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NESTING BEHAVIOR OF WOOD WARBLERS

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THE following paper is based on a study of the nesting behavior of warblers made during the summers of 1942 to 1944 inclusive on the Edmund Niles Huyck Preserve, Rensselaerville, New York. This 500-acre preserve is about 30 miles southwest of Albany, on the Helderberg Plateau on the north side of the Catskill Mountains. The observations extended each year from the first week of June until the last week of July. Seventeen species of warblers were recorded during the three summers, probably all of them breeding, but worthwhile notes were obtained on only the 12, more common, species treated in this paper. The study of several species proved difficult because the movements of the birds in the dense foliage could often be followed only by sound, and the finding of their nests was usually accidental. No attempt at monographic treatment is made here, but the fragments of life history on the various species have been brought together at the end of the paper into a composite pattern of nesting behavior.

This area is in the ecotone or transition between the deciduous forest biome and the coniferous evergreen forest biome. Hemlock, beech, sugar maple, and yellow and white birches are the dominant species. White pine is present but of minor importance. Breeding-bird censuses were taken each year in shrubby fields, in a hemlock-beech forest, and in a forest composed chiefly of deciduous trees. The most time was spent with the birds in a 21-acre hemlock-beech community. This predominantly evergreen forest is not virgin, but some of the large hemlocks are 200 years old and 75 feet in height. The forest floor is covered with a mat of dry brown hemlock needles overlaid in most places with leaves of beech and yellow birch. There is not a great amount of undergrowth nor many herbs, but here and there the young second growth forms a dense stand. Figure 1 shows the degree of mixture of hemlock and beech, as well as the relative size of the trees.

On each survey of this community, the location of every bird observed was marked on a map of the area. After a few such surveys the approximation of marks permitted drawing of territorial boundaries as shown in Figures 1 and 2. This, together with peculiarities of song,



PRAIRIE WARBLER
(*Dendroica discolor*)

**Adult, at nest with young. Lovells, Michigan, June 19, 1944.
Photographed by Bernard Baker.**

made it possible to recognize individuals, although with less certainty than if the birds could have been color-banded. The boundaries of the territories as drawn and the measurements given for them are only approximate, and they may generally be too small. They were most accurately determined in 1942, when the greatest amount of time was spent in this area. It is entirely possible that more time spent in observing the birds in 1943 and 1944 would have shown that some of the territories were larger than they appear on the map. These territories were simultaneously occupied, although not continuously so, during the breeding season. For the Oven-bird and Magnolia Warbler, which have two breeding periods, the territories as mapped include the total area occupied for both broods, since there seemed to be very little change in the boundaries. A very few males, chiefly Oven-birds, were present only during the latter part of the season. Birds whose territorial boundaries were not determined are indicated on the maps by numbers in parentheses placed at the approximate center of the area of their activities.

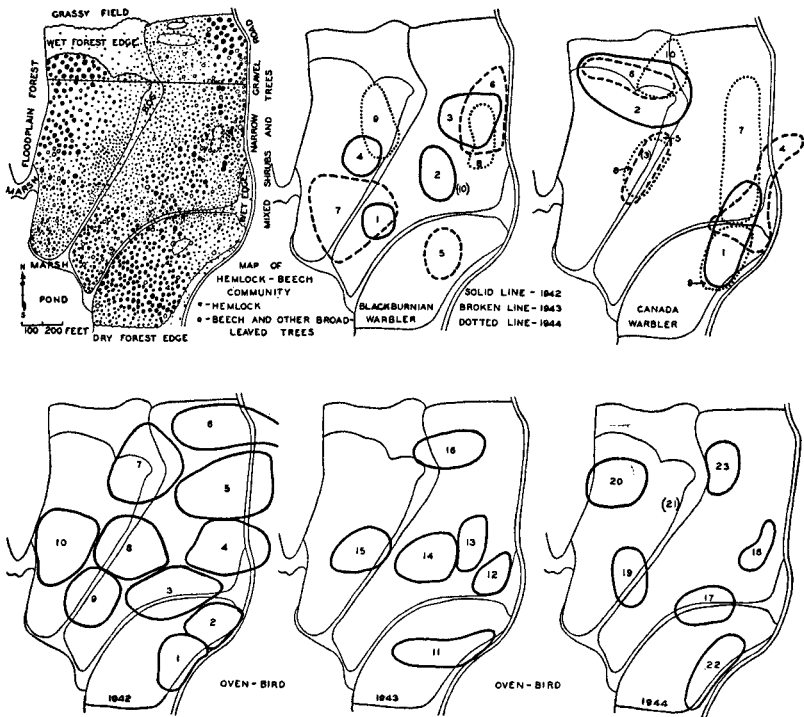


Figure 1. Map of hemlock-beech community and territories of warblers studied. Numbers in parentheses represent territories the exact boundaries of which were not determined.



Figure 2. Territories of warblers in a hemlock-beech community.

BLACK AND WHITE WARBLER

Male Black and White Warblers (*Mniotilta varia*) sing incessantly until mated. They seek exposed singing posts at or near the tops of isolated trees in shrubby fields, and perch crosswise on a branch. One song was syllabized *zii zii zii ziii-eee ziii-eee ziii-eee*, the first three notes being single, the last three double. A variation was a series of about eight short *zii* notes followed by a trill. About the middle of June, when nesting is well along, these warblers become almost entirely quiet and are easily overlooked. At a nest with 5 young about 4 days old, the young were fed twice by the male, 3 times by the female during 2 hours afternoon observation. This seems a very slow rate of feeding, yet the young successfully left the nest on June 29, when 8 or 9 days old.

On June 15, a pair of Black and White Warblers were much concerned over a young Oven-bird not long out of the nest and apparently separated from its parents. The young bird was calling loudly for food. The Black and White Warblers were apparently caring for it, although they were not actually observed to feed it until 3 days later.

NASHVILLE WARBLER

Male Nashville Warblers (*Vermivora ruficapilla*) sang from posts on the forest-edge at heights from 15 to 30 feet. The song consisted of a series of notes of the same pitch followed by a descending trill, probably a variation of the second song described by Saunders (1935: 182). The singing posts are often inconspicuous and the birds difficult to find. Males were observed on two occasions silently chasing other birds for some little distance in what appeared to be territorial competition. When excited, the females flutter their wings. Although adults were seen with food for the young in their bills, no nest was found. Fledglings were observed by the third week in June.

MAGNOLIA WARBLER

Figure 2 shows the territories of 20 male Magnolia Warblers (*Dendroica magnolia*) during the first breeding period. Fifteen of these average 1.8 acres in size. Territory 20, which was in a dense shrubby area and measured only about 0.6 acre, was the smallest. Territory 4 was quite large, probably 3 to 4 acres if one includes the area in the pine-spruce planting across the road where the nest was later built.

Territory is established and defended by song, plumage display, and chasing. Singing posts are most frequently on the outer edge of a hemlock and from 10 to 45 feet above the ground. When vigorous, the song may be repeated 10 times a minute. The song commonly given for territory and mate has been frequently described by others, e.g. *wee-o, wee-o, wee-chy* (Stanwood, 1910:384); there are, however, many variations. Another song for the same purpose, *ta hé ta héch a*, may be the same as the second common song described by Brewster (Griscom, 1938:575). A song given during the progress of nesting or when the bird is patrolling a well-established territory consists of a series of notes (usually four), all of the same pitch: *mae mae mae mae*, or *cheel cheel cheel cheel*. The male Magnolia sings persistently day after day but often in a desultory manner. However, when a new male comes in to establish a territory or a male attempts to expand his territory, singing may be very vigorous and stimulate the males of this species over the entire woods to join in and assert their claims. Such responses show how closely knit and balanced a society these birds form when there are several territories in a comparatively small area.

When another bird of the same species intrudes in spite of the warning song, the male in possession of the territory flits nervously but silently around from branch to branch with tail spread, showing its white markings. Occasionally the resident male will fly out at the other male with tail and wings spread in display and then circle back without giving real chase. On several occasions when more vigorous resistance was required, the male suddenly stopped singing (sometimes uttering a

few chirps) and gave full chase to the intruder without any attempt at plumage display. Once a male chased two male Black-throated Green Warblers that were squabbling near-by.

During the mating period, when a female enters the territory, the male stops singing and begins a display which is more complete than that used in territorial defense. With spread tail and wings the male follows the female through the trees from branch to branch, or sometimes flies directly at her. Nice (1926:193) has described a *kree-ee kree-ee* note given by the male when "courting" his mate late in the nesting period.

When nervously excited, the female also displays, at least to the extent of flitting her tail and exposing its markings. There was no evidence that the female recognized the limits of the territory that the male established. When leaving the nest during the incubation period she sometimes went well outside the male's domain. But she did resent intrusion in the immediate vicinity of her nest. Twice during the incubation period a female drove off male Magnolia Warblers that had been attracted by her scolding of me.

The behavior of the adults was watched at only one nest, and this for only 2.5 hours two days before, and for 2 hours shortly after, the eggs hatched (both times in mid-morning). During the first observation, the female incubated steadily for 2 hours with hardly a restless movement, left for 20 minutes and then returned for another attentive period. The male did not come near. During the second observation, the female brooded the newly hatched young for 20 minutes after being away 13 minutes, left for 4 minutes, brooded again for 24 minutes, was gone for 5 minutes, then back to brood for 12 minutes, when her stay was interrupted by the male's appearance. During the next half-hour the young were fed twice by the male, 3 times by the female, and the female brooded for 2 periods of respectively 13 and 10 minutes. Observations of Stanwood (1910:386), Mousley (1924:280), and Nice (1926:196) indicate that the incubation period lasts about 12 days and that the young leave the nest 8 or 9 days after hatching.

The Magnolia Warbler begins nesting rather early, and fledglings were found in 1942 on June 15; in 1943, on June 24. Second broods are regularly attempted, and the males sing energetically during the latter part of June while re-establishing their territories and acquiring mates. Singing continues until the end of July.

BLACK-THROATED BLUE WARBLER

One male Black-throated Blue Warbler (*Dendroica caerulescens*) was in the northeastern corner of the hemlock-beech study-area at the beginning of June, 1942; on June 18 a second male intruded on the area of the first male without being molested but later became estab-

lished with a female just to the south. In this species the males seem more tolerant of each other than in most species of warblers. Once, for example, a male was observed singing and feeding 15 to 20 feet up in a beech when another male, likewise singing, was 30 feet up in the same or in an adjacent tree; the two birds appeared to pay no attention to each other. It was common to find two males thus singing near each other, and birds often shifted around in an apparently aimless manner. Males were frequently observed far from their usual posts (often as much as 500 or 600 feet); they sang as they gradually worked their way back. Probably with this species, as with some other warblers, the concept of "home range" should be retained, since it is doubtful whether the entire area, often several acres, over which the birds wandered was regularly used and defended. Some competitive singing between males and chasing of one male by another was observed, but the actual portion of the home range that was defended as territory was not satisfactorily measured.

There are two common and easily recognized songs in this species, and each song has variations. Both songs may occasionally be given by the same bird, but usually one or the other song predominates with any one male. One song is given slowly and has a harsh quality; *wheer wheer wheeee* (Chapman, 1907:137). Usually there are three *wheer's*, but one male gave only one. The other song is faster, and the notes are sharper: *zee zee zee zee zeeeee*. Both songs end with an upward slur that involves all of the last note and sometimes with the second song includes several of the preliminary *zee* notes.

On June 10, 1943, a male and female were observed feeding together, the female energetically, the male half-heartedly. The male appeared excited but sang little. Once he flew to the limb beside the female, partially spread his wings in display, then left. Very soon he sang softly once, then flew to the female, uttered several chattering notes, displayed his wings, chased her two or three feet into denser foliage, and apparently copulated with her. He continued his display, without singing, and finally chased the female some distance away. Four days later, another male, considerably outside his usual area, was observed chasing a female. He was very excited; he did not sing but uttered the same peculiar chattering notes. Again copulation apparently followed. These chattering notes are the same as the alarm notes described by Harding (1931:517) as a series of *thck's*. On July 10, a pair was observed feeding young near this location.

In 1943, the behavior of birds at a nest was watched from the time the nest was begun, on June 29, until the young left on July 25. The nest was in an upright fork of a purple-flowered raspberry in a deciduous forest and was only one foot above the ground. During 36 minutes of observation on the first day, the female did all the nest-building, making 21 visits; the male did not appear. The female once chased away a male Chestnut-sided Warbler that came too near the nest. Because of

the lateness in the season this may have been a second attempt at nesting. Elsewhere in the woods on this same morning, another pair of adults was observed carrying food.

On July 1, the nest was fully built but empty. During 71 minutes of observation, the female came once and sat in the nest for 7 minutes, squirming and kicking around part of the time. The male came twice when the female was absent and sang near-by, but did not approach the nest itself. Presumably the first egg was laid the next day since there were two in the nest at 8:16 A.M., (E.S.T.), July 3. During 94 minutes observation on that day, the male was absent, and the female came to the nest once, sitting quietly on the eggs for 20 minutes.

On July 5, there were 4 eggs in the nest, and incubation was well under way. During 5.3 hours of observations made at various times of day, and spaced at 3- and 4-day intervals throughout the incubation period, the attentive periods averaged 28 minutes in duration, varying between 22 and 40+ minutes, and the inattentive periods averaged 9 minutes, varying between 5 and 15 minutes. The male was not recorded a single time during this period either around the nest or singing near-by. This does not agree with observations by Harding (1931:513, 516), who observed the male taking part in nest-building and feeding the female while she incubated.

Two young had hatched by 12:50 P.M. on July 16; at 8:00 A.M. the next morning the third young had appeared, and at 4:45 P.M. the fourth was out of the shell (an incubation period of 12 days). One young had disappeared by July 23, but the other three had matured sufficiently to leave the nest early in the morning on July 26. Thus their nestling life was 9 and 10 days long.

During the period of hatching on July 16 when there were 2 young and 2 eggs in the nest, the attentive periods of the female were 11, 25, and 10.5 minutes in length and the inattentive periods, 3, 8, 2.5, and 6 minutes, indicating a shortening and a greater irregularity of both periods compared with attentive and inattentive periods during incubation. During 68 minutes, the female fed the 2 young 5 times. The male was not present.

Approximately 1.7 hours were spent in observation at the nest, beginning at 9:10 A.M. on July 20, when the young were 3 and 4 days old. The female was at the nest for periods of 19, 11, and 37 minutes, although much of this time she stood on the rim and worked with her bill inside the nest. The irregularity in the length of her attentive periods was due in large part to the male's coming to the nest with food and interrupting her stay. The male fed the young 6 times, and the female fed them 3 times. The male invariably sang as he approached the nest, and this appeared to be a notice for the female to prepare to leave. The song was given softly and was often incomplete.

On July 23, when the young were 6 and 7 days old, the female brooded 13+ and 10 minutes during the 105 minutes of observation

beginning at 8:33 A.M. She fed the young 4 times and the male fed them 3 times. The male's behavior when approaching the nest alone was the same as before; twice the male and female came to the nest together. The young now had their eyes open, and the tips of their pin feathers were beginning to break open. They left the nest 3 days later. During the 3.4 hours observation on July 20 and 23, the young were fed on the average once every 13 minutes. This is in marked contrast to the average interval of 2.4 minutes recorded by Mousley (1924:274).

BLACK-THROATED GREEN WARBLER

Twenty-one territories of the Black-throated Green Warbler (*Dendroica virens*) averaged 1.6 acres in extent and varied from 0.6 to 2.5 acres in size (Figure 2). Territory 1 represents an unusual case since the territory was occupied consistently only until June 10. After that it appeared that the male had a mate with a nest across the road in a dense pine-spruce planting. On July 3 a male with the same type of song and accompanied by young out of the nest was in the original territory. Territory 15, a very small one, was also only temporarily occupied.

Territories are especially important with this species, and intrusions by other males are met with vigor. The male immediately gives chase and drives the other bird to the boundaries of his area. If the intruder remains in the vicinity, intermittent chasing may continue for several hours. There may be chipping notes given, but there is no singing nor usually any special plumage display. Once a male was observed to dart after another male and then to hover for an instant. Competitive singing sometimes occurs between males on adjacent territories when no trespass is involved. On June 28, 1943, two, or possibly three male birds were in a part of the hemlock-beech forest three or four hundred feet away from the nearest active territories. There was some chipping but no singing, although the birds seemed aware of each other's presence. This is apparently an instance of wandering by males outside of established territories, which is common in warblers although this wandering tendency is less marked in this than in some other species.

There are two main variations in the song melody of the Black-throated Green Warbler, as has been frequently noted by others. This fact, together with secondary variations in the song and the male's persistence within mapped territories, permitted recognition of pairs throughout most of the season or until they began to wander with their young. Sixteen of 27 males sang a song described by Pitelka (1940:14) as: *zrrr-zrrr-zu-zu-zwee*. Some males uttered this intermittently amidst a constant stream of low chips. The first, second, and last note are rasping in character. The second note, as given in this region, is higher than the first in pitch, not lower as Pitelka diagrammed it for birds in Michigan. This rendition is somewhat similar to the third

example of the second type of song described by Saunders (1935:191). As one moves away from a male the last note is lost to audibility first, then the first and second notes, while at a still greater distance the more metallic third and fourth notes alone can be heard. There is less variation in this song than in a second song. Eleven males had a song described *zee zee zee zee zu zwee* by Pitelka. In this song the fifth note (*zu*) was on a lower pitch than the others and was occasionally doubled; some males uttered three or five instead of four preliminary notes. In both the *zrrr* and the *zee* types of song the last note is slurred upward. The song of any one individual was almost exclusively one or the other type (or a variation of one type). In 1942, there were only one or two doubtful instances of a male uttering both types of song; in 1943, at least 3 males sang both types of song rather frequently. Singing persisted even after the young left the nest or until mid-July.

Two pairs in 1942 had young out of the nest on June 23, another pair on July 3, and others soon after. In 1943, such families were not seen in the hemlock-beech forest. Perhaps they were there, though not seen by the observer, but since red squirrels were unusually abundant that year, and the population of Black-throated Green Warblers was considerably reduced in 1944, there is reason to think that much of the nesting was unsuccessful. This species apparently raised only one brood in a season.

During 2.5 hours of nest observation divided between 2 afternoons the young were fed 6 times by the male and 7 times by the female with the sex doing one feeding undetermined. This was at the rate of once every 11 minutes. Part of the female's time, however, was occupied with brooding.

BLACKBURNIAN WARBLER

Since the Blackburnian Warbler (*Dendroica fusca*) frequents the highest stratum of the tree tops, observations of this species were particularly difficult. Nine territories were marked out, mostly from the location of songs heard, and their average size was relatively small, 1.3 acres (Figure 1).

Saunders (1942:253) describes the song of these birds in southwestern New York as a series of two-note phrases followed by a trill which is commonly lower in pitch than the rest of the song: *tsita-tsita-tsita-tsita zzzzzzzzz*. At Rensselaerville the trill is more commonly a slur rising in pitch, although one unmated male, perched on a projecting dead limb high above the forest canopy, sang an elaborate song with a trill descending in pitch and ending with a final *tsee*. After a male acquires a mate and settles down, the song often consists of the initial series of double notes only. By the end of June or the first week of July, singing ceases except for occasional notes.

A nest was found on June 18, 35 feet up in a hemlock in an inaccessible location 6 feet out on a horizontal limb. Its construction was nearing completion with the lining being inserted. In 82 minutes of observation the female visited the nest 7 times. The male occasionally sang near-by and once alighted near the nest, but the female spread her wings and chased him away as if she would not tolerate his presence in the immediate vicinity. On June 21, during 15 minutes of observation, neither adult visited the nest, but a non-singing bird, possibly the female, was seen to chase a male Black-throated Green Warbler out of the territory. On June 24, incubation apparently was under way. During 53 minutes of watching in mid-afternoon, the female incubated twice (for 10 and 18 minutes), and was inattentive for 15 and 10 minutes. The male sang periodically nearby. The next morning the female, while under observation, incubated for one period of 30 minutes and was inattentive for periods of 9 and 10 minutes. The male was not seen.

CHESTNUT-SIDED WARBLER

In 1940, Eugene P. Odum, then resident naturalist on the Preserve, noted the arrival of the first males of the Chestnut-sided Warbler (*Dendroica pensylvanica*) on May 14 and the first females on May 22. In 1942, the first females must have arrived about the same date since the first young being cared for out of the nest were observed on June 22. However, many females were delayed in starting to nest; in six instances signs of first mating behavior with arrival of females in the males' territories were observed, on June 5, 8, 10, 12, 12, 12. The sexes are not always easy to distinguish in the field, although the male has a darker back and a brighter crown. Only the male sings, as is true also with the other wood warblers, and the female is usually shy and retiring, keeping well down in the low bushes and briers.

The unmated male on his territory, which is typically an open shrubby field containing patches of briers, bushes, and scattered trees, spends much of his time singing from tops of bushes or from the lower branches of trees. During the early season the song may be given 5 or 6 times a minute and may be heard at any time of day. The song is of two types. In the establishment of territories and advertising for mates it is characteristically clear and loud and may be heard at some distance. Jones (1900:35) has given the best rendition of it, *te te te te wee chu*, with the fifth note accented and of higher pitch. Developing gradually from this song as the season progresses is one of a different character that Saunders (1942:254) renders, *wayo wayo wayo wayo weeo weeo wayo wayo*. Commonly the last two notes are not given, and *weeo* is more nearly *whaea*. This second song is more common after incubation is well established, is not given so vigorously or sharply, and seems to indicate a lower emotional level. It serves as a signal of territorial possession rather than of competition, although two males on adjacent

territories were once observed giving this song alternately when only 30 feet apart.

Ordinarily there are several song posts habitually used by the male on his territory, and he sings successively from one, then another, until he completes the round of his possessions. Where the territories of two males lie close together, the males occasionally compete in song. On several occasions one male was seen to chase another out of his territory, once fully 200 feet. In this singing, chasing, and competition between males there is no special plumage display aside from that which occurs with the normal movements of parts of the body.

The female enters the territory quietly and inconspicuously by short flights from branch to branch through the bushes and trees. When the male sees her, he becomes silent and may dive at her or chase her from limb to limb. As his excitement grows, he makes a plumage display. This may occur as he alights near the female at the end of a dive from a high perch; it lasts only a few seconds. The tail feathers are spread, the wings extended, and crown feathers erected. The wings and tail quiver up and down. The female may display in return, though less vigorously. Doubtlessly this plumage display is mutually stimulating and leads to the emotional pitch necessary for coition. After one such dive by a male a series of chattering notes was heard, but copulation, if it occurred, could not be seen in the dense foliage. There is no singing during the display, although subsequently the male may fly excitedly around, give his first song described above, and chase other birds that normally he would not notice.

The male accompanies the female in the search for a nest-site, following her closely from tree to tree or bush to bush. There may be occasional singing, but they are mostly quiet, and they carry on some feeding. The male may slightly spread and droop his wings and partly raise his tail in a manner typical of pre-copulation behavior in other species. The female appears more intent than the male in the search for a nest-site. One nest was later found in a brier patch about 50 feet away from where a vigorous dive and plumage display by a male had been seen. However, the female looks for, and often establishes, nest-sites outside of the male's original territory. The male is somewhat attentive to the female during nest-building and egg-laying, but his enthusiasm is less sustained. He continues to sing during the incubation period, although he is quiet for long stretches of time. These quiet periods become more frequent as incubation continues.

Previous to the mating period, the male's territory, in three instances that were measured with some accuracy, covered 1.2, 1.3, 1.3 acres respectively, and two other known territories were about the same size. Another territory was estimated at 2.5 acres. During the incubation period, or during protracted pre-mating periods, the male greatly extends the area over which he roams, going well outside his previous

territorial boundaries. This was observed repeatedly and regularly with several males. They wandered from 200 to 700 feet, and covered from 2 to 12 acres, or even more. On these long excursions the male sings his *wayo wayo* song more frequently than the *te te* song, although they may both be given. This singing, however, is much less vigorous and less frequent than on the territory itself; there may be long periods of silence; or the male may not sing at all. There is no evidence that these larger areas are defended, although the desultory singing may serve to ward off intruders. It is best at present to designate this area simply as the bird's "home range" and to limit the term "territory" to that portion of the home range where singing is vigorous and regular or where there is chasing or other types of defense. The home ranges always extended into free and unoccupied areas. In no case did the home ranges of two males overlap, although this may have been because the birds were few and fairly scattered.

On June 22, 1943, a nest was found just being built at the edge of a shrubby field, in the triangular fork of a bracken fern only 2.5 feet from the ground. The female was working on the nest foundation at the time, coming to the nest with materials at about one-minute intervals. The next afternoon the nest was well formed, and the female was busy finishing the interior. She made 9 trips in the first 52 minutes of observation but was then absent for the next 38 minutes. The male sang unexcitedly and made some attempt to follow the female. Once he looked into the nest when the female was away. Another time he followed the female to the nest and displayed to her on its rim, uttering a *tsiip*. Early on June 25, the nest was practically complete, and the female apparently brought no new material, although she would sit in the nest and work at the lining. She made six visits in an hour. One visit was interrupted when she gave chase to a male Golden-winged Warbler (*Vermivora chrysoptera*) that came within a foot of the nest and again a minute later when it came within 15 feet. The male could be heard singing his *wayo wayo* song in the distance but was not seen near the nest.

The first egg was found in the nest early the next morning. During an hour's observation a male sang in the distance. The female came to the vicinity of the nest 6 times but only once went to the nest itself; then she sat on the egg for 2 minutes. Once she chased away a yearling male Redstart that came within 20 feet of the nest. The third, and last, egg was in the nest on June 28, and incubation had begun. All eggs were hatched by July 9 (an incubation period of 11 days); two of the young were so much larger than the third that they had probably hatched the day before.

Four and a half hours of observation, divided fairly evenly on the afternoons of June 28, 29, July 1, and 7, gave an average of 13 minutes for 11 attentive periods, and 8 minutes for 10 inattentive periods (ex-

cluding one long inattentive period of 23 minutes on the first day of incubation). A male could frequently be heard singing in the distance but was not observed near the nest. It appeared that the male's territory was chiefly to the north, and this nest-site was on the very edge of it or may even have been outside of it as originally established. The female almost invariably went north (in the direction of the territory) when she left the nest.

At another nest, under observation in 1942 for 8.7 hours scattered in morning and afternoon throughout the incubation period, the attentive periods averaged 21 minutes in length and the inattentive periods a little over 6 minutes. The female during incubation at this nest seemed quite independent of the male. Although the male occasionally sang near the nest, only twice in 21 times that she was observed to leave the nest did she appear to do so because stimulated by the male's presence. These departures ended attentive periods of only 11 and 16 minutes. The longest period observed was 27 minutes. The inattentive periods varied between 4 and 9 minutes.

The eggs in the 1942 nest, perhaps because of accidental jarring by the observer, did not hatch. On the day the young were found hatched in the 1943 nest, the male was back helping to feed them. In 1.4 hours of watching during the afternoon he brought food for the young 3 times and the female brought food twice. The female brooded 2 times (26 and 34 minutes) with inattentive periods of 11 and 13 minutes. On the morning of July 12 when the young were between 3 and 4 days old, the female during an hour and 26 minutes of observation brooded for one long period of 35 minutes after the preceding brooding period had been cut short at 4 minutes by the arrival of the male. It is of interest that this female's attentive periods while brooding the young were considerably longer than while incubating the eggs. On this same date the female fed the young 4 times and the male fed them 7 times, once interrupting his feeding to drive off a yearling male Redstart. The young were gone on July 16, only 7 and 8 days after hatching, and it is uncertain whether they left naturally or were taken by a predator.

Another nest was found on June 17 with young one or two days old. When first discovered, the female flushed from the nest, fluttered along the ground as if wounded, uttered scolding notes, and the male approached within a couple of feet. During an hour's observation in the afternoon, the female came to the nest 6 times (not certainly with food each time) and brooded twice for periods of 12.5 and 21 minutes, the brooding periods being interrupted or terminated when the male arrived with food. The male sang frequently and fed the young 5 or 6 times. On my return to the nest on June 24, 7 days later, the young were gone. On two or three occasions the male has been seen caring for the young out of the nest, and it is likely this duty continues to be shared by both sexes until the young become independent.

OVEN-BIRD

Although territories for the Oven-bird (*Seiurus aurocapillus*) in the hemlock-beech study area were mapped (Figure 1) and several nests were located, little attention was paid to its behavior. Chasing, however, was frequently observed, and the "flight song" was heard several times. One performance was especially spectacular. There was a swift musical jumble of notes, apparently given at the beginning of the flight, for immediately afterwards the bird came into view, doing a loop that extended from the level of the tree tops (30 feet high) down to the ground. The bird seemed to have its wings folded close to its body and to be making a swift dive.

Apparently two broods are raised. The size of 21 territories varied from 0.25 to nearly 3 acres and averaged 1.6 acres. Song was greatly reduced after mid-July.

LOUISIANA WATER-THRUSH

A single nest of the Louisiana Water-thrush (*Seiurus motacilla*) was found on June 10, but unfortunately not until the four young were 5 or 6 days old. Three days later, the young were fed 7 times in 53 minutes of observation. Apparently most of the feeding was done by the female; a male was singing in the distance a large part of the time. The young were still in the nest on June 15 when they were at least 10 days old. The exact time of their leaving was not determined.

YELLOW-THROAT

The Yellow-throat (*Geothlypis trichas*) begins nesting early, for the first young were out of the nest by June 15 in 1942. On June 19, there was considerable commotion among the Yellow-throats inhabiting the shrubby-field study-area. There seemed to be an influx of new males, and adults with their young were roaming around on each other's territories and upsetting the normal equilibrium. It was also obvious that the males were making an effort to reestablish territories and secure mates for a second brood. There was chasing of one bird by another in wide circles and considerable singing both of the normal song and of the flight song. The excitement continued at a slightly lower level during the rest of the month and into early July when the second nestings were under way. In 1943 and 1944, this period of excitement and readjustment for second broods was again evident during the third week of June.

Although male Yellow-throats commonly sing from close to the ground or from low bushes, they mount higher under the influence of competition, even to 40 feet or more. As if this were not sufficient, they also have a song given during either a vertical flight or a horizontal one that begins with their usual song and ends with an outburst of ecstasy after which the bird flutters down to the ground or to an exposed perch. One horizontal flight song at a height of fully 100 feet was observed at

7:00 P.M. These flight songs may be heard well past the middle of July.

Territories were not mapped for this species, but in 1942, 7 pairs were fairly uniformly spaced over an area of 5 or 6 acres, which would make their territories less than an acre in size. The incubation period at one nest was 12 days long.

CANADA WARBLER

Male Canada Warblers (*Wilsonia canadensis*) have a clear, abruptly tumbling song (Saunders, 1935:217) that they commonly utter at a rate of 6 times per minute when advertising for a mate. Soon after a mate is secured they usually become very quiet. Since the young of one nest left on June 19, and at another nest they were nearly ready to leave on June 23, nesting must begin soon after the middle of May.

In spite of persistent singing, one male in 1942 was unable to secure a mate until the third week in June. The size of his singing area was only about 0.6 acre, but after nesting began he wandered over 2 acres, although then he was usually quiet. Another male, with a nest, roamed over 3 acres or more, an expansion of an earlier singing area. This again appears to be an example of a larger area being used after nesting has begun. With this species, however, there is some evidence that the entire larger area is vigorously defended against intruding males by scolding notes and by silent chasing. In Figure 1, the entire larger areas are mapped.

REDSTART

Two male Redstarts (*Setophaga ruticilla*) in yearling plumage were regularly observed in the same thicket or patch of trees and evidently had established territories and nests. Other singing males in yearling plumage appeared to move around considerably and were apparently without mates. The majority of the males were in full adult plumage, however, and showed no wandering tendencies. In 1944, none of the estimated 10 males on the Preserve was in yearling plumage.

Adult males in this species are strongly territorial in behavior, defending their possessions by song, color displays, and chase. There is a variety of songs, a common one being: *zwee zwee zwee ze ze zump* with the fourth and fifth (*ze*) notes at higher pitch than the first three, and the last note at a lower one. Another series of notes at the same pitch resembles a song of the Black and White Warbler. Redstarts sing from perches up to 40 feet from the ground.

Chasing occurs on slight provocation and is not accompanied by singing though it may be preceded by sharp scolding notes or by a period of competitive singing. One male was seen to chase another for fully 200 feet. Redstarts were also observed to fly after Oven-birds and juvenile Hairy Woodpeckers. These chases are straight and rapid, and there is no plumage display except that which is incidental to movements of wings and tail.

A special flight maneuver has been described by Hickey (1940:255) that serves primarily as a threatening plumage display. These darting flights were observed in the present study only once or twice and only between males. In Hickey's words they consist of "short, horizontal, semi-circular flights made with stiffened wings and out-spread tails. These performances were frequently observed between males, less commonly between females and never between a male and a female where a question solely of territory was involved. . . . Low, repeated *quit quit* notes could be heard when the displays were concluded and the birds returned to their perches. As far as could be observed, these same performances seemed to serve as some part of the male's courtship of females. . . . The size of territories was usually about one acre or less. . . . Their boundaries were observed in two cases to break down on June 17, when young were being fed in the nest."

In courtship activities, a male in full adult breeding plumage may fly after a female, alight beside her, and spread his tail, showing its brilliant coloration. His wings may not always be extended, and he does not sing. He may retain the pose for several seconds before they both fly away.

Two nests were found in 1943 and one in 1944. On the mornings of June 12 and 17, 1943, during 119 minutes of observation at a nest containing eggs, the female's 10 attentive periods averaged only 9 minutes in length; 11 inattentive periods averaged only 2 minutes. The male sang nearby, and on the latter date came to the nest and flitted around it.

At the 1944 nest, 153 minutes of observation in both morning and afternoon on the second, third, seventh, and eleventh days of the incubation period covered 5 attentive periods that averaged 18 minutes and 6 inattentive periods that averaged 7.5 minutes. There was one exceptionally long inattentive period of 19 minutes. In this nest the fourth egg was laid on June 6. Since 3 of the young hatched on June 17 and the last not until June 18, it is probable that rather steady incubation began with the third egg and that the incubation period is 12 days long. The young left on June 27, which gave them only 10 days for development in the nest. In 53 minutes of observation in late morning when the young were 3 and 4 days old the female brooded 3 times for periods averaging 15 minutes, with inattentive periods averaging 4 minutes. The female's brooding was interrupted by the male bringing food. This he passed to the female who then fed the young. When the female was absent, the male fed the young directly. The male brought food 12 times, the female only once; this gives an average of once every 4 minutes for feeding the young.

There were half-grown birds in the third nest when it was found. On June 22 and 26, 94 minutes were spent watching the nest, beginning about 9:30 A.M. each day. On the first date the female brooded 3 times

for 5, 6.5, and 2 minutes, with the male coming to interrupt her each time as he brought food for the young. Her inattentive periods were 2, 1.5, and 15 minutes long. On the first day the male fed the young 5 times, the female fed them 4 times; on the second date, the male fed 6 times and chased away a female Yellow-throat and an unidentified bird; the female fed the young 4 times. When a disturbance was made near the nest, both adults came scolding and flashed their tail markings as they flitted through the branches.

DISCUSSION AND SUMMARY

Although there is variation in details from species to species, nevertheless there is sufficient agreement to permit description of a general pattern of nesting behavior for wood warblers. The following remarks are based primarily on the original observations reported here.

Song is used for marking out and advertising a defended territory. When song is not sufficient to keep an intruder away, chasing results. There is no evidence that fighting or physical combat between males takes place, except possibly in the Oven-bird (Hann, 1937:151). Song is distinctive for each species, and variations in the song are often characteristic of different individuals. Geographic variations in song also occur, since descriptions given by different authors vary in important details. In addition to proclaiming territory, song is used to attract the female but not as a primary stimulus leading to coition. After mating is completed, singing is less enthusiastic and less frequent and there are sometimes modifications in the character of the song. During the incubation period, the singing of the male helps to maintain the territory and in some species or in some pairs has an influence in modifying the female's attentive behavior. Singing greatly decreases at the time the eggs hatch but may be renewed with vigor between a first and second brood.

Nearly all wood warblers are strikingly marked and often brightly colored, especially in the male. Nichols (1913) lists three principal functions for warbler coloration: concealment, recognition, and advertisement and display of the male. The coloration is displayed to advantage by spreading the tail, extending the wing, and erecting feathers on the crown or elsewhere on the body. A partial display may be given when the male is excited by an intruding bird, but it reaches a climax when the male is exciting a female toward coition. This display takes the place of a mating song, although notes of excitement may be uttered preceding coition. In the Redstart, and to a lesser extent in Magnolia and Black-throated Green Warblers, a darting semi-circular flight with full display of color has developed for intimidation of intruders in territorial defense. Coloration doubtlessly also serves for recognition of species and sex by the birds themselves.

In addition to the defended territory, some warblers (Chestnut-sided, Black-throated Blue, Black-throated Green, and yearling Red-

TABLE 1
ATTENTIVE BEHAVIOR IN EIGHT SPECIES OF WOOD WARBLERS

	Incubation				Brooding				Feeding young					
	Total obser- vation	Average periods			Total obser- vation	Average periods*			Total obser- vation	No. of young	Age of young days	Times fed		Rate per hour
		Atten- tive	Inatten- tive			On nest	Off nest					♂	♀	
			min.	min.			min.	min.						
Black and White Warbler	—	—	—	—	—	—	—	120	5	4	2	3	2.5	
Magnolia Warbler	144	120 ^a	20 ^a	114	16	6	—	114	?	0-1	2	3	2.6	
Black-throated Blue Warbler	323	28	9	168	19	7	—	100	4	3-4	6	3	5.4	
Black-throated Green Warbler	—	—	—	—	—	—	—	105	3	6-7	3	4	4.0	
Blackburnian Warbler	110	19	11	—	—	—	—	153	?	?	6	7	5.5 ^b	
Chestnut-sided Warbler	266	13	8	170	25	15	—	84	3	0-1	2	2	2.9	
	520	21	6	—	—	—	—	86	3	3-4	7	4	7.7	
Louisiana Water-thrush	—	—	—	57	17	6	—	—	—	—	—	—	—	
	—	—	—	—	—	—	—	57	4	1-2	6	6	12.6	
Redstart	119	9	2	—	—	—	—	53	4	8-9	?	?	7.9	
	153	18	8	53	15	4	—	—	—	—	—	—	—	
	—	—	—	—	—	—	—	94	?	4-8	11	8	12.1	

* During the first four days.

^a Probably not representative for the species.

^b Includes one additional feeding by an adult whose sex was not determined.

starts) have a wider area—a "home range"—over which they wander, sometimes singing, sometimes not. This wide home range may begin to develop during protracted pre-mating periods but more commonly does so after incubation is begun by the female.

The female takes no part in defense of the male's territory and may disregard its boundaries. However, she vigorously defends a smaller area around the nest, especially during the egg-laying and incubation periods, from both sexes of the same and of other species of wood warblers. This defense is less vigorous after hatching of the eggs. "Injury feigning" behavior may occur in the presence of predators.

The female usually builds the nest alone, although occasionally the male may help. The female is responsible for incubation of the eggs, but the male helps to feed the young. Four days commonly elapse between the start of nest-building and the laying of the first egg. Full incubation behavior is established when the last egg is laid, or occasionally earlier, and the incubation period is normally 12 days long. After hatching, the young remain in the nest 8 to 10 days.

Periods of attentiveness and inattentiveness are well marked, especially during incubation and brooding of the young. In different individuals and species, the average length of the attentive period during incubation varied from 9 to 28 minutes and of the inattentive period from 2 to 11 minutes (Table 1). Brooding and non-brooding intervals vary over approximately the same range. The adult male usually feeds the young at least as frequently as the female and often more frequently, since part of her time is given to brooding. The average rate of feeding varied from 2.5 to 14.7 times per hour.

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