A LIFE HISTORY STUDY OF THE YELLOW-THROAT

BY ROBERT E. STEWART

During the spring and summer of 1938, I studied the habits and behavior of the Northern Yellow-throat (Geothlypis trichas brachidactyla) in southern Michigan. General observations were made throughout Washtenaw, Jackson, and Livingston counties, and detailed notes were obtained on a breeding population of Yellow-throats in a marshy area adjacent to Geddes Pond, one mile east of Ann Arbor. Nesting activities were studied from blinds placed within a few feet of active nests in the Geddes Pond area. Supplementary information on nest-building, egg-laying, and incubation periods of a closely related subspecies, the Maryland Yellow-throat (Geothlypis trichas trichas), was recorded at Arlington, Virginia, in 1940, and at the Patuxent Research Refuge near Laurel, Maryland, in 1947. Grateful acknowledgment is made to Dr. Josselyn Van Tyne for helpful advice given during the course of this study.

BREEDING SEASON

The resident male Yellow-throats were found to establish breeding territories almost immediately upon their arrival in the spring. At Ann Arbor, in 1938, the first record of a Yellow-throat in the spring was on April 29. On April 30, another was seen and on May 1, three were found with established territories adjacent to each other. The three birds were definitely resident males as they remained in their respective territories during the summer. They were easily recognized because of their distinctive songs. It would appear, therefore, that some of the resident males arrive on their nesting grounds at least as soon as, if not before, the transient males that nest farther north. Breeding territories were occupied and defended by male Yellow-throats from the time of their arrival in the spring until the advent of the post-nuptial molt which occurred during the first two weeks of August. At this time, territorial boundaries were no longer recognized and most of the Yellow-throats, even those still caring for young, wandered about a good deal.

In 1938, most female Yellow-throats arrived about one week after the first general appearance of the males. One lone female was seen on May 3, but this was, no doubt, an unusually early arrival as no others were seen until May 7. This early female was also peculiar in that it remained unattended by a male for over two weeks after its arrival although it was surrounded by males.

The first nest, containing eggs, was found on June 3. On June 7, another nest, containing nestlings, was located, while on June 10, a pair of Yellow-

throats was found tending young birds out of the nest. These records would indicate that the nesting actually started during the middle of May, probably about May 15. A nest with 4 eggs was reported near Ann Arbor on May 23, 1903 (Wood, 1951:417). July 27 was the latest date on which a nest with viable eggs was observed, and young birds were last seen as nestlings on August 3. From the evidence presented, I think that the period in 1938 during which occupied nests occurred extended from approximately May 15 to August 7. Adults were observed tending young out of the nest as late as August 20, and on August 29 an adult male was observed feeding a young Cowbird (Molothrus ater).

Навітат

The typical Yellow-throat habitat in southern Michigan develops on sites with damp or wet soil. It is characterized by a mixture of dense, rather lush, herbaceous vegetation and woody plants, chiefly shrubs and small trees. This type of habitat is usually found along the margins of streams, ponds and lakes, in open bogs, and in seepage areas below springs. In life form the habitats were found to range from an open savanna-like type with scattered groups of shrubs or trees from 3 to 15 feet in height, to a fairly dense thicket of small woody plants, usually less than 3 feet in height. Although definite evidence is lacking, it may be, as suggested by Kendeigh (1945b:430), that the habitat requirement of the Yellow-throat is the dense growth of low vegetation, which is more prevalent in wet areas, rather than the moisture itself.

Numerous species of plants characterize Yellow-throat habitats. The following names of some of the more numerous ones are taken from Gray's Manual of Botany (Fernald, 1950). Near Ann Arbor the more important woody plants include Salix cordata, hoary willow (Salix candida), speckled alder (Alnus rugosa), red osier dogwood (Cornus stolonifera), shrubby cinquefoil (Potentilla fruticosa), and buttonbush (Cephalanthus occidentalis). The many kinds of herbaceous species were found to be extremely variable in their occurrence and abundance from one area to another. In the Geddes Marsh area the more important herbaceous species are as follows: Dryopteris Thelypteris, Sphenopholis intermedia, Glyceria striata, Leersia oryzoides, Calamagrostis canadensis, Carex cristatella, Carex stipata, Carex vulpinoidea, Carex steralis, Carex stricta, Carex leptalea, Eleocharis palustris, Juncus Dudleyi, Juncus nodosus, Thalictrum polygamum, Anemone canadensis, Fragaria virginiana, Desmodium spp., Pycnanthemum virginianum, Pedicularis lanceolata, Galium boreale, Eupatorium purpureum, Eupatorium perfoliatum, Aster puniceus, Aster novae-angliae, and Solidago spp. The predominant herbaceous plants are grasses, sedges, rushes, composites, and a few representatives of other families.

The local distribution of Yellow-throats overlapped the local ranges of numerous other species of birds. Since the areas occupied frequently included portions of marsh, sedge-meadow, shrub swamp, and forest edge, many of the associating species were those that are characteristic of these various habitat segregates. Due to the lack of uniformity of most of the areas occupied by Yellow-throats the species composition of birds was found to vary greatly from one place to another. The more common associating species were: Traill's Flycatcher (Empidonax traillii), Long-billed Marsh Wren (Telmatodytes palustris), Short-billed Marsh Wren (Cistothorus platensis), Cathird (Dumetella carolinensis), Yellow Warbler (Dendroica petechia), Red-winged Blackbird (Agelaius phoeniceus), Cowbird (Molothrus ater), Cardinal (Richmondena cardinalis), Indigo Bunting (Passerina cyanea), American Goldfinch (Spinus tristis), Eastern Towhee (Pipilo erythrophthalmus), Henslow's Sparrow (Passerherbulus henslowii), Field Sparrow (Spizella pusilla), Swamp Sparrow (Melospiza georgiana), and Song Sparrow (Melospiza melodia). Other birds occasionally noted within Yellowthroat habitats include: American Bittern (Botaurus lentiginosus), Black Duck (Anas rubripes), Marsh Hawk (Circus cyaneus), Ring-necked Pheasant (Phasianus colchicus), Virginia Rail (Rallus limicola), and Sora (Porzana carolina).

POPULATION

The Yellow-throat, one of the more common species of the warblers (Parulidae) that nest in the Ann Arbor region, varies greatly in abundance from one area to another, depending on habitat conditions. A census of breeding Yellow-throats in the Huron River valley was conducted in an area comprising six adjoining sections (six square miles) that extend eastward from Ann Arbor. These sections were covered systematically on foot and all habitats that appeared suitable for Yellow-throats were thoroughly searched during several visits. Because of the intensive coverage, I think that the census totals are fairly accurate. The total number of territorial males in the entire area was found to be 58 (average of 9.7 males per square mile). These birds were unevenly distributed, being concentrated in their restricted habitats which occurred only along portions of the Huron River and its tributaries. An indication of this variation in occurrence and abundance is shown by the number of territorial males in each of the six sections: 21, 10, 9, 9, 9, 9, 0.

Although most of the areas of Yellow-throat habitat in this region are quite local and restricted in size, there are a few fairly large tracts that are popu-

lated by them. One such area, which covered a little more than one square mile was adjacent to Portage Lake in Jackson County. More than half of this area was made up of suitable habitat and here the birds were nesting in profusion. While no detailed census was made of this plot, I estimate that well over 100 territorial males were present.

In the Geddes Marsh study tract all of the habitat that appeared to be suitable for breeding Yellow-throats was occupied by them. This would indicate that the local breeding population in 1938 had reached the saturation point. The total area of suitable habitat was approximately 16 acres, while the number of territorial males present was 11. On the basis of these figures, the population density of territorial males on land that supports appropriate habitat is about 69 per 100 acres.

All of the 11 territorial males in the Geddes Marsh study tract were mated. One male was definitely polygamous, having two mates, while nine males were monogamous. The remaining male was also probably monogamous since not more than one female was seen in its territory at one time. However, two nests were found in its territory within a very short period which might indicate the presence of a second female. Young birds were fledged from the first of these nests on June 22 while on June 27 the other nest was found a relatively short distance from the first, containing two young Cowbirds and one Yellow-throat egg.

SONGS AND CALL NOTES

Upon their arrival in spring, the male Yellow-throats frequently sang while establishing their territories. The songs were then continued through summer until the advent of the post-nuptial molt in August. The latest adult song was heard on August 19. These songs apparently serve as proclamations of ownership of territory and, in the spring, probably also function in advertising the male's presence to any newly-arrived females.

The typical common song may be represented phonetically either as wit-cha-ree, wit-cha-ree, wit-cha-ree, wit or as wheet-to, wheet-to, wheet-to, wheet-to. However, there are many individual variations in the number of phrases, the number of syllables in each phrase, and in the tone and pitch. In the Geddes Marsh area, seven males had songs that were composed chiefly of three-syllable phrases while four males had songs made up of two-syllable phrases. The song of each male was distinctive enough to be readily recognized.

Ordinarily the males paused only momentarily to sing and then continued with whatever activity they were engaged in. Occasionally they stopped for a much longer period to sing, generally mounting to a perch several feet higher than usual, and there bursting forth in song at fairly regular intervals,

remaining stationary throughout. Mousley (1919) studied the relationship between location of favorite singing trees and nest sites. His observations on four nests showed distances between singing trees and nests of 4, 7, 10, and 11 yards. In the present study, most males were observed to sing in spurts, singing actively at fairly regular intervals for a considerable period and then abruptly ceasing to sing for another period. While actively singing, the interval between songs frequently was from 10 to 20 seconds with the period of song delivery lasting from 1.5 to 3 seconds. In mid-July, the total number of common songs sung by one male during nine hours of observation in the afternoon was 558 (an average of 62 per hour). The greatest number of songs recorded for this bird during one five-minute period was 26 (an average of one song every 12 seconds); the longest period of silence lasted for 85 minutes.

Male Yellow-throats were also occasionally observed performing flight songs. The procedure usually was for the bird to start from a perch in a low shrub, rise with undulating flight to a height of from 25 to 100 feet and then swoop downward to a new perch near the ground. During the ascending part of the flight the bird uttered several sharp, short notes which resembled the sounds, teenk, teenk, teenk. Near the apex of the flight, a somewhat discordant, garbled group of call notes, song phrases, "chuckles," and "gurgles" were uttered; during the descent the bird was completely silent. A modification of the typical flight song was noticed once when a male was observed singing the characteristic notes while flying to a perch near the top of a tall willow tree. The season of the flight song coincided with the season of the common song, although my records indicate that flight songs were given more frequently in late July and early August than earlier in the season. Usually more flight songs were heard in the afternoon and evening than in the morning. In nine hours of observation during which the songs of one male were recorded (see above) only 10 flight songs, or one flight song to 56 common songs, were given.

Another type of song which seemed to be more or less intermediate in character between the common song and flight song, was heard from a few adult males during the last half of July. This song was made up of a conglomeration of many unharmonious, squeaky, harsh, and melodious notes and was sung in diminished volume while the bird was perched. Several young males in first-winter plumage, were also heard singing similar songs during the first two weeks in September. Their songs were not very loud and lacked the well-balanced timing of the common song of the adult.

The vocabulary of call notes, which is shared by both sexes, is quite varied. Apparently many of these notes either have special functions or represent outward expressions of distinct "emotional states" of the bird. Probably the

most common of the call notes may be described phonetically by the sounds stagt - stagt. They evidently represent expressions of "suspicion" or "distrust" and sometimes of "annoyance." The sudden appearance of anything at all unusual or unnatural is likely to evoke an outburst of stagts. Sometimes a female when closely followed by a male will give vent to a few stagts as if she were annoyed with him. Often other birds of even smaller size were greeted with these notes when they approached a Yellow-throat too closely.

The harsh notes ste-de-de-de-de-de-deet are used by Yellow-throats when they appear to be communicating with each other. They are given in rapid succession and considerable effort seems to be involved in their utterance, as is evidenced by the noticeable vibration of the tail and lower part of the bird's body. Occasionally these notes are abbreviated to a mere ste-deet. They might be considered as being true call notes, since they are often employed by either sex in calling the mate. In spring, before the arrival of the females, these same notes were often used in verbal duels between two males in such a manner that they seemed to represent notes of challenge. Sometimes such a verbal duel would lead to actual physical combat. The use of these notes by a Yellow-throat as warning signals to its mate was also apparent since the presence of an enemy, such as man, seemed to furnish the stimulus for their delivery as if the bird were attempting to warn its mate of impending danger. The incubating female also appeared to use these notes as a warning to the male whenever he attempted to sing too close to the nest. If the male failed to heed the initial warning, the female would repeat the notes.

The alarm notes of the Yellow-throat may be represented by the sounds steek-steek or shtip-shtip or speenk-speenk. They were uttered only when the bird was "alarmed" or "frightened," such as when the nests or young were approached too closely. The barely audible notes, cheche-che-ca-r-r, che-che-ca-r-r, which are delivered in a slow and drawn-out fashion, might be considered to be "parental love" notes since they were often uttered by the parents while attending the young in the nest. Still another call, represented by the sounds zee-eet, zee-eet, zee-eet, was sometimes given by the adults when approaching fledglings with food.

TERRITORIES

The resident males, upon their arrival in spring, almost immediately began to establish their breeding territories. For one of the first arrivals, this seemed to be a rather simple procedure. The bird merely picked out a plot of ground which it deemed suitable, and then defended the plot against other males. This newly acquired "sovereignty" was proclaimed by almost continual song. For later arrivals the establishment of territories appeared to be

more complicated because much of the suitable habitat had already been claimed for territories by earlier males. As a result the late-comers often had to struggle vigorously to obtain adequate territories of their own. This often entailed a shifting of the boundaries of territories already established and sometimes resulted in a reduction in their size as well. In New York, Kendeigh (1945a:158) noted a period of territorial readjustment for second broods shortly after the first broods left the nest.

Observations of encounters between two established males along the border between their respective territories indicated that the males became extremely nervous and fidgety when they met. They moved quickly around each other, darting and alighting here and there, and at the same time displaying a peculiar flicking movement of the wings and tail. Ordinarily, while going through these antics the birds were completely silent, although on a few occasions one was heard singing a low, barely audible song. This display of rivalry apparently was usually mere "bluster and bravado" since actual physical combat was seldom noted. As a prelude to an encounter of this type the rapidly repeated challenge or warning notes were often uttered by both males when they were first approaching each other.

I seldom saw a male trespassing on another male's territory. When this happened, however, the intruder usually was soon discovered by the owner. Then the trespassing male was likely to retreat hastily with the other male darting after him and if the intruder was overtaken a short but vicious battle would ensue. In all cases observed the original owner emerged as the victor.

The territories of ten monogamous males in the Geddes Marsh study area were found to range in size from .8 to 1.8 acres (mean, 1.26±.12 acres; standard deviation, .39). The territory of the one polygamous male in the Geddes Marsh area occupied 3.4 acres—nearly twice as large as any of the others. The home ranges of the two females in this case were entirely separate from each other; the birds probably were unaware of each other's presence. This male's favorite singing perch was located near the top of a large dead tree midway between the home ranges of the two females. The male and one of his mates were color-banded in order to facilitate identification.

During most of the summer the male Yellow-throats seemed to be completely tolerant of neighboring species of birds. However, during early May, before the arrival of most of the females, the territorial instincts of the males were at a peak and as a result the birds were somewhat pugnacious, even toward other species. At this time male Yellow-throats were observed on a few occasions chasing four other species: Black-capped Chickadee (*Parus atricapillus*), Yellow Warbler, Field Sparrow, and Henslow's Sparrow. Yel-

low-throats were in turn observed being chased by Catbirds and Song Sparrows.

In only one instance did I see a male showing antagonistic actions toward a female. This took place while I was walking near a nest containing young birds. My presence caused such a commotion from the parent birds that a neighboring female was attracted to the spot. The attention of the two parents then was turned toward this new trespasser. The female parent became especially excited and soon both females were actively chasing each other back and forth through the area. The male meanwhile stood passively by, watching, and occasionally voicing his displeasure with a few characteristic stagts. Finally, as if losing his patience, he darted after the intruder with determination that could not be denied, forcing her to flee to her own territory.

Courtship

Courtship activities began as soon as the females arrived. Ordinarily after a few preliminary bouts between contending males along the boundary between their territories, the newly-arrived female chose her mate (or territory) with little delay, usually within a day or two. As soon as a male acquired a mate, he exercised a constant vigil over all of her activities for the next six or seven days, closely following her wherever she went. At this time the male frequently attempted to induce the female to copulate. Accompanying such attempts he was seen to exhibit the same peculiar flicking movement of the wings and tail as was seen in connection with the inter-territorial encounters between two males. In an experimental study on sex recognition in birds (Noble and Vogt, 1935:281), the male Yellow-throat was found to attack mounted male specimens and to attempt copulation with female specimens. However, when a black mask was placed on a female specimen, it was attacked, indicating that Yellow-throats recognize sex, at least in part, by color pattern.

The rivalry between two males which were attempting to court the same unmated female in a disputed area between their territories provided an amusing spectacle. The two males, when not fighting, would often chase each other around and about the ever-moving female, flying in a most peculiar manner all the while. Both would fly very slowly and jerkily with a pronounced and continual flopping (up and down motion) of the tail for short distances. The female meanwhile acted as though she were oblivious of all this fuss and attention.

During the courtship period, the males ordinarily sang very little, if at all. Several times, however, a male was observed endeavoring to sing a barely

audible song, but in each case was "severely reprimanded' by the female through the medium of the harsh-sounding warning notes. After six or seven days the courtship period ended almost as abruptly as it began, with the vigorous renewal of songs by the male.

NESTS

Locating a suitable nest site as well as the actual building of the first nest takes place during the courtship period. Knight (1908:561) found that the building of the nest was performed solely by the female. Field observations in the present study, too, indicated that the female was entirely responsible for these activities. The building of two nests was closely watched, one at Arlington, Virginia, in 1940 and one at the Patuxent Research Refuge, Maryland, in 1947. In each case, only the female was observed carrying materials to the nest. During these visits the males were not observed to approach the nests nearer than about 20 feet.

The Maryland nest had been barely started when it was first discovered in the evening of May 21. By the end of the following day the body of this nest was fully formed but the lining had not been inserted; on the evening of May 23, the nest appeared to be complete, indicating a nest-building time of about two days. Surprisingly, the first egg was not laid in this nest until May 29, eight days after the start of the nest. The first egg in the Virginia nest was laid three days after the nest had been completed. Conclusions of Knight (1908:561) were considerably at variance with my observations since he reported that this species requires a week to ten days for nest-building.

In total, 23 nests were located in Michigan in 1938. The situations in which the nests were found varied considerably. Most of the nests were found on or near the ground (within three inches) and were supported on all sides by herbaceous plants, usually sedges and grasses of various species. Two nests were found at the base of bushes, braced on all sides by the up-growing limbs, and several were situated on top of marshy hummocks. Almost all were located in damp situations; two nests were just above water with a depth of a half inch or more. Only two nests were placed higher than three inches above the ground; the rim of the highest one of these measured 14½ inches from the ground. This nest, built in tall weeds in late July, may have been placed higher because the undergrowth of vegetation within a foot of the ground was scanty. Nests which were placed above the ground were apparently supported by being merely wedged in between dense shoots and stems of vegetation as no intertwining nesting material could be found around these supporting structures.

Considerable variation was found in the shape and size of the nests, although most of them appeared to be rather bulky compared to the nests of

other warblers. Many were in the form of circular cups while others were found with two sides somewhat compressed. One nest bore a distinct resemblance to the nest of the Oven-bird (Seiurus aurocapillus). This nest was on top of a small hummock; it was rather sparsely roofed over with loosely entwined grasses and sedges in such a way as to leave an opening on one side only. Other nests of this type have been reported previously by Audubon (1831:121) and Cook (1893:118). Measurements were made of 12 nests: the outside diameter ranged from 6.8 to 10.8 centimeters (average, 8.5); the outside depth ranged from 6.0 to 12.0 centimeters (average, 8.2). The dried weight of 14 nests collected ranged from 6.7 to 16.8 grams (average, 12.1).

Most of the nests were found, upon dissection, to be composed of three layers or shells, each made up of dry plant remains. The outer shell, which usually comprised most of the bulk and about 70 per cent of the weight, was composed of matted leaves of deciduous trees and shrubs and coarse stems and leaves of many of the larger grasses, sedges, rushes, and cat-tails. The outer shell of any one nest was composed either of a mixture of all or most of these materials or was built predominantly of one type of material. The outer shells of a few nests that were constructed almost entirely of the leaves of narrow-leaved cattail (Typha angustifolia) were noticeably smaller and more compact than the others. The middle shell ordinarily comprised about 20 per cent of the weight of the nest and consisted of medium sized leaves and stems of grasses and sedges. One nest was examined in which the middle shell exceeded the outer shell in weight. In this case the outer shell was made up of leaves and coarse stems of weeds, sedges, and grasses while the middle shell was constructed of the matted leaves of deciduous trees and shrubs. The inner shell or lining of most nests comprised about 10 per cent of the weight and consisted of fine grasses and sedges and sometimes a few fine rootlets. Several horse-hairs were also found in the lining of one nest. In a few nests the distinct layering of different types of materials was not evident; instead, there was a gradual diminution in size of materials from the outside to the inside of the nest.

EGGS AND INCUBATION

In the Michigan area, in 1938, the full clutch was determined for 12 nests that had not been parasitized by the Cowbird. Six of these nests contained 4 eggs, 5 contained 5 eggs, and one contained 6 eggs (average, 4.6). The number of eggs laid in first nests seemed to be greater than in succeeding ones. Six of the 12 nests were found in June and of these, one contained 4 eggs, 4 contained 5 eggs, and one contained 6 eggs (average, 5.0). The

other 6 nests were found in July and of these, 5 contained 4 eggs and one contained 5 (average, 4.2).

Records of two nests, one each in Virginia and Maryland, disclosed that after the first egg was laid, one egg was laid on each succeeding day until the full clutch was reached. The time of laying was found to be between 7:00 p.m. and 9:00 a.m. for one egg in the Virginia nest, and between 7:30 p.m. and 8:10 a.m. for one egg in the Maryland nest. The approximate incubation period in both of these nests was about 12 days, or, more specifically, between 11 days, 9½ hours and 12 days, 13½ hours for the Virginia nest and between 11 days, 3 hours and 12 days, 19¾ hours for the Maryland nest. This is in agreement with the observations of Knight (1908:561), Burns (1915:286), and Kendeigh (1945a:159) who also reported the incubation period to be 12 days.

Field observations in the present investigation substantiate the statements by Knight (1908:561) and Chapman (1907:254) that incubation is performed entirely by the female. A total of 17 hours and 50 minutes was spent in a blind recording the incubation schedule of three females in the afternoon. These birds averaged 46, 68, and 70 minutes, respectively, for each setting and 12, 17, and 18 minutes, respectively, for each period spent off the nest (Over-all average of 61 minutes for each setting and 16 minutes for each period off the nest). The longest period that a female spent on the nest at one setting was 84 minutes, and the shortest when undisturbed was 38 minutes. The longest and shortest periods spent off the nest were $26\frac{1}{2}$ and 11 minutes, respectively.

Ordinarily in leaving the nest, when not disturbed, the female hopped to the rim, then to the ground and then by a series of hops made her way through the weeds and sedges for 10 feet or more before flushing. On a few occasions, however, the female flew directly from the nest. Always in approaching the nest she was observed passing through the vegetation close to the ground. Often the male would accompany her to within a few feet of the nest. Upon entering the nest the female almost invariably faced in one direction and then turned and faced in the opposite direction before settling down. While setting on the eggs the female frequently shifted her position and sometimes acted rather restless. Often she would pick at and eat ants or other small insects which were crawling on the rim of the nest or on adjacent vegetation.

Young

The young Yellow-throats normally remain in the nest for eight or nine days after hatching, usually between 196 and 216 hours. During this period they undergo rapid growth and development. The hatching weight is pre-

sumably not much less than the egg weight. Eleven eggs that were weighed were found to range from 1.45 to 1.81 grams (average, 1.66). Several young not more than a few hours old were weighed and the smallest of these weighed 1.80 grams. The weights of five nestlings and certain linear measurements of two nestlings were taken at the end of each day of nest life. The averages of these measurements are shown in Table 1.

TABLE 1
GROWTH OF NESTLING YELLOW-THROATS

The state of the s								
	Days of Nest Life							
	I	2	3	4	5	6	7	8
Weight (in grams)	2.0	3.2	4.8	6.6	8.1	9.4	10.0	9.8
Total length (mm.)	31.5	35.0	42.2	50.2	58.5	63.2	66.5	70.0
Tarsus (mm.)	6.5	8.6	11.4	13.6	16.1	18.5	20.2	21.7
Culmen (mm.)	3.5	4.6	5.6	6.3	6.9	7.3	7.5	7.7
1st primary (mm.)	.4	.8	2.5	4.3	7.6	11.2	15.2	18.0

The data show that these birds actually quintupled in weight in only six days (from the first to the seventh day). The rapid growth is also indicated by the linear measurements. It is interesting to note that there was a slight loss in weight on the eighth day. Possibly this was due to a reduction in frequency of feeding on the eighth day as the nestlings approach nest-leaving.

The behavior and appearance of the nestlings changed almost as rapidly as their size. The development of the juvenal plumage has been described in a previous report (Stewart, 1952). At the end of the first day the nestlings were truly helpless. Their eyes were closed and they sprawled on their bellies. They did open their mouths in response to sound or touch and occasionally they uttered barely audible seeps. At this time the legs and toes were light flesh color with lemon-yellow claws, the bill was light tan with a nearly black egg tooth, the edges of the mouth were cream-colored, and the inside of the mouth was bright peach. By the third day the nestlings were able partly to support themselves on their tarsi. The eyes were opened on the fifth day, the claws were becoming flesh-colored, and the young birds were able to crawl a little by using their legs and wings. On the sixth day they could support themselves readily on their tarsi, and on the seventh they could perch on the rim of the nest. By the eighth day the young were calling chac-chacchac-perhaps these are hunger notes. At this time they were apt to leave the nest upon the slightest provocation. This agreed with the findings of Shaver (1918), who observed that the young left the nest on the eighth day.

Both sexes fed the young. Often only one insect would be brought to the nest at a time, especially if it was large, while at other times the bill of the adult would be crammed with small insects. Occasionally, the adults would

experience difficulty in feeding large insects to the young; in these cases the insects would have to be broken up or partly masticated before the young birds could swallow them. Twice a female was observed attempting to feed large katydids (Tettigoniidae) to the young. She was not successful and finally ate them herself. In an intensive study of one nest, Shaver (1918) found that during the first few days of feeding, the male fed the young much more than the female. This was explained by the fact that the duties of the female in brooding kept her close to the nest during this period. Often food was brought to the nest by the male and delivered to the female who, in turn, apportioned it among the young.

After feeding the young, the adult carefully inspected the nest for droppings. The excreta were either eaten by the parent or carried several yards away and then dropped. They were more commonly eaten during the first few days of nest life and more commonly carried away during the last few days. Shaver (1918) found that the act of feeding furnished the stimulus for the evacuation of excreta which usually occurred shortly after the food was swallowed.

The schedule of feeding was studied at three nests. One nest, containing three eggs and one young, not more than a few hours old, was watched for 2 hours and 32 minutes. During this interval the female fed the young bird seven times (one feeding per 22 minutes). Another nest containing four young about two days old was watched for 3 hours and 53 minutes. These young were fed 17 times during this period (one feeding per 14 minutes). Both the male and female actively participated, the male feeding nine times and the female, eight times; usually two young were fed at each feeding. The third nest containing two young which were about six days old was watched on two consecutive days for a total of 2 hours and 23 minutes. A drop nest trap had been placed over this nest and as a consequence the male did not approach close enough to feed the young. The female did not seem to mind the trap and went directly to the nest without hesitation. During this period she fed the young 26 times (one feeding per 5½ minutes). The data from the last two nests would indicate that the rate of feeding increases with the age of the nestlings through the first seven days of nest-life.

After the young have reached the age of two days, the female apparently does little or no brooding during the daylight hours, although it is probable that this activity is greatly influenced by weather conditions. At the nest containing three eggs and one young not more than a few hours old (see above), the female averaged 17 minutes for each period of brooding and 8 minutes for each period spent off of the nest. On several occasions on hot, sunny days, a female was observed standing on the rim of her nest with wings outspread as if she were attempting to shield the young birds from the

sun. Usually while doing this she would hold her bill open and pant as though suffering from the heat. After dark, the female has been observed to brood the young every night except the last (Shaver, 1918).

Adults were observed to take care of the young for at least two weeks after the young leave the nest. There is some observational evidence that the adult male sometimes assumes more responsibility for the care of the young after they have left the nest than does the female. Possibly, this is because the female often begins to prepare for her next nest without much delay and has little time for attending to the first brood. One interesting observation was made of a fully-grown immature bird approaching an adult female while she was caring for nestlings of her second brood. The female ignored the young bird for awhile and then called to it with a few soft low notes and gently pecked it a few times on the head, whereupon the young bird flew away. Stone (1937:838), while observing the actions of an adult male accompanying a brood of stub-tailed fledglings, noted that the adult, while actively moving about, constantly flirted its tail to one side or the other and nervously flapped its wings, so rapidly as almost to escape detection. This behavior is similar to that displayed by males during inter-territorial encounters or when courting a female.

NESTING SUCCESS

Of the 12 breeding females definitely identified in the Geddes Marsh area, 10 (83 per cent) were successful in raising young beyond the nestling stage during the summer. Each female seemingly attempted to raise two broods, but apparently few actually attained this goal. Only one of the Geddes Marsh females was known definitely to have raised two broods beyond the nestling stage.

The number of nests built and number of clutches of eggs laid by a female in a season probably depends to a large extent on the degree of success attending each attempt. In the Geddes Marsh area, three females were known to have built at least three nests each, and four females constructed at least two nests each. The shortest interval known to elapse between the destruction of one nest and attention given by the female to a new nest was somewhat less than 10 days. The interval between the start of two consecutive nests, when the first had been successful was determined in one instance and found to be aproximately 28 days. Consecutive nests built within one territory were placed without any apparent relation to each other.

The histories of 19 nests were followed to their conclusion in the Geddes Marsh area. The eggs of 11 (58 per cent) of these nests hatched, and 7 nests (37 per cent) produced fledgling Yellow-throats. In total, the 19 nests pro-

duced an average of only one fledgling Yellow-throat per nest. However, it must be remembered that most female Yellow-throats build several nests (possibly averaging about three) during the season, thus accounting for the maintenance of the population level.

The heavy parasitism by the Cowbird is an important factor in connection with the high mortality rate of the eggs and young. Of 22 nests found in Michigan in 1938 containing eggs or young, 10 (45 per cent) had been parasitized by the Cowbird. In these 10 nests the number of Cowbird eggs or young ranged from one to three (average, 1.8 per nest). In the Geddes Marsh area, nine nests had been parasitized by the Cowbird and of these only one produced a fledgling Yellow-throat. On the other hand, ten nests in the Geddes Marsh area had not been parasitized and of these six produced fledgling Yellow-throats. The average number of fledgling Yellow-throats produced per nest parasitized by the Cowbird was only .1, while the average number produced per non-parasitized nest was 1.9. The average number of Cowbirds fledged in the parasitized nests was .4 per nest.

The causes for the destruction or disappearance of many of the eggs and young were not ascertained. Several of the nest were found greatly disheveled, indicating that some predatory animal may have been responsible. Other nests were found intact and thus furnished no clue as to what the marauders might have been. Two nests had been badly smashed as if some large mammal had stepped on them. Another nest was over-run with a mass of small ants. One nest containing four young gradually became tilted to one side, eventually causing one of the nestlings to fall out.

SHMMARY

Investigations concerning the life history of the Yellow-throat were made in southern Michigan during the spring and summer of 1938. Supplementary information was also obtained at Arlington, Virginia, in 1940 and at the Patuxent Research Refuge, Maryland, in 1947.

Resident males established territories almost immediately upon arrival in spring. In southern Michigan some resident males arrived at least as soon as, if not before, transient males. Most females appeared on their nesting ground about a week later. Adults were engaged in nesting activities from the time of their arrival in spring until the advent of the post-nuptial molt in late summer.

Typical Yellow-throat habitat consists of a mixture of a dense herbaceous vegetation and small woody plants in damp or wet situations.

At Ann Arbor, the Yellow-throat was a common breeding species in its restricted suitable habitat. The population density in one area of suitable habitat was about 69 territorial males per 100 acres. Of 11 territorial males

that were intensively studied, one was polygamous (with two mates), nine were monogamous, and one was probably monogamous (with at least one mate).

The song of the individual Yellow-throat was heard throughout the breeding season except for the courtship period. Two major types of song were the common song given while perched, and an occasional, more elaborate, flight song. Most males sing in spurts, singing at fairly regular intervals for a considerable period and then abruptly ceasing for another period. The vocabulary of both sexes included several types of call notes that appeared either to have special functions or to represent outward expressions of distinct emotional states of the bird.

Resident males were antagonistic toward each other throughout the breeding season. Most remained on well-established territories during this period. Territories of 10 monogamous males ranged in size from .8 to 1.8 acres but the territory of one polygamous male occupied 3.4 acres. The behavior of males during inter-territorial encounters was similar in some respects to their behavior when courting females.

While courting females, the males are very attentive and seldom sing for about one week. During the courtship period the female locates the nesting site and builds the nest without assistance from the male.

Nests, constructed of dried plant materials, were situated on or near the ground and were supported on all sides by stems of herbaceous plants or limbs of shrubs. Many nests were composed of three layers with the coarser materials being used in the outer layer.

The full clutch of eggs in 12 nests ranged from 4 to 6 (average, 4.6). Early clutches seem to be larger than later ones. After the first egg is laid, one is laid on each succeeding day until the clutch is complete. Incubation period is about 12 days. Incubation is only by the female. Records of day-time incubation schedules of three females about half way through incubation indicate that the periods spent on and off the nests average about 61 and 16 minutes, respectively.

Young Yellow-throats usually remain in the nest for eight or nine days. During this period they grow and develop rapidly. Their weight quintuples in six days. Both sexes are active in feeding the young and in removing excreta from the nest. Records of feeding at three nests showed a range of one feeding per $5\frac{1}{2}$ minutes to one feeding per 22 minutes, the rate increasing with age of young. Adults care for the young for at least two weeks after the young leave the nest.

Ten of 12 females that were intensively studied were successful in raising young beyond the nestling stage. Only one of these raised two broods, although three females built at least three nests each. In 19 nests, 11 (58 per

cent) produced nestlings and 7 (37 per cent) produced fledglings. In total, the 19 nests produced an average of one fledgling Yellow-throat per nest. Of 22 nests that were found near Ann Arbor, 10 (45 per cent) had been parasitized by Cowbirds. Nine of the ten parasitized nests produced an average of .1 fledgling Yellow-throat per nest, and ten nests that had not been parasitized produced an average of 1.9 Yellow-throats per nest.

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