A LIFE HISTORY STUDY OF THE LOUISIANA WATERTHRUSH

BY STEPHEN W. EATON

THE Louisiana Waterthrush (*Seiurus motacilla*) has been a favorite with naturalists in eastern North America for many years, yet little has been published on its life history except by Chapman (1907) and Bent (1953).

Ithaca, New York, is an ideal place to study the Louisiana Waterthrush. Along almost every stream which cuts steep banks in the hills sloping toward Cayuga Lake, the Louisiana Waterthrush finds a favorite place to rear its young. Steep slopes leading to the floors of the glens facilitate observation of the streams where the birds spend most of their time. Birds building nests or feeding in the glens can be watched from the slopes with the aid of binoculars.

About 345 hours were spent in the study area from April through August during 1947, 1948 and 1949.

In 1947 one nest was watched until the young left the nest, and in 1948 and 1949 my study area was expanded to include 10 small glens in which eight pairs were nesting. These glens were numbered from 1 to 10 for the purposes of the study. Glen No. 1 is the ravine by which Dr. Arthur A. Allen's house is located, No. 2 is the next one north and so on to No. 10, which is approximately 2.4 kilometers north of No. 1 (Fig. 1). In width the study area was approximately 0.8 kilometers from east to west.

Streams in the headwaters of the Susquehanna River system were visited on three occasions. In one of these streams, 24 kilometers south of Ithaca (Prospect Valley), I saw my first Louisiana Waterthrushes of the 1949 season on April 12. On April 26, 1948, I had found a pair building a nest in the same valley, two days before any nests were found started in the Ithaca area. A glen 4.8 kilometers north of Glen No. 1, nicknamed "Chironomus Glen," was often visited to collect birds for the purpose of checking on food habits, habits of the sexes, and molt. Coy Glen, a deeper, longer ravine just southwest of Ithaca, was visited twice to see how many pairs occupied 1.6 kilometers (1 mile) of suitable habitat.

Near Cienfuegos, Cuba, between December 24, 1948, and January 2, 1949, I spent approximately 15 hours along a 1.6-kilometer stretch of fresh-water stream observing the birds' behavior in winter (Eaton, 1953).

Sixteen nests were located during the three-year period; four of these were under observation from nest-building until the young left the nest. The most satisfactory way to find nests was to locate birds building early in the morning. If not found at this time, the nests were difficult to locate until adults were feeding young. When the young were about four days old the nests

YOUNG LOUISIANA WATERTHRUSH
(Seiurus motacilla)

An individual in full juvenal plumage, painted from life by William C. Dilger.

were located easily if water in the streams was low. The parents left fecal sacs in the stream within a few feet of the nest. These caught in a backwater not far downstream and were easily seen.

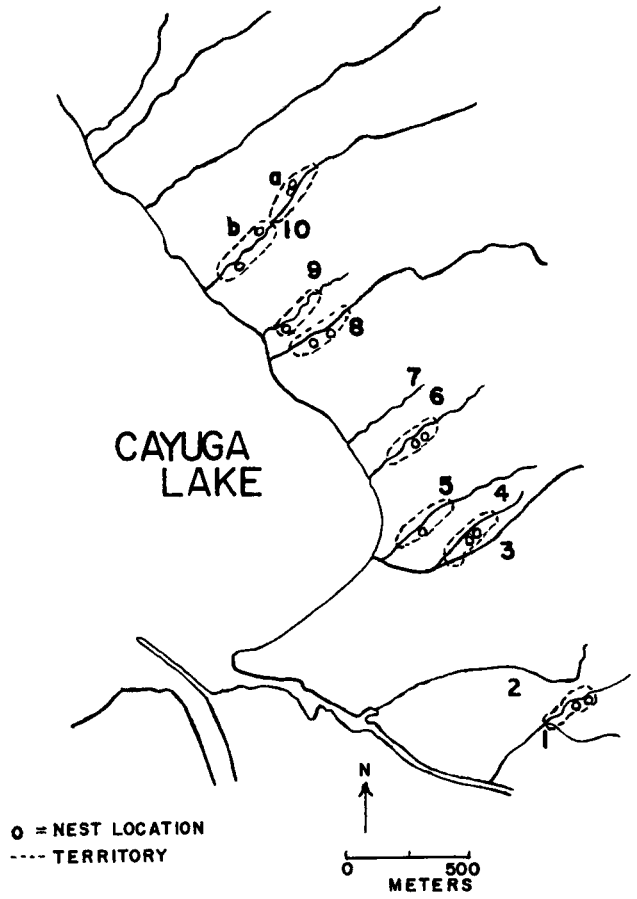

FIG. 1. Map of southeastern corner of Cayuga Lake, near Ithaca, New York. Eight pairs of Louisiana Waterthrushes nested in the ten numbered glens. One nest was located in this area in 1947, nine in 1948, four in 1949. Additional information on these nests is presented in Table 3.

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VARIATION

Ridgway (1902) considered the species as monotypic. He compared samples from the Mississippi Valley and from the Atlantic side of the Appalachians and found no reason to name these populations. I used slightly larger samples and came to the same conclusion.

Individual Variation.—This species has much less variation in color than has the Northern Waterthrush (*Seiurus noveboracensis*). The breast and superciliary feathers are white to buffy cream according to the season. Some variation in streaking is evident. A few individuals show light streaking on the throat, a character that is regular in *S. noveboracensis*. Other variable parts of the color pattern are the amount of white striping from the bill over the forehead and crown, and the amount of buffy wash on the flanks and undertail coverts.

Seasonal Variation.—In fresh fall plumage this bird is beautiful with its olive upperparts and buffy cream underparts. Birds I collected in Cuba during December and January had lost little of this fall coloration, and Ridgway (*op. cit.*: 639) wrote ". . . I could not find that there is any difference in plumage according to season, some birds taken in April and May being quite as strongly colored as any autumnal or winter specimen." In late May and June, however, the plumage becomes very worn. The upperparts become browner and the underparts lose the buffy-cream "wash" of the fall. Some birds show a buffy collar about the neck, and sometimes individuals become almost bald on the back of the head.

Age Variation.—Birds in first fall plumage have rufous edgings on the tertials, and lack white tips on the inner vanes of the outer one to three pairs of rectrices. Nine juveniles from the Ithaca region, collected shortly after assuming most of the first fall plumage, show no trace of white in the tail. A bird raised in captivity until it had assumed the first fall plumage showed no white tipping. Twenty-eight of 51 birds (55 per cent) collected in April, May and June showed the white tipping; 23 (45 per cent) lacked even a trace. A bird banded as a six-day-old nestling in 1947 was collected on April 28, 1949, and he showed distinct white tipping. This white tipping of the rectrices, then, serves to separate first-year birds from those which have completed the first post-nuptial molt. This is a generic character occurring in *Seiurus noveboracensis* (Eaton, 1957*a*) and *S. aurocapillus* (Eaton, 1957*b*).

Arrival of Males

The first males arrive in the Ithaca area about April 11 (15-year average from Cayuga Bird Club records), but do not become common until about April 25. They usually appear the morning after a warm night with strong south winds. Below is a summary showing dates of first arrival for individuals in the study area. Numbers represent dates in late April except where marked M, which indicates a date in May.

Glen No.	1	2	3	4	5	6	7	8	9	10
1948	29			18	30	3 (M)	28	25	28	28
1949	13 (M)			24	22	22		15	18	22

After the males arrive, temperatures may drop well below freezing, and snowstorms often occur at this time of year. If the weather is cold the birds do not often sing, and when they do the volume of their songs is much reduced. If the day is warm with a strong south wind, the birds will sing loudly. The cold weather they encounter in April does not seem to be a mortality factor. During snowstorms with the temperature at 27°F., I have watched them feeding along the floor of the glen, flipping leaves on the surface of the water and poking their bills into crannies. The only noticeable effect of the weather was the suppression of song.

The males take possession of territory immediately upon arrival and will sing from trees five to 10 meters above the ground. These advertising songs are given throughout the day with short interruptions for feeding. Frequency of song is about five times per minute, and each song is about three seconds in duration. While singing, the bird sits on a horizontal limb with tail depressed and head thrown back so that the bill is pointing skyward.

Arrival of Females

In 1949 the first female was seen near Ithaca on April 27, and was already paired to the male in Glen No. 4. It was quite easy to tell when pair formation was accomplished because the male ceased his regular advertising song. Before the females arrive the male in a glen sings consistently throughout the day, stopping for only a few minutes of each hour to feed. At this time males were observed singing even from the ground while feeding, although such observations were unusual. After pair formation is accomplished, males assume an entirely different behavior. They follow the females in the glens, walking a few meters behind and occasionally make a "zizzing" sound. If a male is not following a female he will be perched above her in a tree, and when she has passed beyond him a few meters he will often dive toward her. Near the end of this dive he utters a sputtering noise followed by a "zizzing" sound which seems to come from both male and female. This is perhaps

homologous to the "pounce" of the Song Sparrow, *Melospiza melodia* (Nice, 1943:174). The advertising song is rarely heard again until incubation starts, and even then it is never as loud nor as frequent as it was before the female's arrival. In late June and early July songs were heard occasionally. These songs were found to be from males feeding semi-independent young. A recrudescence of song occurred during the first half of August when the males had completed their post-nuptial molt.

During 1948 the glens were inspected daily for the arrival of the females. Females arrived over a span of 9 days; the males over a span of 15 days. Below is a summary of females' first appearance in the study area in 1948. Sex was determined by behavior.

Glen No.	1	2	3	4	5	6	7	8	9	10
April	29			27				27		
May						3	1		5	

Territory

The territory is long and narrow, following the course of a fast-flowing stream. Along 1.6 kilometers (one mile) of continuously favorable streamside habitat in Coy Glen four pairs were found nesting in 1948. In the study area suitable habitat (exclusive of Glens No. 8 and No. 10) extended approximately 500 meters east from the lake; and one pair was found nesting in all but Glens 2, 3, and 10. In Glen No. 10 two pairs were found nesting in 1948 and 1949, but here favorable habitat extended approximately one kilometer back from the lake. Nests were found only 200 meters apart along this stream; a 30-ft.-high falls marked the boundary of their territories. None was found nesting in Glens 2 and 3.

From these data it appears that one pair of Louisiana Waterthrushes will occupy approximately 400 meters along a stream during the nesting season. Usually nests are located near the center of the territory or 400 meters apart, but in one case (Glen No. 10) they were as close as 200 meters (Fig. 1).

The male of the pair in Glen No. 4 included the lower part of Glen No. 3 in his territory (Fig. 1). Early in the spring of 1948 he also included Glen No. 5 in his territory, but when his female arrived he was not again seen in Glen No. 5. Another male occupied Glen No. 5 after April 30. The male of Glen No. 4 used the unoccupied Glen No. 3 as a feeding area, while his mate used that part of Glen No. 4 upstream from the nest as a feeding area. In Glen No. 10 the female of pair No. 10*a* in 1949 (Fig. 1) collected food for the young downstream from the nest, while the male went approximately 200 meters upstream to get his. This was probably because water in the glen was very low after a prolonged dry spell, and aquatic food was scarce in the vicinity of the nest. In most cases birds were observed feeding in areas along

the stream not so far from the nest. When feeding young they seemed to have distinct foraging areas, one member of the pair usually collecting food upstream, the other downstream.

If another bird of the same species entered the territory a vigorous fight ensued, and the defending male (and perhaps female) always won by driving the other bird out of the ravine and back through the woods in spectacular aerial chases. These fights occurred more often either before the females arrived or during incubation than later, after the young had hatched. On May 4, 1949, in Glen No. 8, I watched a particularly lively scrap which recalled the fights of Snow Buntings (*Plectrophenax nivalis*) as described by Tinbergen (1939:15–16). The male in Glen No. 8 was singing his advertising song when another male (identified by song) came into the glen from the direction of Glen No. 7. The male of Glen No. 8 immediately flew toward the intruder and started to chase him. One bird landed in the center of the highway that crossed the glen at this point and struck a defiant pose—tail up, body crouched and bill horizontal to the ground. The other bird flew down to a point not more than two inches distant and faced the bird on the road. They remained motionless, bill toward bill, for a few seconds and then started to fight. They jumped into the air with a jumble of wings and much "zizzing" and chipping. Then, still locked together in some manner, they drifted over to some nearby hawthorn bushes and fell to the ground. When it was over the Glen No. 8 male resumed his singing and the other bird flew south through the woods toward Glen No. 7.

Pugnacity of the males in the territory was usually less vigorous than that described above. On April 15, 1949, I watched the same male of Glen No. 8 successfully rout an itinerant male. The two birds flew up and down the glen and through the trees on the talus slopes for about three minutes. The distance between the birds in flight was about one to three meters, and the bird behind matched each turn of the bird in front. Sometimes during these chases advertising song was heard. Once, while I was sitting in a blind about 10 meters from a nest, a bird dived toward me from the top of the slope, and, swooping up over me, uttered a beautiful song. It was similar to the perch song but more hurried. Such songs, given on the wing while chasing other birds (or intimidating a blind), I have termed *pursuit* songs because they are somewhat different from the perch or *advertising* song and decidedly different from the *flight* song. The pursuit song is given while the bird is in normal bounding flight; the flight song is given while the bird is flying with rapidly beating wings. All these vocalizations seem to function in maintenance of territory.

Flight Songs

During the three-year study I failed to see Louisiana Waterthrushes sing

the typical *seiurian* flight song. Ovenbirds and Northern Waterthrushes often sang them at dusk (Table 1). They initiated the flight song by showing increased excitement on or near the ground, their chipping becoming louder and more frequent. Then suddenly they leapt into the air and flew in labored flight over the treetops. This flight was usually parallel to the tops of the trees but sometimes almost straight upwards. Only rarely were the flights under or through the tree canopy. While on this flight Ovenbirds and Northern Waterthrushes uttered a finchlike twittering which ended or was interjected by a recognizable species song. When this was completed they would drop to the ground, or to a low perch about 100 meters from the starting point, but within their territory.

Along a tributary of the Allegheny River near Olean, New York, where I am now living, I have heard the Louisiana Waterthrush give three typical flight songs in the past five years. The whole performance was like its congeners' but louder, longer and more vigorous. Initial chipping started along the stream border, becoming louder and more frequent, followed by the horizontal, labored flight above the trees, twittering song, regular song and the drop to the stream border, approximately 200 meters from the start. The performances were given within the territory. In this area the population of Louisiana Waterthrushes is much lower than in the Ithaca region generally, but this is not stated to imply a solution. Hann (1937) has noted that the Ovenbird gives its flight song more often in some geographic areas than in others.

Habitat

The 10 glens in the study area are post-glacial gorges. The floors of these glens run in step-like fashion to the lake. A series of two to five falls, formed at more resistant sandstone outcrops along the path of the watercourses, interrupt the smooth flow toward the lake (Fig. 2). Between the falls the water flows along rather flat beds of Devonian shales.

The flora on the acidic slopes between the different glens is mainly a forest of oaks with an understory of ericaceous plants, and *Desmodium* and *Lespedeza*. This contrasts sharply with the flora of the talus slopes leading down to the glen floor. In a strict sense these talus slopes and the stream itself constitute the niche of the Louisiana Waterthrush. On the north-facing slopes the vegetation is usually more dense, and it is here that plants of more northern affinities are found, such as hemlock (*Tsuga canadensis*) and mountain maple (*Acer spicatum*). The south-facing slopes of the glens have fewer trees and are much hotter and drier due to their greater exposure to the sun.

Use of Habitat.—When the males arrive they sing in trees up to 12 meters from the ground or talus slopes (usually about nine meters). When flying

TABLE 1

DAILY PATTERN OF FLIGHT SONG ACTIVITY OF *SEIURUS* RECORDED NEAR ITHACA, NEW YORK, DURING THIS STUDY

Each dash represents a flight or pursuit song; below the totals are the numbers of flight songs heard per month. Ovenbird flight songs were recorded while in Northern Waterthrush habitat and would probably have been recorded more frequently had I been concentrating my efforts on the Ovenbird.

Time	motacilla*	noveboracensis	aurocapillus
0600			
0630			
0700	—		
0730			
0800			
0830			
0900			
0930			
1000	—		
1030	—		
1100			
1130			
1200			
1230			
1300			
1330		—	
1400			
1430	—	—	
1500		— —	
1530		— —	—
1600			
1630		—	
1700		—	
1730		— —	
1800	—	—	
1830			
1900		—	
1930		—	
2000	— —	— — —	— — — —
2030		— — — — — — — — — —	
		— — — — — — — — — —	— — — — — — —
2100		— — — — — — — — — —	—
2130			— — —
2200			
Totals	7	47	16
April	2		
May	5	25	10
June		22	2
July			4

* pursuit songs

from one end of the territory to the other they usually fly between the slopes of the glen where there is a break in the trees. Before the deciduous trees have leafed out in April the birds, when disturbed, will usually seek cover in the hemlocks. Early in the season the waterthrushes feed entirely in the stream. Here they can be seen flipping leaves and picking up the disturbed animals beneath, poking their bills into crannies at the edge of the falls or

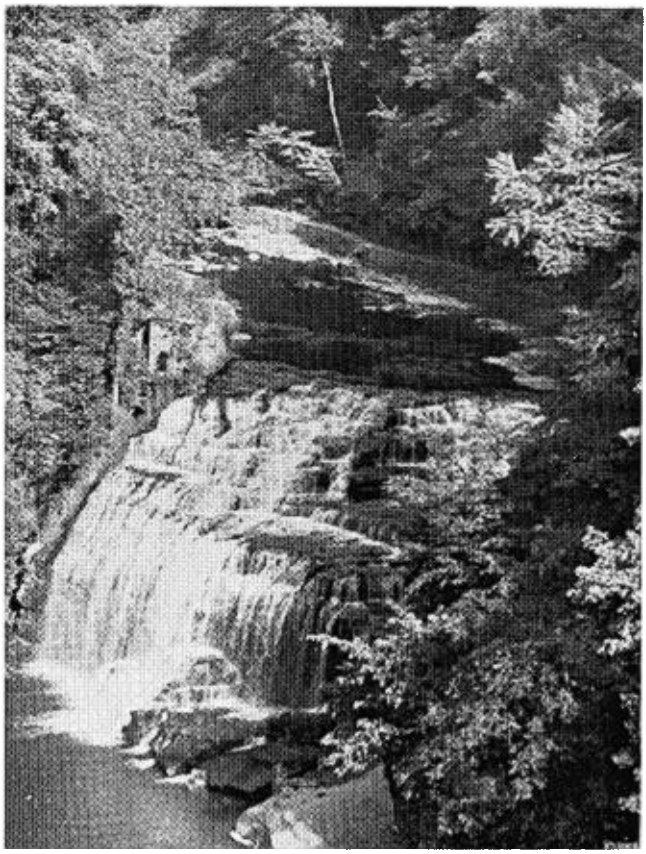

FIG. 2. Fall Creek Gorge near Ithaca, New York, a short distance south of Glen No. 1. This glen is much larger than those in the study area.

picking things directly out of the water from a wading approach. Most often they are observed feeding upstream. Later in the season feeding is less restricted to the stream. Often birds will be seen to jump from the floor of the glen and capture insects on the wing, then return to a flat rock along the stream. The birds appear most at ease on the bare, flat rocks of the glen floors where they run in rapid sprints with tail up and head down.

From the start of incubation until the young are fledged the female roosts in the nest at night. Where the male and female roost at other times was not learned, but near dark on several occasions I saw them fly into hemlocks. A young Louisiana Waterthrush which was kept in captivity for a month always picked a site near the ceiling of the room (2 to 3 meters from the floor).

Nests

In five instances where nest construction was observed both male and female took active parts, but the female was more consistent in her work. Building was watched at various times between the hours of 6:00 and 10:30 a.m. On April 28, 1948, building was observed in Glen No. 8 from 7:25 to 8:43 a.m. At this stage of construction grasses and moss sporophytes were being added and molded into the nest bowl. Nest material was collected within 30 meters of the nest by both members of the pair. During this period of observation the female brought 17 loads and the male 11. Both birds were observed molding the nest material into the bowl, but the female was more thorough in this regard. The bringing of fewer loads by the male does not indicate less activity on his part, for during this time he chased a third waterthrush out of the glen, and also a female Brown-headed Cowbird (*Molothrus ater*) which was watching construction approximately 25 meters from the nest.

On April 26, 1948, nest construction was observed for half an hour near the start of construction. Both birds were dragging wet, muddy leaves into a depression of the bank. Here again the female did much of the work, but the male helped substantially.

Thirteen nests in the Ithaca region were situated on the south sides of ravines, from 0.5 to 4.0 meters above the glen floor. Only three nests were located on the north sides of ravines, and two of these were probably built by the same pair in two successive years. The glen, at the point these nests were located, made an "S" curve and actually ran north and south so that in a restrictive sense the nests were on the east-facing slope of the ravine. In most cases the nests were placed under roots and humus overhanging the banks of the streams, but in two instances they were on small ledges of shale which jutted out from a perpendicular wall.

Nest construction starts with the digging of a shallow cup in the dirt of the bank. Then both partners start hauling in leaves obtained from the surface of the water or from land adjacent to the nest. The cup formed in the bank is filled with these leaves and a few are left in front to form a pathway to the nest (Fig. 3). The number of leaves lining the cup varies considerably, as does the length of the pathway. One nest had leaves arched above

the bowl, and when taken from its location in the bank it looked superficially like the nest of an Ovenbird. The leaves, which constitute the greatest bulk

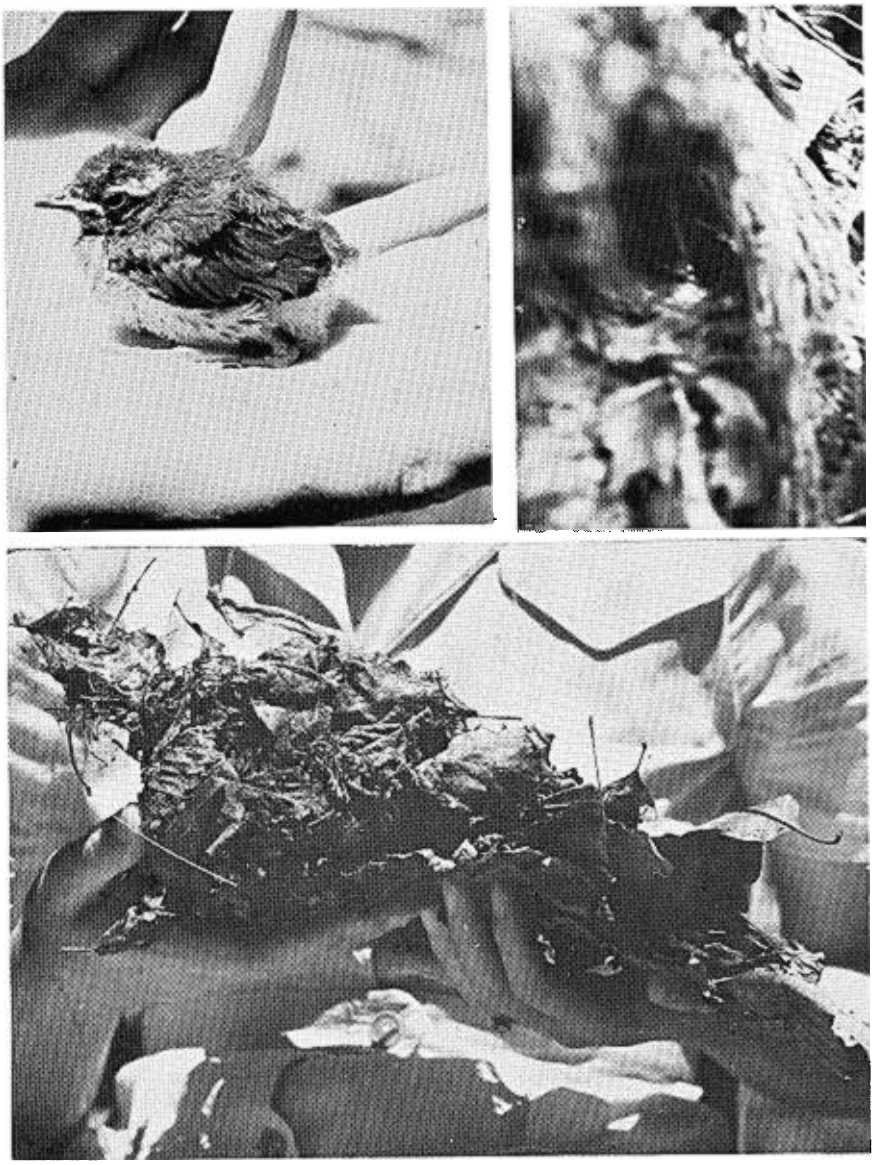

FIG. 3. *Upper left*, Louisiana Waterthrush nestling 10 days old; *upper right*, female incubating with head pointed out entrance. *Below*, side view of nest with pathway on the right and the body of the nest to the left.

of the nest, are continuously molded about the cavity that they fill. In six nests studied carefully, leaves of *Quercus borealis*, *Q. montana*, *Q. alba*, *Ulmus americana*, *U. rubra*, *Acer spicatum* and *A. nigrum* were used. Next, plant stems, pine needles or small hemlock twigs are added to form the outside of the nest bowl. Inside linings are made of small rootlets, small plant stems, horsehair, grass culms or moss sporophytes. One nest about 10 meters away from a discarded chair was lined exclusively with horsehair. Nest sizes are shown in Table 2.

Most first nests were built in the first week of May, but if the first nest was destroyed a second attempt was made. The species is, like the majority of warblers, single-brooded. In 1949 the pair in Glen No. 6 began renesting just one or two days after deserting the first. (I found the second nest with six eggs hatching 18 days after the desertion of the first.) Most nests, except for the lining, are completed in one or two days. The lining is added over a period of two or three days until the first egg is laid.

TABLE 2

MEASUREMENTS OF SIX NESTS COLLECTED AFTER THE NESTING SEASON

	Inside diameter	Depth of bowl	Over-all width	Over-all depth	Length of pathway
	7.5 cm.	4.0 cm.	18.0 cm.	13.0 cm.	15.0 cm.
	7.5	5.0	13.0	7.5	8.0
	7.5	5.0	13.0	9.0	12.0
	7.5	5.0	14.0	8.5	13.0
	7.5	5.0	15.0	7.0	16.0
	7.5	5.0	16.0	9.0	14.0
Average	7.5	4.83	14.8	9.0	13.0

COPULATION

Copulation was seen twice on May 1, 1948, in Glen No. 1. At 10:45 a.m. a female was seen sunning, occasionally preening and scratching her head. At 11:08 she began feeding. At 11:15 she hopped up on a fallen log adjacent to the stream. A male suddenly appeared, chipping loudly. The female crouched on the log and the male mounted with wings vibrating, only partially opened. After two seconds the male flew a few feet away to a shrub, sang once and went back to copulate again. After this action the male flew across the stream. The female sat quietly for a few minutes, then walked up the bank a short distance and started to preen again. At 11:25 she started feeding in the stream again. Five minutes later she started alternately sunning and preening until about 12:00 when she started feeding again. The male

returned about 12:30 p.m. and they flew off together. Two days later I found the nest of this pair approximately 20 meters upstream from the site of copulation; it contained one waterthrush egg and three Cowbird eggs.

Eggs

Brown-headed Cowbirds made the study of clutch size difficult because they apparently removed waterthrush eggs. Only five undisturbed nests were studied: one held 5 eggs and four held 6 eggs, for an average clutch size of 5.8 eggs (Table 3). The nest with 5 eggs was in Glen No. 1. This

TABLE 3

SUMMARY OF DATA ON NESTS OF THE LOUISIANA WATERTHRUSH

Year	Location[1]	Eggs		Young fledged	
		Waterthrush	Cowbird	Waterthrush	Cowbird
1947	8	6	0	6	0
	Cascadilla	?	(1)[2]	0	(1)[3]
1948	1	(1)	3	0	2
	4	(4)	1	1	1
	5	1	0	0	0
	6	6	0	0	0
	6 (2nd nest)	5	2	3	2
	8	(3)	3	0	0
	9	(3)	0	3	0
	10a	(5)	1	4	1
	10b	(4)	1	4	1
	Coy Glen	6	0	6	0
1949	1	5	0	5	0
	4	(2)	4	1	3
	10a	(3)	2	3	2
	10b	6	0	6	0
Totals	16	60	18	42	12

[1] Numbers refer to glens or glen-pairs, and names to those glens outside the study area.
[2] Number of eggs actually laid is unknown.
[3] Successful fledging of young is doubtful.

clutch was completed on May 29, 1949, about three weeks later than the normal first nest. In this case the male was first noted on May 13 and the nest was completed except for the lining on May 23. I believe the male in Glen No. 1 the previous year was killed by a car, because an adult male was found dead by Dr. Brina Kessel Roof not more than 50 meters from the nest. Both parents nesting in Glen No. 1 in 1949 lacked white tipping on the tail, so it was assumed that they were first-year birds which had replaced the pair of 1948 (Table 3).

Near Branchport, New York, on May 17, 1905, C. F. Stone (Unpublished

notes) found four nests in one afternoon and evening. Each of three nests contained 6 Louisiana Waterthrush eggs and one nest contained 3 Louisiana Waterthrush eggs and 1 Cowbird egg.

From these data it appears that 6 eggs is the normal first clutch of undisturbed nests in the central New York region. Chapman (1907:229) said that, in a carefully selected series of 45 sets, four were of 6 eggs, 35 of 5 eggs and six of 4 eggs. The average clutch size of the population in the Finger Lakes region, then, is higher than that reported by Chapman. This may be due to a response to compensate for excessive parasitism by the Cowbird or to the fact that this population is at the northern extremity of the species' range. *Seiurus noveboracensis* in the Ithaca area (Eaton, 1957*b*) was found to have a clutch size of 4.2 eggs (based on nine clutches). There that species is at the southern extremity of its range and is nearly free of parasitism by the Cowbird.

Incubation

In all cases incubation was done by the female, and she began the day before the last egg was laid. I never collected a male which showed signs of an incubation patch.

Like most ground-nesting birds the female Louisiana Waterthrush is a close sitter, sometimes even allowing one to touch her on the back before she drops to the stream bed with wings and tail spread and feathers of the back elevated. All females observed incubating kept their heads pointed directly out of the nest opening and their tails pointed up at the rear of the nest (Fig. 3). Whenever I approached a nest and moved my head from side to side, a few inches from the female's head, she would slowly turn her head, keeping her bill pointed at the nearest part of my face. Sometimes I could get one to swing her head as much as 60 degrees. This may indicate the species possesses binocular vision rather close to the tip of its bill, an aid in stream-side feeding.

Individual birds varied in amount of injury-feigning shown after leaving the nest. Some left the nest by dropping to the flat rocks and then walked off a short way like a mouse with back slightly hunched, but most birds half-spread the wings and tail and walked down the shallow stream without uttering a sound. When the water level was high, as after a rain, the birds sometimes walked in this manner right up the sides of the steep slopes. One bird observed spread only one wing, but the rest spread both. As incubation progressed there appeared to be an increase in intensity of this behavior.

When approaching the nest during incubation the female flies to a point about 10 meters upstream or downstream from the nest, then walks to a point directly below. From this point she hops either directly to the pathway

leading to the nest or to a point nearby from which she walks to the nest. The "take-off" to the nest from the glen floor is usually made from the same spot each time.

Accurate information on length of incubation (last egg laid to hatching of last egg) was obtained at six nests. Eggs were marked as soon as possible after laying. In four clutches they hatched in 12 days; in one, 13 days; in another, 14 days. The 14-day incubation length was obtained from a nest containing one Louisiana Waterthrush egg and 3 Cowbird eggs (which hatched in 13 days). The young hatch over a 24-hour period, the last egg laid being the last to hatch.

While the female is incubating the male becomes inconspicuous. Sometimes he sings, but never as loudly or as often as before the female arrived. Only once did I see a male feed an incubating female, and this was when the eggs were due to hatch in 24 hours. Chapman (1907:229) quotes a similar observation by Verdi Burtch, "May 21, 1899, I saw a male feeding a female which was sitting on five eggs two of which were hatching." Skutch (1954:383) interprets similar behavior in Central and North American parulids as anticipatory feeding of the young rather than true nuptial feeding. This interpretation seems to contradict the "releaser" concept as described by Tinbergen (1951).

The Nestlings

After the eggs hatched the female ate the egg shells, usually at the nest. Once a young Cowbird kicked out the shell of a recently hatched waterthrush egg so that it was about six inches from the nest. When the female returned she fed the young in the nest, then picked up the egg shell in her bill, dropped to the stream below the nest and proceeded to eat the shell. She first crushed it with her bill and then ate it in two portions.

When young hatch, their dark grey (almost black) down stays wet for a few hours, and the skin appears much redder than when a day older. The average weight of seven nestlings at hatching was 2.2 grams. One egg just before hatching weighed 2.5 grams. Young hatch with natal down about 10 mm. long in tufts just dorsal to the orbits, in the occipital region, and on the dorsal, humeral, alar and femoral tracts. Down was always absent on the ventral tracts. Soon after hatching the young could raise their heads and gape. Both parents started feeding the young small insects which they brought held cross-wise in the bill. If the female was brooding, the male usually gave the food to her and she rose and fed the young. Both parents ate the feces of the young for the first three days after hatching. On the fourth day the fecal sacs were well formed and were usually dropped in the

stream below the nest before the birds flew to their food-collecting areas. Occasionally, however, they carried them to the food-collecting area.

Rates of Feeding Young.—On June 7, 1948, a nest containing two young Cowbirds and five Louisiana Waterthrushes (two of which hatched during the period of observation) was watched between 10:10 a.m. and 12:45 p.m. In this 2½-hour period the young were fed 11 times. The female fed the young 6 times, the male fed them 3 times, and twice the male fed the brooding female which then fed the young. On June 9, 1948, the same nest was observed from 12:35 p.m. to 1:35 p.m., and during this time both parents fed the young a grand total of 10 times. On June 12, 1949, a nest in Glen No. 1 was observed from 4:40 to 6:17 p.m. It held five two-day-old waterthrushes. During the observation period the young were fed 19 times (both parents involved). On June 17, 1948, a nest in Glen No. 10 contained four young waterthrushes, about eight days old, and one young Cowbird. From 11:25 a.m. to 12:25 p.m. the female fed 10 times and the male 9 times.

The following observations were based on 13 nestlings in three different nests, except for those 10 days old.

One day old—Average weight 4.1 grams. Feathers of all tracts but the caudal visible beneath the cuticle.

Two days old—Average weight 6.4 grams. Sheaths of primaries protruded about 5 mm. from the epidermis. Young capable of righting themselves by using the head, wings and feet. Papillae of rectrices did not protrude.

Three days old—Average weight 8.5 grams. Eyes obviously opened at this time. Sheaths of the primaries protruded about 6 mm. Rectrices started to protrude and young seemed stronger and more lively.

Four days old—Average weight 10.6 grams. Primaries entirely sheathed and about 12 mm. long. Sheathed feathers of the alula stood out prominently, about 6.5 mm. in length. Their legs were stronger, but the young birds still were unable to sit up.

Five days old—Average weight 13.3 grams. Contour feathers of all tracts starting to break through their sheaths.

Six days old—Average weight 15.7 grams. Eyes more protruded. Longest primary about 25 mm. Young not yet capable of sitting up on their tarsometatarsi.

Seven days old—Average weight 16.9 grams. Young could now sit up on tarsometatarsi.

Eight days old—Average weight 16.9 grams. Eyes more protruded. Longest primary averaged 26.0 mm. but still entirely sheathed. Tail wiggled continuously, apparently with the rhythm of respiration.

Nine days old—Average weight 17.1 grams. Young just beginning to stand on their toes. Primaries unsheathed for about 14.0 mm. A small amount of natal down left on juvenal feathers, mostly on capital tract. Young occasionally stood up in nest to preen. Some young, if too disturbed, left nest on ninth day.

Ten days old—Too few weights for an average but one bird still in the nest weighed 17.1 grams. At five nests where birds were not unduly disturbed and age was known, young left on the tenth day. At this time the parents became greatly excited and bold. When young left the nest they flew a short way and the parents lured them toward the shelter of shrubbery above the stream.

The Fledglings

For two or three days after leaving the nest the young did not travel far. They were usually found perched in the shrubbery up on the talus slopes. Sometimes they surmounted the crest of the ravine and were found in the oak forest, but this was exceptional. Adults at this time collected food along the stream and flew from there up to the young. In two days the young could fly about 15 meters in sustained flight. When on the ground they walked and moved their caudal region up and down continuously. Once when I startled a young bird it "froze." Soon it became used to my presence and started tail-wagging. If I moved or made a noise it stopped wagging its tail and looked intently in my direction. The *fourth day* out of the nest the young started preening more often, could fly and perch more skillfully, and the rectrices showed about 2 mm. beyond the upper and lower juvenal coverts. After dozing on a perch they stretched by extending both legs to their full length.

On the *fifth day* out of the nest a bird I kept in captivity (called Louie, sex unknown) voluntarily took its first bath. Its rectrices were about 5 mm. longer than surrounding juvenal feathers. The *sixth day* Louie first scratched its head. Louie flew in the characteristic "bounding" flight of the species, similar to that of the Common Goldfinch (*Spinus tristis*). On the *seventh day* out of the nest the primaries exceeded the secondaries by about 10 mm. Louie was taught by Dr. Ernest P. Edwards and Margery Cummings to catch flies which collected at windows. While perched on one's finger it would reach up and dexterously grab the fly in its bill, hold it a few seconds to kill it and then bolt it down. If led to its feeding tray, which was filled with *Chironomus* larvae, it would pick up its own food. Before this time it would not feed itself, but would eagerly devour food stuffed in its mouth with a pair of forceps. The *eighth day* Louie stood on one foot for the first time, and at night was seen roosting with its bill tucked under its scapulars. The *ninth day* Louie followed people around the room and begged for food. At a similar age young waterthrushes in the field were first seen following the adults on their food-searching missions. On the *eleventh day* Louie started feeding more on its own, but would gladly accept food from anyone.

On the *thirteenth day* Louie's tail was about 40 mm. long and all rectrices were coming in simultaneously. The first-winter feathers were first noted as pin feathers on the crural tract. It started to preen and bathe more frequently. Louie's wing (chord measurement) was 75 mm. long. On the *fifteenth day* out of the nest Louie showed first-winter feathers on the outside of the ventral tracts under the bend of the wing. On the *22nd day* Louie was first noted to pull at leaves and flip them over. On the *27th day* Louie was almost indistinguishable from an adult. Its bill measured 10.0 mm.; wing 80.0 mm.; tail 56.0 mm. and tarsus 24.0 mm. The only feathers lacking to complete the first winter plumage were the upper and lower tail coverts and the major coverts. All juvenal major coverts were lost on this day. Louie was released in a local glen and was watched for about half an hour. It immediately started feeding along the stream and seemed in a healthy state.

The sequence of events described above agreed well with observations on color-banded young in the field. The brood from nest No. 10*b* in 1948 was observed from June 18 to July 9 at frequent intervals. For the first 10 days

one parent with two of the four young from this nest could be found within 70 meters of the nest adjacent to the stream. One of these young was last seen being fed by an adult about 100 meters downstream in the same glen on July 9. What I assumed was the other parent was seen feeding one of these four young (color-banded) in Glen No. 7 on July 8 and 9 about 1 kilometer from the nest site. This was about a week before the young had reached the independent stage.

A month after leaving the nest the young birds started to wander unattended by adults. One bird, banded in Glen No. 6 just before leaving the nest on June 12, was seen 4.8 kilometers north on July 19. It remained in this glen for 4 days. Another bird banded as a nestling in Glen No. 9 on June 9, was seen in Glen No. 1 on July 14, 2.0 kilometers from the nest site.

By the middle of July many of the small streams in the area dry up and considerably restrict available feeding habitat. Birds were seen feeding along the lake shore or the woods adjacent to the streams. The greatest concentration of Louisiana Waterthrushes (exclusive of family groups) I have observed anywhere was seven individuals along 100 meters of stream in Chironomus Glen on July 23, 1948. These were independent young and molting adults, and were attracted there by the abundant blood worms (*Chironomus*). Drainage from a large dairy farm caused this unusual concentration of worms and, consequently, of the waterthrushes.

Food

Food of Nestlings.—Two young killed by an unknown predator in a nest in Glen No. 4 on June 4, 1948, contained the following food items in their stomachs (per cent by bulk): one stomach contained 5 per cent gastropods, 5 per cent Coleoptera adults, 5 per cent grit and 85 per cent undetermined insect fragments; the other contained 10 per cent Coleoptera adults, 5 per cent grit and 85 per cent undetermined insect fragments. A Brown-headed Cowbird found dead in a Louisiana Waterthrush nest on July 16, 1947, had in its stomach: 28 per cent Diptera larvae (15 per cent Stratiomyiidae, 3 per cent Tipulidae and 10 per cent unidentified), 10 per cent Diplopoda, 2 per cent Geometridae larvae, 2 per cent Plecoptera, 1 per cent *Asellus*, 2 per cent spiders, 2 per cent Membracidae, 1 per cent Tricoptera, 2 per cent grit and 50 per cent unidentified.

Food of adults in New York.—The stomachs of 15 adults were examined (Table 4). These were collected near Ithaca, April through August, 1947–49. The high per cent of occurrence of chironomid larvae was due in part to the fact that nine birds were collected in Chironomus Glen where this food is abundant. Besides dipterid larvae the principal food (as ascertained from the stomachs) was coleopterid adults. Although Plecoptera and Ephemerida

were identified in only one stomach these insects were a favorite food item —particularly during April and May. Often after a "hatch" of these aquatic insects waterthrushes were seen feeding on slow-flying stonefly and mayfly sub-imagos and adults. They take many nymphs too, but at restricted times, i.e. a day or two before a species is due to emerge. Adults also were seen to capture and eat earthworms.

Food of Adults in Winter and on Migration.—The food of this bird in Cuba differs markedly from that eaten in New York. In the stomachs of four out of eight birds I collected near Soledad small amphibian bones were present. These were probably small frogs (*Eleutherodactylus* sp.) which were common along the fresh water streams. Crustaceans (probably crayfish), weevils, small aquatic snails and small aquatic beetles were also eaten. Grit was present in seven of the eight stomachs examined.

TABLE 4

FOOD ITEMS FROM 15 ADULT LOUISIANA WATERTHRUSHES TAKEN NEAR ITHACA, APRIL THROUGH AUGUST

	Average per cent by bulk	Per cent occurrence
Diptera		
Stratiomyiidae	44.0	13.3
Tipulidae	5.0	20.0
Chironomidae	40.0	73.5
Hemiptera	5.0	6.7
Tricoptera	42.0	13.3
Coleoptera adults (undeter.)	12.6	30.0
Hydrophilidae	25.0	20.0
Elateridae	3.5	13.3
Rhynchophora	2.0	6.7
Neuroptera (*Sialis infumata*)	35.0	6.7
Plecoptera	40.0	6.7
Ephemerida	45.0	6.7
Diplopoda	20.0	6.7
Grit	6.0	54.0
Undetermined fragments (mostly insects)	58.5	94.0

Wetmore (1919) reported finding the following items in the stomachs of five specimens collected in Porto Rico: water beetles (Parnidae), leaf beetles, flies, treehopper, spider remains, bits of scorpions, snails, *Eleutherodactylus* and seeds.

Hix (1916) watched a bird in Central Park, New York City, which caught a fish about 1½ inches long. This bird picked off the flesh with its bill. Howell (1932) found the following items in four stomachs of birds collected

in Florida: dragon flies, crane-fly larvae, grouse locusts, beetles, bugs, ants, caterpillars and scale insects. Two of the birds had eaten small mollusks, and one had eaten a killifish (*Fundulus*).

Parasitism by the Brown-headed Cowbird

Nine of 16 nests (56 per cent) in the Ithaca region were parasitized by the cowbird. These nests contained from one to four cowbird eggs, with a total of 18 eggs (Table 3). Twelve young cowbirds were raised to leave the nine nests. One young was killed by human interference, one young died in the nest (cause unknown), three eggs were deserted (after the female waterthrush was killed), and one egg failed to hatch.

If we assume that the average clutch size of Louisiana Waterthrushes is 5.8 (see page 223), the waterthrushes should have laid 93 eggs in 16 nests. The actual number incubated, however, was only 60 waterthrush eggs. If these assumptions are correct, the cowbirds probably dumped one third of the total from the nests and substituted only 18 of their own. This habit of egg removal by the cowbird is not its only bad one. On one occasion a young cowbird apparently killed three or four young waterthrushes at about the time they would have left the nest. In three other cases young waterthrushes were found below the nest apparently jostled there by their larger (cowbird) nestmates. One of these waterthrushes was six days old when pushed out. When I inspected this nest on June 13, 1948, I found the young bird about six inches below the nest. At first it appeared to be dead, but when I picked it up it moved its limbs slightly. It was cold to the touch and weighed about 4 grams less than the two waterthrushes in the nest. After about a half hour in my hand, it started to revive and soon was begging for food. I returned the young to the nest and in two days it weighed almost as much and appeared as healthy as the other young.

Fat Deposition

Wayne (1910) said that *Seiurus motacilla* is always exceedingly fat in July and August, but lean in the spring (in South Carolina). Christy (1897) wrote that an adult female which he shot near La Vega, San Domingo, on April 19 was so extraordinarily fat that he had the utmost difficulty in preparing it. Near Gulfport, Mississippi, on October 29 Burleigh (1944) shot a bird which was very fat and apparently normal in every respect. Paul S. Martin (pers. comm.) said he shot a female near Gomez Farias, Tamaulipas, Mexico, in April, 1948, which was "little fat."

The birds which I collected during this study were classified as to amount of fat deposition (Table 5) by the system suggested by McCabe (1943).

From these data it appears that birds start fat deposition in late July and

TABLE 5

FAT CONDITION OF LOUISIANA WATERTHRUSHES COLLECTED IN NEW YORK (APRIL–AUGUST) AND CUBA (DECEMBER–JANUARY)

	New York					Cuba
	April	May	June	July	August	Dec.–Jan.
no fat	1		3			1
little fat				6	3	4
moderate fat					1	2

August, following the molt, and during migration are sometimes found in an extremely fat condition. When birds arrive on their nesting grounds they have lost this fat. Birds collected in Cuba in winter showed only a little more fat than they did on their breeding grounds; however, none was collected in winter with a classification greater than "moderate fat."

WEIGHT

Weights of 22 individuals collected near Ithaca, New York, and six near Soledad, Cuba, show some seasonal variation, correlated with fat deposition and the reproductive cycle (Fig. 4). Although my sample is meager when broken down by sex and month I feel it worth presenting.

MOLT

Post-juvenal molt—This molt involves the contour feathers, the upper and lower tail coverts and the major wing coverts. One from a total of 10 Louisiana Waterthrushes that I collected during the progress of this molt showed evidence of renewal of tail feathers. This bird had one white-tipped tail feather on one side which was one half the length of the others. Similar

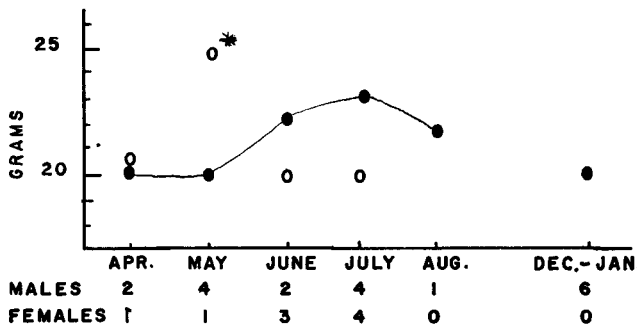

FIG. 4. Weights of adult Louisiana Waterthrushes collected near Ithaca, New York (April–August) and Soledad, Cuba (December–January). * female with egg in oviduct; ● male weights; O female weights.

partial replacement of tail feathers in *Seiurus noveboracensis* was noted by Eaton (1957*a*:234). Stewart (1952) in a careful study of this molt in the Yellowthroat (*Geothlypis trichas*) proved this species to have a complete post-juvenal molt. Dwight (1900:282) thought the Yellow-breasted Chat (*Icteria virens*) the only warbler to have a complete post-juvenal molt. Additional selective collecting during the progress of this molt may reveal a greater number of warblers replacing wing and tail feathers as well as contour feathers, especially among ground- and shrub-frequenting species.

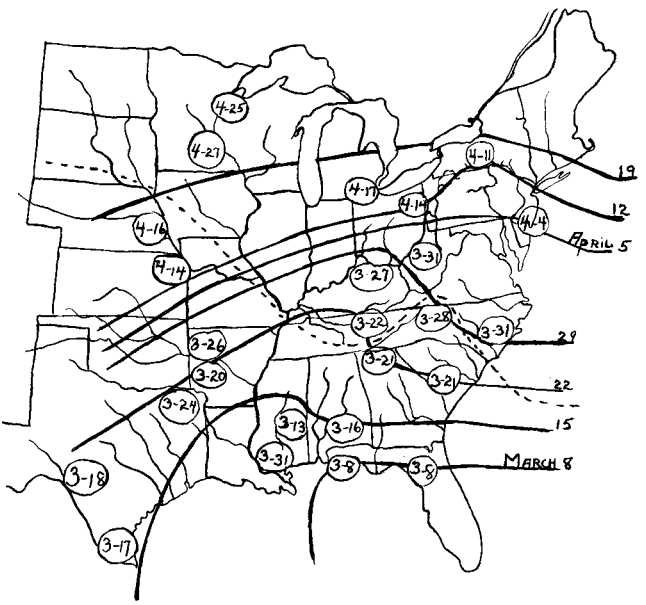

FIG. 5. Map showing average first arrival dates for the Louisiana Waterthrush in the United States. Dates above dotted line are average dates for more than five years of observation; dates below dotted line fewer than five years. Data are from the U.S. Fish and Wildlife files.

Post-nuptial molt—First evidence of this molt was obtained on July 9, 1948. A female collected near Ithaca was replacing the inner two primaries of each wing. All adults collected later in July were in a later stage of molt. The completion of this molt in the males is often heralded by a recrudescence of song in early August. The Northern Waterthrush (Eaton, 1957*b*) started its molt in the Ithaca region as early as June 9.

ECTOPARASITES

Peters (1933) lists a tick, *Haemophyalis leporis-palustris*, taken from a Louisiana Waterthrush at Packard, South Carolina. Dr. Elizabeth M. Boyd kindly identified feather

mites which were on all Louisiana Waterthrushes I collected (on primaries 4 and 5). These were *Pterodectes bilobatus* and were also found on *S. noveboracensis* and *S. aurocapillus* (Eaton, 1957*b*). K. C. Emerson identified Mallophaga which I collected from a few specimens as *Bruelia* sp.

Summary and Discussion

It is of interest to compare the essential differences in breeding biology of the Ovenbird in Michigan (so ably described by Hann) and the Louisiana Waterthrush. Below is a summary of the important dissimilarities brought out by these studies.

	Ovenbird	Louisiana Waterthrush
Flight song	frequent	rare
Singing after pair formation	often	seldom
Territory	rectangular, 0.2–1.8 ha.	400 meters long, following stream
Nest location	under litter of broad leaves	over foundation of broad leaves
Nest constructed	by female	by male and female
Female's position during incubation	flank toward entrance	head faces out entrance
Young first capable balancing on "tarsus"	4 days	7 days
Young at 8 days	primaries 20 mm. long, over half unsheathed	primaries 26 mm. long, still completely sheathed
Young leave nest	at 8 days	at 10 days
Males sing after post-nuptial molt	seldom	often
Nesting Success	43.5 per cent of 161 eggs fledged	70 per cent of 60 eggs fledged
First arrives Gulf coast (U.S. Fish and Wildlife files)	April 5	March 8
First arrives in Michigan and New York	April 29	April 11
Dates of first eggs	May 23–July 2	April 30–May 26
First arrives Central America (Skutch, *in* Bent, 1953)	first week October	late August

Most of these differences can be explained as adaptations for the successful rearing of young in the specific nesting habitat and the utilization of unlike food sources.

Dissimilarities in territory shape may account for the greater attentiveness of the male Louisiana Waterthrush to the female following pair-formation. At this time there is a marked suppression of song in the Louisiana Waterthrush; and the male Louisiana Waterthrush aids substantially in nest building, whereas the male Ovenbird does not. Perhaps the fact that Ovenbird territories are usually surrounded by as many as 4 neighboring males requires

that the male expend more energy in singing to maintain the territory. The Louisiana Waterthrush territory follows the course of a stream so that normally one male must maintain his territory at 2 ends (or against 2 males instead of 4). Territory shape may also have something to do with the near absence of the flight song in the Louisiana Waterthrush. Visual contact of the female by the male following pair-formation seems to be more important here than vocal contact. Nest building by the male and tail-wagging may be added evidence for the importance of this visual contact.

The Buff-rumped Warbler (*Basileuterus fulvicauda*) of Central and South America inhabits the fast flowing stream-sides of montane forests. This warbler belongs to a wide-ranging, flycatching genus of tropical parulids which are mainly arboreal. This species, however, feeds along the stream margin, wags its tail, has a loud voice and both male and female build the nest (Skutch 1954:346–356). These characteristics, which it shares with *Seiurus motacilla*, are examples of convergence—the stream-side habitat being the selective agent.

The nest of the Ovenbird is beautifully concealed on the open floor of the forest by a roof, whereas the Louisiana Waterthrush utilizes overhanging rock ledges or humus and builds a substantial floor of broad leaves for a foundation and pathway to the nest.

The Ovenbird sits sideways to the entrance during incubation perhaps either to conceal the orange crown patch, as suggested by Hann, or because it may have keener monocular vision in this position. The Louisiana Waterthrush female faces directly out the opening and appears to utilize binocular vision while incubating. The white markings above and below the eye and the superciliary stripe help camouflage her in this position.

Incubation lengths did not appear to be different in the two species. Kendeigh's (1952) summary indicates 12 days as an average incubation length in North Temperate wood warblers. Skutch (1954) has discovered that some tropical parulids may incubate up to 17 days.

Ovenbird young leave the nest in eight days whereas the Louisiana Waterthrush left in 10. Nice (1943) suggests such differences are correlated with amount of predation on the nestlings, which view is supported here by the higher percentage of 60 Louisiana Waterthrush eggs successfully fledged.

Motor coordination in the hind limb appears to develop more rapidly in the Ovenbird as Hann's young Ovenbirds could sit up on the "tarsus" in four days and my waterthrushes could not do this until the seventh day. The primaries became unsheathed earlier in the Ovenbird (eighth day or earlier) and not until the ninth day in the Louisiana Waterthrush. However, the latter appears to be able to fly at an earlier age. Motor coordination in the forelimb appears to develop earlier in the Louisiana Waterthrush.

The Louisiana Waterthrush initiates the reproductive phase of its life history about one month earlier than the Ovenbird (Fig. 5). This timing is maintained through nesting, the molt and the return to Central America. This month's difference is certainly now a hereditary one and probably timed to exploit two quite different food sources at the critical time of feeding young in the nest and during the post-juvenal molt. Stone flies, mayflies and other aquatic insects reach a peak of emergence at this latitude about the last week in May and the first week in June. The Louisiana Waterthrush exploits this source. The Ovenbird, along with many other species of the mature broad-leaved forests, exploits the lepidopterid larvae abundant from late June to early August.

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