when the young were large; occasionally he did some singing while on guard.

Nestling period.—Ten young birds left the nest at the age of about 12 to 14 days. Two left at about 12 days, two at about 12 and 13, one at 13, two at 13 or 14, and three had been in the nest 12 and 13 days when I caused premature departures.

FLEDGLING PERIOD

Feedings.—Both parents feed the fledglings. The females of two pairs helped to feed their first broods even while building their second nests; they made feedings at least as late as the second day before, and the day before, they resumed laying. When the young of single or final broods are all out of the nest each parent cares only for certain ones, and there may be a very similar division of the care of first broods; my observations on this point, with color-banded adults (one exception) and young are:

First broods: With one brood of three, the male alone was seen to feed two fledglings (12 and five observations) but the female helped to feed the third (two feedings by her, five by male seen) through the second day before she again began laying, after which the male alone was seen to feed that bird too (six more observations). This is an elaboration of my statement (1943:79).

With a brood of four, I saw only one feeding of each fledgling, but the male fed two of the birds and the female the other two.

Single or final broods: I had already seen the care of one second brood divided between the parents (1943:79), and Weaver (1949:112) has reported this for an unspecified brood. Two further sets of observations on single-brooded pairs are:

An already-color-banded fledgling that I caught and held for half an hour in an effort to decoy the unbanded female was attended only by the male; its most persistent calls during his absences never brought the female. Later I again briefly watched that fledgling and again the male was the parent in attendance. I saw another of the brood cared for by the unbanded female; once the male drove off a Robin that alighted near this fledgling, but it ignored the fledgling itself.

At another nest I took particular pains with this point. When two of the three young

had left the nest the male fed both; I do not know whether the female fed either. The male also helped the female feed the final nestling during at least part of its last day in the nest. This third bird vanished immediately upon leaving the nest. The parents then divided the care of the other two; I watched feedings on all of 12 days that the young remained in the territory, and saw the male feed one of them 85 times and the female feed the other 28 times. On the way to his bird with food the male once hopped close past the female's but ignored it.

Period of dependency and stay in natal territory.—One first-brood fledgling was partly independent by the age of 21 or 22 days, and two final-brood fledglings by 23 to 25 days. Three first-brood fledglings were last seen when about 22 to 24 days old, and four single- or final-brood fledglings when about 21 to 27 days old, in contrast to the 28 to 32-day ages I previously observed (1943:80–81). The two single-brood young that I watched most closely developed self-sufficiency as follows:

One first seen to peck at ground at age 17 or 18 days, definitely picking up inanimate things at 18 or 19, apparently eating at 24 or 25, last seen to be fed by parent and last seen in territory at 26 or 27 days.

Other first seen to peck at ground at age 19 or 20 days, apparently eating at 23 or 24, last seen to be fed at 24 or 25, last seen in territory at 25 or 26 days.

NUMBER OF BROODS; NESTING SUCCESS

Full-season observation of nine pairs in which one or both birds were color-banded showed two broods to be the rule. Three pairs raised two broods and two more pairs had unsuccessful second nestings. Only two pairs disappeared after successful first nestings, though two other pairs disappeared after unsuccessful ones.

Seventeen out of 26 nests (65 per cent) in which eggs were laid produced young; at least nine of the 26 (34 per cent), and possibly 11, were completely successful. Nine nests (34 per cent) were total failures. Two additional nests were deserted before being completed. Of the nine nests that were total failures, three were destroyed by storms and two by unknown predators, three were deserted—one after a Brown-headed Cowbird parasitized it, one after an egg disappeared, and one for an unknown reason—and at one the single egg failed to hatch.

Of 44 eggs laid in 15 nests, 39 hatched (89 per cent), and 35 young were raised (80 per cent of the eggs, 90 per cent of the hatch).

SONG

On the ground.— I have seen males sing on the ground eight times while foraging. One date was in April, five in May, one in June and one in July. The song has usually been intermittent but of good quality. The stage of the breeding cycle was: day after arrival, bird unmated, 1; mate building, 2; mate laying, 1; eggs hatching, 2; unknown, 2.

In flight.—Four times in June and July I have seen birds sing in flight—just one to a few phrases. One bird was pursuing or pursued by another Wood Thrush, one may have been trying to draw a fledgling Cowbird farther away from me; the other two were undisturbed, as far as I could tell.

Atypical Song.—Twice I have heard atypical song. On a May 11 one bird's phrases sounded, at a little distance, like a succession of *weet tyer's*; however, heard from very close by they had a fair vibrancy and some phrases were more typical. On a July 8 a bird had in its song some whistled, rather rapid *too-wee too-wee's*.

Another singing female?—Since I have seen one female that did much singing (Brackbill, 1948) and another that gave some single song-like notes (1943:82), it seems worth noting that in 1949 I suspected still another female of doing some singing fairly similar to that of the first bird referred to here, but only rarely instead of frequently. The days on which I heard such song were May 21, the sixth day of full-clutch incubation; May 24, the day following desertion of the storm-damaged nest, and June 5, the fourth day of full-clutch incubation at a new nest. I never succeeded in locating the bird that was giving the notes I heard; however, on May 22 I saw this female give, from the nest, two loud, raspy *tsee* notes that in quality were nearer to the suspected songs than to any other Wood Thrush utterances I have ever heard.

COWBIRD PARASITISM

Brown-headed Cowbirds parasitized three of the 37 nests, laying one egg in each, and in each case it appeared that this inhibited the laying of the Wood Thrush.

Nest 1: May 11, nest seems complete. May 12, inspections at 6:35 a.m. and 5:43 p.m. show no egg. May 13, a Cowbird egg present at 6:04 a.m., and only that marked egg present at 5:40 p.m. May 14, at 8:05 a.m. the thrush on the nest but only the Cowbird egg present; between 9:35 and 10:17 a.m. the thrush laid an egg. The thrush incubated those two marked eggs through the evening of May 17, then abandoned the nest.

Nest 2: May 16, nest with one thrush egg found; I marked the egg. May 17, second thrush egg laid and marked. May 18, Cowbird egg laid and marked; steady incubation was under way by this morning, my first opportunity to watch. No further eggs appeared. The first thrush egg hatched the night of May 28–29, the Cowbird egg on May 29, and the second thrush egg on May 30. The Cowbird disappeared when four days old; both thrushes were raised.

Nest 3: May 19, nest with one thrush egg and one Cowbird egg found. The thrush egg did not hatch. The Cowbird hatched May 28 and was raised.

The fact that no marked eggs disappeared from Nests 1 and 2 seems to show that the abnormally small thrush clutches were not the result of egg destruction by the Cowbirds.

Cowbird incubation and nestling periods.—Assuming a laying hour of about 5:00 a.m., which Hann (1941:211–212) found to be usual, the incubation period of the Cowbird egg in Nest 2 was about 11½ days, for it was

laid May 18, incubated at once, and hatched at 1:25 p.m. on May 29—that is, at that hour I found the nestling enclosed in just one half of its shell.

The nestling period of the Cowbird in Nest 3 was 12 days.

Wood Thrush feeds with female Cowbird.—The thrushes of a fourth nest did not seem to regard Cowbirds as enemies. During the building and laying periods at their nest a color-banded female Cowbird often fed in my banding trap just 20 yards southeast of their nest, and occasionally single males accompanied her and sometimes sang. The thrushes never showed concern; indeed, just two days before she laid her first egg the female thrush once fed in the trap along with the female Cowbird, while a male Cowbird stood just outside and the male thrush foraged a few yards away. Leaving the trap, these Cowbirds always flew in directions other than north; apparently the boundary of their range fell just short of including the thrushes' nest, and it was not parasitized.

SUMMARY

Wood Thrush nest sites are chosen by the female; the male can influence her choice. Building is done by the female; rarely a male may work, but except during site selection none has certainly been seen to gather material. Height, placement, size and manner of building are described; like the American Robin, this species makes regular reversals of direction when molding. Nests are essentially complete after three days' work; slight touches are commonly given on two or three more days.

Sexual flights, other possibly stimulatory acts, and an attempt at copulation are described. One egg is laid daily, beginning one to three days after essential completion of the nest. Observed clutch size was 1 to 5, with 3 and 4 most common; clutches smaller than 3 all followed some disturbance of the breeding cycle. Laying is usually done between 9:00 a.m. and noon, but sometimes not until early afternoon; it is done earlier on cool than on warm days. Two broods are usual; second clutches were begun 9 to 12 days after first broods left the nest, but sooner when first nests were destroyed during incubation. Cowbird parasitism apparently inhibited Wood Thrush laying at all of three nests.

The brood patch develops within the week before laying starts. Incubation is by the female alone, beginning usually on the second laying day, and always before completion of the clutch; its gradual increase is described. Roosting on the nest begins with either the first or second egg. Some figures on amount and rhythm of incubation are given. Hatching most often occurs during daylight, and is spread over as much as 39 hours. The incubation period is about $12\frac{3}{4}$ days; an infertile egg was incubated 25 days; the female's incubating behavior is described. The incubation period of a Cowbird egg hatched by Wood Thrushes was about $11\frac{1}{2}$ days.

One male learned of hatching by seeing the nestling and seeing his mate feed it, when it may have been but 17 minutes old; the male first fed it 17 minutes after that; it was fed three, probably five, times in its first hour. Feces are usually eaten, occasionally carried away. Brooding is by the female alone, throughout the nestling period of 12 to 14 days. The nestling period of a Cowbird raised by thrushes was 12 days. The thrushes do not seem to recognize the Cowbird as an enemy.

Both parents feed the fledglings, but not indiscriminately: the broods are divided between them, except that just before females resume laying they apparently stop feeding first broods. Several fledglings became partly independent at age 21 to 25 days, were last seen to be fed at 24 to 27, and were last seen at 21 to 27. Figures on nesting success are given. The male's activities during each phase of the breeding cycle are described. Song on the ground and in flight, and possible song by a female, are recorded.

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