

# A LIFE HISTORY OF THE MOURNING WARBLER

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DURING the summers of 1956 and 1957 I studied the breeding biology of the Mourning Warbler (*Oporornis philadelphia*) at the University of Minnesota Forestry and Biological Station in Itasca State Park, Minnesota. Here, in contrast to much of the breeding range of the species, the Mourning Warbler is one of the commoner nesting warblers. During the spring of 1957 I made observations on migrating Mourning Warblers at Urbana, Illinois. In February, March, and April, 1959, I made scattered observations of the species in its winter range in the Panama Canal Zone. Since no comprehensive life history study of this species has been published, an attempt is made here to summarize available information related to the aspects of the breeding biology investigated in the present study.

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## METHODS

During the summer of 1956 three nests (#1, #2, #3, 1956) were studied from blinds situated close to the nests. In 1957 two additional nests (#1, #2, 1957) were studied, one with the aid of an itograph, a device for automatically recording visits to the nest by the parents. This itograph was a modification of the type used by Hann (1937), and consisted of a hardware-cloth cage fitted over the nest, and a battery-run recorder located in a nearby blind. The cage over the nest had a single opening through which the parents entered and left. The record obtained, however, did not distinguish between birds entering or leaving. Because of this, difficulties of interpretation were encountered. During incubation these difficulties were greatly reduced by the observer frequently visiting the blind and marking on the record whether the female was on the nest or not, thus providing reference points for interpreting adjacent records of entrance or departure of the parents. After the young had hatched and both parents were actively feeding the young, as well as the female brooding for longer periods of time, interpretation was more difficult. For this reason data from this period are more approxi-



MOURNING WARBLER (*Oporornis philadelphia*).  
Male at nest with young. Photographed by Hal H. Harrison.

mate, and have been summarized separately from data obtained from direct nest observation.

During both summers observations were also made on the behavior and ecology of the pairs with nests under observation and of other territorial pairs throughout the park.

#### RANGE AND MIGRATION

The breeding range of the Mourning Warbler extends, in the north, from west-central Alberta eastward through central Saskatchewan and Manitoba, northern Ontario, and central Quebec to Newfoundland and Nova Scotia, and in the south, from northeastern North Dakota eastward through the northern parts of Minnesota, Wisconsin, and Michigan to northern Pennsylvania and southern New York, with a southward extension in the mountains to West Virginia (for detailed account, see A.O.U., 1957). In the southern extension of the range the species breeds only at higher elevations. In Massachusetts it occurs mostly above 1600 feet, although occasionally as low as 940–960 feet (Eliot, 1941). In western Pennsylvania the lower limit is about 1100 feet (Todd, 1940). In West Virginia (Brooks, 1940) and Maryland (Stewart and Robbins, 1947) the 3000-foot contour is the lower limit of the species.

The winter range, although poorly known, seems to extend from southern Nicaragua to Colombia, western Venezuela, and northern Ecuador (A.O.U., 1957). In the Panama Canal Zone, from February to April, 1959, I found the species to be a not uncommon winter resident in the lowland areas from sea level to about 500 feet. During this period the species was observed five times in edge areas with dense brush or tall rank grass. Miller (1947) reports that in the Magdalena Valley of Colombia they frequented low tangles and understory vegetation in damp woodlands. In Costa Rica Skutch (in Bent, 1953) states that low dense thickets and fields overgrown with tall weeds and rank grass are favorite habitats. He states that he has observed them mainly in the lowlands up to 4000 feet, but that they are still one of the commoner wintering warblers at 3000 feet.

The migration route of the species is primarily through Central America (Stevenson, 1957). In general it is one of the later migrants, leaving the winter range in March and April (Bent, 1953) and arriving at the latitude of Champaign, Illinois, and central and northern Ohio about May 11 or 12 (Smith, 1930; Jones, 1914; Borrer, 1950). Observations of Soper (1949) and Peters and Burleigh (1951) at the extremities of the breeding range indicate that the species has reached most of this area by the last week in May.

At Urbana, Illinois, during the spring of 1957, 48 individuals of this species were observed between May 10 and May 25. The majority were ob-

served in brushy edges, thickets and understory vegetation in open woods. When first noted, 90 per cent of the birds were in vegetation less than 5 feet in height.

In fall, migration begins early, with immature birds often appearing far south of the breeding range in early August, as, for instance, in Texas on August 4 (Baumgartner, 1951). At Chicago the average fall arrival is about August 25 (Clark and Nice, 1950), and in central Ohio the first birds appear about September 5 (Borrer, 1950). Arrival in the winter range occurs during the last half of September and the first half of October (Bent, 1953).

#### BREEDING HABITAT

The Mourning Warbler is found in a variety of habitats, including brushy woodland clearings (Gromme, 1938; Saunders, 1938; Forbush, 1929; Peters and Burleigh, 1951), forest edges, brushy edges of marshes and bogs (Roberts, 1932), and dense second growth (Roberts, 1932; Todd, 1940; Brooks, 1940). In the present study area, Hickey (1956) found the species strongly associated with clearings, while Kendeigh (1956) noted it most strongly associated with aspen-birch stands.

During the summer of 1957 I obtained data on the general habitat of the species by spot-checks of areas occupied by singing males throughout the park. Males were found in all the major vegetation types, from almost pure stands of red, white, or jack pine to stands of maple-basswood, spruce-fir, aspen and aspen-birch. In most cases these males were associated with edge conditions such as road edges, logging trails, bog borders, clearings, or areas of open woods. Occasionally, however, they were noted where well defined edge conditions seemed to be absent.

The vegetational characteristics of four territories were determined by quantitative measurements of tree density, degree of canopy closure, and type of ground cover. Canopy closure and ground cover were measured by walking parallel line transects 50 feet apart through each territory and counting the number of paces through each condition (open or closed canopy, herbs, shrubs or bare ground). Data on tree density were obtained by a method of stratified random sampling, using 30- by 30-foot quadrats laid out in a manner described by Oosting (1956:50). In these quadrats all trees more than two inches dbh were identified and measured. From these data the number of stems per acre, and the average diameter and the average basal area for each species and each territory were computed.

Canopy closure in these territories varied from 48 to 77 per cent (Table 1). Ground coverage by herbs varied from 41 to 81 per cent and by shrubs from 18 to 59 per cent. These results and a consideration of the features common

TABLE 1  
CHARACTERISTICS OF FOUR MOURNING WARBLER TERRITORIES AT ITASCA  
STATE PARK

	1	2	3	4
Territory size (acres)	1.7	2.2	1.8	1.6
Herb coverage (per cent)	65	43	41	81
Shrub coverage (per cent)	34	53	59	18
Bare ground (per cent)	1	4	0	1
Canopy closure (per cent)	77	48	71	69
Trees per acre	334	211	281	358
Average tree dbh (inches)	7.5	6.3	7.3	8.4
Basal area per acre (ft. <sup>2</sup> )	111.6	51.6	111.7	159.2
Per cent basal area of deciduous species	68	98	18	7
Per cent basal area of coniferous species	32	2	82	93

to the various other locations in which the Mourning Warbler was noted in the park, and to other habitats from which it has been reported, suggest requirements for a partially open canopy and the presence of both herb and shrub cover on the ground. If these requirements are satisfied the species may occur in a wide range of plant communities ranging from almost pure coniferous (Territories 3 and 4, Table 1) to pure deciduous (Territories 1 and 2) and even in relatively dense coniferous forests, provided there are scattered openings.

#### COMPETITION WITH ASSOCIATED SPECIES

On the biological station grounds at Itasca Park, where five territories of the Mourning Warbler were under close observation during the summer of 1957, 11 other species of warblers held territories which overlapped with those of Mourning Warblers. These were the Blackburnian (*Dendroica fusca*), Black-throated Green (*Dendroica virens*), Parula (*Parula americana*), Chestnut-sided (*Dendroica pensylvanica*), Black-and-white (*Mniotilta varia*), Nashville (*Vermivora ruficapilla*), Myrtle (*Dendroica coronata*), and Golden-winged (*Vermivora chrysoptera*) Warblers, American Redstart (*Setophaga ruticilla*), Yellowthroat (*Geothlypis trichas*), and Ovenbird (*Seiurus aurocapillus*). Interspecific aggressive behavior was noted with only two of these, the Yellowthroat and the Chestnut-sided Warbler.

On four occasions (one in migration at Urbana, Illinois) encounters were noted between male Mourning Warblers and Yellowthroats (both sexes). These encounters involved mutual wing-flipping and tail-flipping displays,

usually accompanied by *tshrip* notes (see section on vocalizations), and occasionally chases. The aggressive behavior on the part of the male Mourning Warbler was similar to that shown in encounters with other Mourning Warblers.

Several authors have pointed out the similarity of the habitats of the Mourning Warbler and the Yellowthroat (Roberts, 1932; Todd, 1940). On the biological station grounds at Lake Itasca, Yellowthroat territories overlapped all five of the Mourning Warbler territories studied there, and two of the Yellowthroat nests were known to be located inside Mourning Warbler territories. There was no evidence of mutual exclusiveness of territories.

One example of aggressive behavior was noted between the Mourning Warbler and the Chestnut-sided Warbler. On June 19, 1957, in an area where territories of the two species overlapped, the male Mourning was observed to chase the male Chestnut-sided briefly. In the same area, these same two birds were observed singing in a clump of shrubbery where the nest of the Chestnut-sided was located. At this time the male Mourning Warbler gave a series of soft, gurgling phrases rather than the typical territorial song. There was no evidence of mutual exclusiveness of territories between these two species either, and on the biological station grounds the territory of one pair of Mourning Warblers almost completely overlapped that of a pair of Chestnut-sided Warblers.

#### FOOD HABITS

Few food habits data are available for this species. In eight stomachs of adult Mourning Warblers from the vicinity of Lake Nipagon, Ontario, Ken-deigh (1947) found that spiders, various beetles, and Lepidoptera constituted over 50 per cent of the contents. Other insects typical of the ground and low vegetation were present in smaller amounts. Saunders (1938) and Roberts (1932) report that nestlings are fed mainly on Lepidoptera larvae. This item was commonly brought to the young in the present study, but numbers of other small insects were fed as well.

#### RELATION TO PREDATORS

Two of the nests under observation during 1956 fell victim to predators. One, from which eggs were taken, was in an area frequented by two ground squirrels (*Citellus tridecemlineatus* and *C. franklini*), the eastern chipmunk (*Tamias striatus*), the least chipmunk (*Eutamias minimus*), and the red squirrel (*Sciurus hudsonicus*) by day and the racoon (*Procyon lotor*) by night. The nest itself was little disturbed and it seemed likely that one of the smaller mammals was responsible. The second nest, from which nestlings

were taken, was located in an area frequented by red squirrels and least chipmunks. This nest was also little disturbed, suggesting the action of one of these small mammals.

On one occasion, where Mourning Warblers had young just out of the nest, the parents, several Blue Jays (*Cyanocitta cristata*), and several Red-eyed Vireos (*Vireo olivaceus*) were found scolding a large hawk or owl. The Mourning Warblers remained in the dense underbrush and gave loud *tshrip* notes.

Two types of distraction displays were given by the adults in response to the observer approaching the nest or the young birds after they had left the nest. When a nest containing eggs or young was approached the female usually remained on until the observer was quite close. She would then dive quickly over the edge and run away quickly through the ground vegetation, not taking flight until reaching a distance of 20–25 feet from the nest. This escape was very mouse-like, and often a peculiar gait seemed to be used. This behavior may well function as a distraction display based on the resemblance of the female to a mouse scurrying through the leaves, since the action, *per se*, is conspicuous, but the identity of the female as a bird may not be evident. This type of behavior has also been noted by Forbush (1929) and Gromme (1934).

A typical “broken wing” display was also given by the adults, especially during the period just after the young had left the nest. The initial part of the display was most intense. The adults would dash and flop through the ground vegetation, flipping the wings outward from the body, and often holding them out in a dragging position for short periods. During this display *tsip* notes were usually given. This behavior became weaker as the young birds grew older, but was noted for about two weeks after the young had left the nest. In the present study this behavior was noted occasionally during the period when the young were still in the nest. Gromme (1934) recorded this display during incubation, also.

The Mourning Warbler is not uncommonly a victim of the Brown-headed Cowbird (*Molothrus ater*). During the present study one nest was parasitized, containing one egg of the parasite and three of the host. Twelve other instances of parasitism have been reported in the literature, including five (Pitelka, 1939; Roberts, 1932; Lloyd, 1949; Chambers, 1947; Hickey, *et al.*, 1955) not included in summaries by Friedmann (1929, 1931, 1938, 1949).

#### VOCALIZATION

In the following discussion the term “song” is applied to the more complex vocalizations and the terms “call notes” or “notes” to the less complex. These should be understood as simply convenient names for these vocaliza-

tions and not as interpretations of function or motivation. Likewise, the term "territorial song" refers to the complex male vocalization which may be similar in function and motivation to the advertising songs of other species.

The territorial song of the Mourning Warbler is loud and ringing, with a somewhat throaty quality. It consists of 3-7 two-parted phrases, with the accent on the first syllable of each phrase. Typically, the last 1-3 phrases are given on a lower pitch. The length of the song varies approximately from 1-1 $\frac{3}{4}$  seconds (Gunn and Borror in Griscom and Sprunt, 1957). A typical song of the males in the present study area could be paraphrased *whee-o whee-o whee-o, whoo-e whoo-e*. Other common song patterns are given by Gunn and Borror (*op. cit.*). Variations I noted consisted of differences in number of phrases, omission of the changed ending, and differences in pitch and quality.

Only the male sang. He showed definite attentive and inattentive song periods, the latter being devoted mainly to feeding. Attentive periods were long, often over an hour in length, but within these the rate of singing varied. The rate of singing varied from 1-8 songs per minute, averaging about 3.6, giving an interval of about 15 seconds between songs. At times feeding and singing were carried out together in the underbrush, and during these times the rate of song was low (1-2 per minute). High intensity singing (6-8 per minute) was usually noted after territorial encounters.

The height in the vegetation at which territorial song was given varied from near ground level to about 40 feet high in trees. The stratum with the most records (37 per cent of 1200 records) of singing birds was that of low underbrush less than 5 feet in height. The stratum of second highest number of records was that between 20 and 25 feet (22 per cent). At this level the males often perched for long periods and sang rather steadily. The heights of those perches at which males remained and sang steadily for at least 10 songs ("singing perches"), were most frequently between 20 and 25 feet. Kendeigh (1947) found nearly the same distribution of song in relation to height in the vegetation in Ontario, where he noted the average height to be 26 feet, with some as high as 60 feet. Roberts (1932) and Forbush (1929) have also noted the tendency of the males to sit motionless at certain perches, singing steadily for long periods. When disturbed from these perches the males usually flew quickly into the underbrush, frequently to continue singing there.

A definite pattern of movement was followed during the attentive periods of song. At the beginning the male would fly up to a low branch, give a few songs, fly to a higher perch nearby, give a few more songs, and continue this process until reaching a perch 20-30 feet high, from which he would sing steadily for a long time (often 40-50 songs). From here occasional



flights would be made to adjacent trees, or back down into the underbrush, in which case the performance would often be repeated. Trautman (1940) has described this behavior in Ohio in migration.

In the present study singing was less frequent in the afternoon hours. In New Hampshire, Wright (1913) stated that song began about 37 minutes before sunrise. Trautman (1940), however, states that males in migration at Buckeye Lake, Ohio, remained silent during the early morning warbler chorus.

Song declined near the end of the nesting cycle, but did not cease until some time after the young were out of the nest. Roberts (1932) found young awing in late July with the parents still in full song. Saunders (1948a) found the average date of song cessation to be July 16 in Allegany Park, New York. He also noted a revival of song, frequently the flight song, between August 5 and 16 (Saunders, 1948b).

At Urbana, Illinois, in the spring of 1957, migrating males were frequently heard singing. One male was observed to maintain a nearly constant rate of 3-4 songs per minute for almost an hour. Trautman (1940) on one occasion observed 25 males singing at one time in migration in Ohio. Song is rare during fall migration.

The male also possesses a flight song, which is given as the bird flies upward, and ceases when a certain height is reached (Saunders, 1954). At Itasca Park the entire performance was never seen, but was heard on many occasions. Although hard to describe because of its rapidity, the song apparently begins with a series of chipping notes, followed by a rapid version of the territorial song, and ends with a few more chipping notes. A paraphrase of this song might be given as: *chi-chi-chi-chip-chip-cheery-cheery-chorry-chorry-chi-chip*. This song was heard once in mid-afternoon in migration at Urbana, Illinois. At Itasca Park it was heard between June 21 and July 13, but was most common during the first part of July when most pairs were in the latter stages of nesting. It was given at various times throughout the day. On one occasion it occurred at the beginning of a period of territorial song. In the territory of one of the pairs whose nests were under observation the flight song was heard on three occasions during the period when this pair had nestlings or fledglings. The sex of the bird giving this song was noted only twice; it was the male.

A third type of song pattern was heard once in early June. A male gave a soft, patternless series of muttering notes, interspersed with notes resembling soft *tschrip* notes. The significance of this song was not determined.

Two call notes were given by the adults. One was a *tshrip*, loud and rather harsh in quality. It was heard commonly interspersed with the territorial song of the male, and was also frequently noted in both male and female when

disturbed by an observer away from the nest area. It was heard commonly from migrating birds. It may have had some signal function between the male and female, since during the period of incubation, when the male occasionally fed the female, it was noted in association with this behavior (see section on incubation).

The second note, a *tsip*, less harsh, and higher in pitch, was heard commonly when I approached a nest containing eggs or young, or when the young fledglings were approached. It was also given during a territorial encounter between two females.

#### TERRITORIES AND TERRITORIAL DEFENSE

The sizes of ten territories were measured during the summer of 1957. The boundaries of these territories in early June were determined by marking the locations of singing males in the field. At least four hours of observation were spent with each pair, divided among at least three trips. Lines connecting the outermost points, thus giving the maximum enclosed area, were measured with a steel tape, and the direction of these lines noted with a compass. These measurements were then transferred to a map, and the enclosed area measured by dividing the areas into triangles and calculating their sizes.

The ten territories ranged in size from 1.6 to 2.4 acres, averaging 1.9 acres. Near Lake Nipagon, Ontario, Kendeigh (1947) found that during a spruce-budworm outbreak two territories were 0.9 and 1.5 acres in size. Kendeigh (pers. comm.) has suggested that these measurements were probably not as detailed as those of the present study, rather than representing a response to the spruce-budworm outbreak. In New Hampshire the foraging area of a pair was about 1.5 acres (Wallace, 1949).

The territories observed at Itasca Park included the nest site, and were used as foraging areas by the parents.

Two males, studied closely in 1957, defended the entire territory by territorial song early in the nesting cycle, but in the later stages their singing was confined to a smaller portion of the territory. In the period between June 20 and 25 the male of a nest containing nestlings confined his singing to two small areas near the nest, while a second, during the same period, sang regularly only in a small area at the opposite end of the territory from its nest, which contained eggs. Although singing seemed to be confined chiefly to these small areas, territorial encounters were noted in other parts of the territory, suggesting that the entire area was defended against other birds if they were noticed.

In 1957, when the nest sites of only two pairs were known, the males did not

sing in the immediate vicinity of the nest. The closest the two males sang to their nests was 30 feet and 85 feet.

In addition to song, other more aggressive displays were used to defend the territory against intruding Mourning Warblers. Good observations on these encounters were made on only three occasions. One encounter, in June, 1956, took place between two males in thick underbrush. The males hopped rapidly from perch to perch, bobbing their bodies violently. At the same time they rapidly flipped their wings outward and rapidly opened and closed their tails. Frequent *tschrip* notes were given. Occasionally short winding chases through the brush were made. During this encounter, the female of one pair appeared and began begging from the male by fluttering her wings and gaping. After a few minutes the males separated, one beginning to sing rapidly, the other continuing to give *tshrip* notes. After a few more minutes the second male also began to sing. During late June, 1957, a similar encounter was noted between two other males. During July, 1957, an encounter taking place mainly between two females was seen. At this time both pairs had fledglings, and the encounter was probably caused by the movement of one group into the territory of the second. When first seen, both females were in a small tree, and were both giving *tsip* and *tshrip* notes. Bobbing and wing- and tail-flipping similar to that seen in encounters between males were also performed. The two birds gradually hopped higher in the tree, then flew quickly down into the underbrush and engaged in a short, winding chase. Following this they returned to the same tree and repeated the posturing behavior. Both males remained nearby in the undergrowth, giving *tshrip* notes. This encounter continued for over an hour.

Territorial behavior was evident in some migrant birds at Urbana, Illinois. Between May 16 and 24, 1957, a male Mourning Warbler was found daily in a brushy area adjacent to a small stream. On the basis of song pattern I judged this to be the same bird each day. This bird sang regularly in an area about an acre in size. No encounters with other males were noted.

#### TIME OF NESTING

Five nests were found during the course of the present study. The following summary indicates the general course of events at these nests:

No. 1, 1956. Found on June 14, 1956, containing three eggs. A fourth added the next morning. Eggs removed by a predator late in incubation.

No. 2, 1956. Found on June 21, 1956, with three eggs of the owner and one of the Brown-headed Cowbird (latter I removed). Two of the eggs hatched on July 3 (other infertile) but the young later died when they fell from the poorly constructed nest (Cox, 1958).

No. 3, 1956. Found on July 1, 1956, with three eggs which hatched on July 6. The young were later removed by a predator.

No. 1, 1957. Found on June 12, 1957, containing five eggs, one of which disappeared during incubation. The young hatched on June 20 and left the nest on June 28.

No. 2, 1957. Found on July 5, 1957, with four well developed young which left the nest before noon of the following day.

Data on time of nesting in this species are scant. The earliest observed date of a nest with eggs is May 31 (Macoun and Macoun, 1909) in southern Ontario, and the latest is July 15 in Minnesota (Roberts, 1932). The earliest observed date of a nest with young is apparently June 20 in Minnesota (present study), and the latest, July 17 in Minnesota (Chambers, 1947).

#### NEST SITE

Nests of the Mourning Warbler are usually placed on or close to the ground. In the present study, four of the nests rested on the ground surface and one was supported on fallen branches 5½ inches above the ground. Records in the literature are mostly of nests on the ground or a few inches above it. The highest record is of a nest 30 inches off the ground (Roberts, 1932).

The nests are concealed in dense herbaceous or shrubby vegetation in most cases. In the present study, three nests were hidden in dense low herbs of the forest floor, one in dense tall grass in a small forest opening, and one in a dense growth of raspberry (*Rubus* sp.) at the edge of an area covered with this plant. The nests are usually supported laterally by stems of the concealing vegetation.

In the literature nests are usually reported from edge areas such as woodland edges or clearings, logging trails, or edges of bogs and marshes. Tree density and coverage of herbs and shrubs were measured in the vicinity (40-foot radius) of the five nests located in the present study. At these sites the average basal area and the number of stems per acre of trees were noticeably lower than in the previous analysis of the territories as a whole (Table 2). This suggests that at least in an area where the territories of the species are located in woodland which is fairly well developed the nests are placed in a more open part of the territory.

#### NEST STRUCTURE AND COMPOSITION

Nests of this species are rather bulky. Measurements for the five nests in the present study, together with five others reported in the literature (Roberts, 1932; Todd, 1940; Davison, 1891; Bent, 1953) gave average figures of 89 mm. (range 70–102 mm.) for outside height, 130 mm. (range 90–229 mm.)

for outside diameter, 47 mm. (range 38–57 mm.) for inside depth, and 54 mm. (range 44–64 mm.) for inside diameter.

Nests vary widely in composition, depending on the nature of available materials, but are usually described as consisting of leaves, weed stalks, pieces of bark, grasses and sedges, with a lining of fine rootlets, grasses or hair. In the nests I studied leaves were always present, usually as the outer shell of the nest, and varied according to the type available in the vicinity of the nest. Grasses, weed stems, and fibrous tree bark were used to bind the wall together. Linings were of fine weed stems, fine rootlets, grasses, and fine strips of bark.

Weights of four of the nests which had been air-dried for at least two weeks were 11.6, 20.2, 22.6, and 28.0 grams; a nest found by Walkinshaw (1956) weighed 12.2 grams.

TABLE 2

COMPARISON OF TERRITORIES AND NEST SITES\* WITH RESPECT TO TREE DENSITY AND GROUND COVER

	Basal area per acre	Stems per acre	Per cent shrub coverage	Per cent herb coverage	Per cent bare
Territories (4)	108.5 ft. <sup>2</sup>	296	41	58	1
Nest sites (5)	76.5 ft. <sup>2</sup>	219	42	55	3

\*40-foot radius of nest

#### EGGS AND EGG LAYING

Clutch sizes in the present study were 3, 3 (parasitized by cowbird), 4, 4 (brood size), and 5. The average size for these and for 31 other clutch sizes taken from the literature was 3.7, with a variation from 2–5.

In a single observation of the time of laying, the last egg of nest # 1, 1956, was laid between 3:15 and 6:15 a.m.

#### INCUBATION

Hofslund (1954) recorded the length of the incubation period of one pair of Mourning Warblers as 12 days, with the same probable time for a second nest. In the present study, nest # 2, 1956, was found on June 21, and contained a full clutch of three eggs at that time. On July 3, 12 days after the nest was found, the young hatched, indicating a minimum period of 12 days for this nest.

The female may begin incubation before the clutch is complete. At nest # 1, 1956, which was found with an incomplete clutch, the female was

observed on the nest three of the four times it was visited on the day before laying of the last egg.

The female usually approached and left the nest by hopping through the ground vegetation for 10–30 feet, and was never observed to fly directly to the nest. Definite routes of approach to and departure from the nest were used, especially in the immediate vicinity of the nest. On arriving at the nest the female usually paused on the rim and looked into the nest cavity for a few seconds, after which she entered the cavity and settled with a side-to-side rocking motion, spreading the feathers on either side of the brood patch as she did so.

While on the nest the female engaged in various activities such as resettling, preening, particularly around the brood patch, pecking at materials in the nest bottom, and moving the eggs. Occasionally she would “yawn,” briefly close her eyes, or tuck her bill under her wing for a few seconds. During hot periods of the day, or when direct sunlight fell on the nest, she would sit with the bill agape, “panting” almost constantly.

Little or no response was shown to loud calling of other birds at distances over 50 feet from the nest. When other birds or small mammals passed through the vegetation within 5 or 6 feet of the nest, the female usually elevated her head and looked in the direction of the disturbance.

During incubation the female is fed by the male both at and away from the nest. On June 14, 1956, the female of nest # 1 was seen to fly up from the vicinity of the nest to a perch about 5 feet off the ground in a small spruce. The male appeared and the female begged by gaping, fluttering her wings, and uttering soft, throaty, musical sounds barely audible to the observer 50 feet away. The male fed her and flew down to the ground, *tshrip*-ping vigorously. He then flew back up and fed the female twice more. Following this he gave *tshrip* notes from several perches and flew away. The female flew down into the ground vegetation and returned to the nest.

Several times while the observer was watching the incubating female of this same nest from a blind, the male came near the nest and began giving *tshrip* notes. In several instances the female responded by giving similar notes from the nest but did not leave. This response occurred on the average 7.4 minutes after the beginning of an attentive period of brooding by the female (attentive periods averaged 28.2 minutes for this bird). On four occasions when the male appeared and gave *tshrip* notes near the nest the female responded by giving similar notes from the nest and then leaving the nest in less than a minute. The attentive periods terminated by this behavior averaged 13.5 minutes in length, seeming to indicate that these periods were shortened by the appearance of the male and that possibly they also represented times when the male fed the female away from the nest. It is suggested

that the relative strength of the incubation drive (higher when occurring shortly after the beginning of an attentive period, lower later) to the drive activated by the appearance of the male was the controlling factor in whether the female left the nest or not.

The male also fed the female on the nest. This was difficult to observe because of the extreme shyness of the male. When approaching the nest the male occasionally gave low *tshrip* notes, but often appeared silently. The food item brought was most frequently a large green larva. When the male appeared the female either remained in the nest cavity or backed off to the opposite edge of the nest and begged by gaping, spreading her wings slightly and giving soft musical notes. After feeding the male usually remained on the edge of the nest for a few seconds. Sometimes the male apparently followed the female to the nest at the end of an inattentive period to feed her, but this was never seen in entirety. In one instance the female hopped to the edge of the nest with her bill agape, making soft musical sounds. The male was heard giving soft *tshrip* calls in the nearby vegetation, but was apparently frightened by the observer and left.

The function of this behavior may be partly that of anticipatory food bringing as described by Nolan (1958), but since the female was also fed away from the nest, an additional function, perhaps related to the pair bond, is probably involved.

Toward the end of attentive periods of incubation, the female exhibited what might be termed incubation restlessness. From seven to eight minutes before the end of the period the female would begin to shift position and re-settle more frequently. From one to four minutes before leaving she would begin to show nervous turning and tilting movements of the head. This behavior became more and more frequent until she left the nest.

The length of the attentive periods in the three nests studied averaged 35.8 minutes, and ranged from 2-93 minutes (Table 3). In respect to the individual females the average lengths were 60.5, 28.2, and 38.4 minutes.

Inattentive periods averaged 9.6 minutes for all three birds together, and 17.8, 8.7, and 9.2 minutes for the three individual females. In these three birds longer average length of attentive periods was correlated with longer average length of inattentive periods.

Length of attentive and inattentive periods also varied with time of day, probably due to daily changes in temperature. Attentive periods averaged longer in the early morning and evening than in mid-day (Table 4). Data on the length of inattentive periods were less conclusive in this regard, but the longest inattentive periods occurred in the afternoon hours.

Overall attentiveness averaged 77.4 per cent and varied only from 76.4 to 81.9 per cent for the individual birds (Table 3). In relation to time of day,

TABLE 3  
ATTENTIVE AND INATTENTIVE PERIODS AND OVERALL ATTENTIVENESS DURING  
INCUBATION FOR THREE MOURNING WARBLERS AT ITASCA STATE PARK

	# 1, 1956	# 2, 1956	# 1, 1957	Total
Attentive periods				
Number	10	45	38	93
Average length (minutes)	60.5	28.2	38.4	35.8
Range (minutes)	18-93	2-52	14-65	2-93
Inattentive periods				
Number	10	45	39	94
Average length (minutes)	17.8	8.7	9.2	9.6
Range (minutes)	9-29	2-17	3-24	2-29
Overall attentiveness				
Time (minutes)	1081	1844	3251	6176
Time in incubation (minutes)	885	1408	2486	4779
Attentiveness (per cent)	81.9	76.4	76.5	77.4

overall attentiveness was highest in the early morning hours and in the evening, and lowest at mid-day (Table 4).

The length of inattentive periods was found to be correlated with the length of the attentive periods immediately preceding them. Longer attentive periods resulted in longer inattentive periods immediately following them (Table 5), probably due to the build-up of a stronger feeding drive. The reverse relation showed no correlation.

TABLE 4  
ATTENTIVE BEHAVIOR DURING INCUBATION IN RELATION TO TIME OF DAY\*

	4-8 a.m.	8-12 a.m.	12-4 p.m.	4-8 p.m.
No. attentive periods	9	54	13	10
Average length (minutes)	42.6	32.8	37.5	47.7
No. inattentive periods	11	53	14	6
Average length (minutes)	11.1	9.6	12.6	8.5
Total observed time	856	2925	1301	1094
Attentiveness (per cent)	82.9	76.8	74.0	78.6

\*# 1, # 2, 1956; # 1, 1957 (see text)

Itograph records from the nest of pair # 1, 1957, during incubation and early feeding of the young gave information on the time of beginning and ending of daily activity by the female. Between June 14 and 26, the female



returned to the nest for the night an average of about 14 minutes before sun-down (eight records), with a range of 54 minutes before to 15 minutes after. Two records of departure in the morning were 23 minutes before and 15 minutes after sunrise.

On one occasion the female was seen when returning to the nest immediately after the hatching of one young. When she reached the nest she paused on the rim and pecked in the nest bottom for over a minute, then picked up the broken parts of the egg shell, worked them around with a chewing motion for several minutes, and finally swallowed them.

TABLE 5

LENGTH OF INATTENTIVE PERIODS OF INCUBATION IN RELATION TO LENGTH OF PRECEDING ATTENTIVE PERIODS\*

Length of attentive period (minutes)	Number of observations	Average length of following inattentive periods (minutes)
Less than 20	10	6.0
21-30	20	8.4
31-40	23	10.6
41-50	13	12.7
Over 50	9	13.9

\*# 1, # 2, 1956; # 1, 1957 (see text)

#### NESTLING PERIOD

Hofslund (1954) recorded the nestling period in two Minnesota nests as 8-9 days. Cottrille (1958) found that the young left the nest after eight days in one Michigan nest. The young successfully fledged at a known age in only one nest in the present study. In nest # 1, 1957, the first young hatched between 2:10 and 2:25 p.m. on June 20, and the remaining young hatched before 7:30 a.m. on the following day. On the afternoon of June 28 the young left the nest, at an age of between seven and eight days. These young survived and the family group was observed until the young achieved independence.

During this period the adults approach the nest silently. The external stimulus causing the young to gape is therefore tactile and/or visual. Before and shortly after the eyes of the young were open they gaped in response to movement of the nest by the observer. Gaping was seen at irregular intervals when the parents were absent, possibly in response to movements of the other young or to slight movement of the nest by wind. Occasionally the young failed to gape when the parent appeared. In these cases the adult

would hop around the edge of the nest, or back and forth between the nest and an adjacent perch until the young gaped.

After feeding, the adults paused on the edge of the nest for a few seconds. Fecal sacs were expelled by the young during this period. Only the young which had been fed were observed to produce fecal sacs. During the first part of the nestling period the fecal sacs were eaten by the parents. On the seventh day after hatching a fecal sac was carried away from nest # 1, 1957, suggesting that this may be the pattern during the later stages of the nestling period. Production of fecal sacs was lowest in the early morning (Table 7).

The appearance of the male with food while the female was brooding often seemed to result in the female's leaving the nest. In 15 of 27 observations, the female left within two minutes of the arrival of the male. When the female did not leave, she generally would rise and back off to the edge of the nest, often showing begging behavior by gaping in the direction of the male and fluttering her wings. In most cases the male fed the young directly, but he often responded to the female by giving her at least part of the food. On these occasions both would then feed the young.

Sometimes the female did not rise off the nest when the male appeared. When this happened the male usually gave the food to the female who then rose and fed the young. Once, however, the male hopped around the edge of the nest, and when the female rose slightly, fed the young beneath her. Another time, the male fed two young, but still had some food left. The female begged, the male gave the food to her, and she ate it. The female occasionally begged after the male had fed the young and had no food left.

When the food item was large, and the young had difficulty swallowing it, the parents frequently removed the object and reinserted it in the same or a different mouth.

Behavior of the female on the nest during brooding was similar to that shown during incubation. When direct sunlight fell on the nest the female spent much time standing over the young with her wings spread slightly, usually panting.

In direct observations on feeding behavior, the average rate was 2.5 feeding visits per nest per hour during the first four days after the young had hatched. This value ranged from 2.2 to 4.3 per nest per hour in the three nests studied (Table 6). Feeding rate varied with the time of day, the lowest rate being observed in the early morning hours (Table 7). Factors related to this low rate may be high brooding attentiveness in the female, and possibly more active territorial defense by the male at this time.

A fairly complete record of nest activity was obtained with the itograph for the nestling period of nest # 1, 1957. In this record two jogs close together indicated a bird leaving the nest soon after arriving, and were assumed (sup-

TABLE 6

RATE OF FEEDING OF YOUNG IN THREE NESTS OF MOURNING WARBLERS DURING  
FIRST FOUR DAYS OF NESTLING PERIOD\*

	# 2, 1956	# 3, 1956	# 1, 1957	Total
Time observed (minutes)	1172	240	180	1592
Feeding visits by male	26	10	5	41
Feeding visits by female	17	1	8	26
Total feeding visits	43	11	13	67
Feeding visits/nest/hour	2.2	2.8	4.3	2.5
Feeding visits/young/hour	1.2	0.9	1.1	1.1

\*Direct nest observations only

ported by observations from the blind while the itograph was recording) to represent a feeding visit. These are summarized in Table 9 as "apparent feeding visits." However, since the female sometimes brought food at the beginning of an attentive period of brooding (represented by a single jog), the total number of feedings could not be determined. Since brooding visits (summarized in Table 9 as "apparent female brooding visits") became less frequent toward the end of the nestling period, the number of "apparent

TABLE 7

BROODING ATTENTIVENESS, RATE OF FEEDING OF YOUNG, AND RATE OF FECAL SAC  
PRODUCTION DURING FIRST FOUR DAYS OF NESTLING PERIOD IN  
RELATION TO TIME OF DAY\*

	4-8 a.m.	8-12 a.m.	12-4 p.m.	4-8 p.m.
<i>Brooding attentiveness</i>				
Attentive periods	6	26	26	31
Average length (minutes)	20.5	20.5	19.5	14.0
Inattentive periods	6	28	27	34
Average length (minutes)	8.7	8.6	8.0	6.7
Observation time (minutes)	205	805	743	747
Attentiveness (per cent)	71.2	69.4	72.0	63.7
<i>Feeding rate and rate of fecal sac production</i>				
Observation time (minutes)	137	672	627	235
Total feeding visits	2	23	32	10
Feedings/nest/hour	0.9	2.0	3.1	2.6
Feedings/young/hour	0.5	1.2	1.0	1.1
Fecal sacs/young/hour	0.2	0.8	0.7	0.7

\*# 2, # 3, 1956; # 1, 1957 (see text)

TABLE 8  
 BROODING ATTENTIVENESS IN RELATION TO AGE OF YOUNG\*

Age (days)	Attentiveness		Duration of attentive periods		Duration of inattentive periods	
	Observation time (minutes)	Brooding (per cent)	Number	Average length (minutes)	Number	Average length (minutes)
0	361	68.4	14	17.9	14	7.8
1	1081	63.7	44	15.3	47	8.0
2	690	78.7	24	20.4	26	5.8
3						
4	785	33.1	10	24.2	11	18.2
5	542	37.1	17	11.4	16	16.6
6	308	25.3	7	11.1	7	26.7
7	371	12.1	6	7.7	7	47.1
8	429	3.3	3	4.7	3	135+

\*# 2, # 3, 1956; # 1, 1957 (see text)

feeding visits" approximates the true feeding rate more closely at this time. Thus the six-fold increase in the rate of "apparent feeding visits" between the first and eighth days probably represents an increase in the true feeding rate of about four times.

TABLE 9  
 RATE OF FEEDING OF YOUNG AS RECORDED BY ITOGRAPH FOR NEST #1, 1957, IN  
 RELATION TO AGE OF YOUNG

Age (days)	Time recorded (minutes)	Apparent feeding visits*	Apparent female brooding visits*	Apparent feeding visits/nest/hour	Apparent feeding visits/young/hour
0	405	4	13	0.6	0.2
1	605	17	30	1.7	0.4
2					
3					
4	489	35	4	4.3	1.1
5	226	13	7	3.4	0.9
6	308	30	8	5.8	1.5
7	371	57	7	9.2	2.3
8	429	79	3	11.0	2.8

\*See text

Brooding tended to remain high during the first three to four days after hatching, but declined rapidly after this. The length of attentive periods varied between about 15 and 25 minutes during the first four days but decreased rapidly after this (Table 8). Inattentive periods remained short

during the first few days after hatching, and then increased rapidly in length. Overall attentiveness was 63.7 to 78.7 per cent during the first few days and declined to 3.3 per cent on the last day.

#### FLEDGLING PERIOD

Observations of the activity of the young after they had left the nest were difficult because their movements were confined to thick underbrush. In addition, the adults usually showed alarm reactions when the family group was approached.

The family group of nest # 1, 1957, was followed for three weeks after it had left the nest on June 28. Although the birds were not marked, confusion with other groups was improbable, since the fledglings from the only close neighbor were of a much different age.

During this three-week period the family group remained within the general area of the territory of that pair, with most of the observations of the group being within 150 feet of the nest site.

When the young left the nest, they were unable to fly, and showed very little development of the tail feathers. By July 4, the tail feathers still showed little development, but the young could fly about 30 feet with a fluttering, uneven flight. On July 12 they were able to fly well and were heard giving weak *tshrip* notes. On July 18, the last day they were seen, they were completely feathered out and were foraging independently, although still accompanied by the adults.

The postnuptial molt of the adults apparently began at about this time. On July 18, two males (one the male from nest # 1, 1957) which were still in company with young birds were just beginning to molt. On July 25, 1957, two females were seen, one in light and one in heavy molt. Dwight (1900) stated that the postnuptial molt occurs in August, but observations of Saunders (1948a), with which those of the present study agree, suggest that it begins as early as mid-July.

#### SUMMARY

The breeding biology of the Mourning Warbler was studied in Itasca State Park, Minnesota, during the summers of 1956 and 1957. Observations on migrants were made at Urbana, Illinois, during the spring of 1957, and on wintering birds in the Panama Canal Zone during the early part of 1959.

In both breeding and winter ranges and in migration the species is a typical inhabitant of forest edge communities. Breeding territories were found in a wide variety of plant communities, where requirements of a partially open canopy and a mixture of herbaceous and shrubby ground cover were satisfied.

Aggressive encounters were noted with Yellowthroats and Chestnut-sided

Warblers, suggesting interspecific competition. Territories of these two commonly overlapped with those of the Mourning Warbler, however.

Vocalizations of the species include a male territorial song, a male flight song, and two call notes in both sexes.

Breeding territories are established and are defended by male song and aggressive displays by both sexes. The average size of the territory is 1.9 acres. The territorial song is given most frequently from low underbrush and from definite song perches 20–25 feet high. The rate of song varies from one to eight songs per minute. It is most frequent in the morning. Song declines during the nesting cycle but does not end until sometime after the young have left the nest. After nesting is well underway the size of the area regularly defended by singing is apparently decreased. Singing was not heard in the vicinity of the nest. A temporary territory was apparently established by a male in migration at Urbana, Illinois.

Nesting was begun mostly in June at Itasca Park. Nests were hidden in thick vegetation on or a few inches above the ground in a more open part of the territory. Leaves, grasses, weed stems, and fibrous bark were the principal items used in nest construction, with fine plant materials used as a lining. Clutch size averaged 3.7 eggs, ranging from two to five. The eggs are probably laid in the early morning. Nest parasitism by the Brown-headed Cowbird is not uncommon. Two nests in the present study were lost to predators, probably small mammals. Two types of distraction displays were shown by the adults when the nests were approached, one possibly based on the resemblance of the female leaving the nest to a small mammal scurrying through the leaves, and the second based on the resemblance of the actions of the adults to those of wounded birds.

Incubation lasts about 12 days, is carried on entirely by the female, and may begin before the clutch is complete. Attentive and inattentive periods averaged 35.8 minutes and 9.6 minutes, respectively, with overall attentiveness averaging 77.4 per cent. Attentiveness was highest in the early morning and evening. The male feeds the female at and away from the nest during incubation. Once the female was observed to eat the egg shell when the young hatched.

The nestling period lasts seven to nine days and the young are fed by both parents. The rate of feeding increases about four times during the period. The rate is lowest in the early morning. Fecal sacs are eaten by the adults at first, but may be carried away later. Brooding by the female is high for the first few days, but decreases rapidly later. The young are unable to fly when they leave the nest, and the family group remains together in the vicinity of the nest for a period of about 2–3 weeks, until the young have achieved independence.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ILLINOIS, URBANA, ILLINOIS, OCTOBER 6, 1959

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### NEW LIFE MEMBER



S. Dillon Ripley, a member of the Wilson Ornithological Society since 1946, is Director of the Peabody Museum, New Haven, Connecticut. Dr. Ripley received his baccalaureate degree from Yale University, and his doctorate from Harvard University. He is especially interested in avian speciation and ecology, and in waterfowl conservation. From these interests his researches have resulted in the publication of 150 technical papers and bulletins and three books: "Trail of the Money Bird," "Search for the Spring Babbler," and "A Paddling of Ducks." In addition, he is President of the International Council for Bird Preservation, a Fellow of the A. O. U., and a member of Sigma Xi, A. A. A. S., Zoological Society of India, B. O. U., French Ornithological Society, S. African Ornithological Society, etc. The photograph shows Dr. Ripley with an Andean Goose on a private preserve in Litchfield, Connecticut, where he rears waterfowl and other birds.