

A STUDY OF NESTING ANT-TANAGERS IN BRITISH HONDURAS

By EDWIN WILLIS

From the middle of February to early in August, 1957, I studied Red-crowned and Red-throated ant-tanagers (*Habia rubica* and *Habia gutturalis*) at Gallon Jug, British Honduras. Earlier articles have described voice and courtship behavior (Willis, 1960a) and foraging habits (Willis, 1960b and 1960c). Here nesting will be considered.

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BREEDING SEASON

About a dozen closely-observed pairs of ant-tanagers began nesting in late March in the dry season and continued through June and July, the first and wettest months of the rainy season. The distribution of 22 nests of Red-crowns according to the quarter-month when a clutch was completed was: April—1, 2, 2, 1; May—1, 1, 2, 0; June—2, 1, 1, 2; and July—2, 3, 1, 0. The distribution for nests of Red-throats was: May—2, 1, 3, 3; June—5, 5, 2, 3; and July—2, 1, 1, 0. During the last half of July, I stopped searching for nests, so that ant-tanagers may have nested more commonly at that time than my records indicate. Other ornithologists have reported nests of ant-tanagers elsewhere in Central America as early as late March and as late as August. Since ant-tanagers utter dawn songs mainly while nesting, dates of breeding can be approximately determined by listening for such songs.

SEARCHES FOR NEST SITES

On eight occasions I saw pairs of Red-crowns that were looking for nest sites. The female did the most active searching. Chattering frequently, she sat in one crotch after another in saplings or forks of limbs. At times the male flew to a limb near her and called; less often he spread his tail or wings as well. After the female chattered and flew away, he sat down at the same spot and pecked at the air in the same fashion as she had, seemingly moving strands of nesting material. He usually gave only faint *chook* notes and day songs except when investigating a site. Then he chattered as volubly as the female. On only one occasion, March 30, did a female carry fine strands to several sites as she searched.

LOCATION OF THE NEST

Generally nests of ant-tanagers were set against the stems of saplings on small branches or on the petioles of large leaves, although four nests of Red-crowns were on the forks of branchlets up to half a meter from the trunks. A few Red-crowns built above the crotches of saplings in such a way that the nests were supported only by vertical branches. But the loose and leafy nests of Red-throats were supported at the bottom by twigs, vines, or petioles.

Many nests (table 1) were in wild coffee (*Rinorea guatemalensis*), the most abundant sapling of the forest at Gallon Jug. Twigs of wild coffee commonly spread in whorls of six or so from the stem and provided excellent supports for nests. *Piper psilorhachis* or Spanish elder, the next most common sapling, and *Pouteria Meyeri* or fever grip, the

TABLE 1
SITES OF NESTS OF ANT-TANAGERS

Plant ¹	Number of nests of Red-crowns	Number of nests of Red-throats
<i>Rinorea guatemalensis</i>	7	17
<i>Piper psilorhachis</i>	5	1
<i>Pouteria Meyeri</i>	5	1
<i>Bactris mexicana</i>	0	3
<i>Cryosophila argentea</i>	0	2
<i>Cupania guatemalensis</i>	0	2
<i>Psychotria grandis</i>	2	0
<i>Bursera simaruba</i>	1	0
<i>Pseudolmedia</i> sp.	1	0
<i>Manilkara zapotilla</i>	1	0
<i>Chamaedorea concolor</i>	1	0
<i>Pouteria Durlandii</i>	0	1
<i>Ouratea Peckii</i>	0	1
<i>Aspidosperma megalocarpon</i>	0	1
<i>Terminalia</i> sp.	0	1
<i>Coccoloba</i> sp.	0	1
Unknowns 1, 2, 3	1	2

¹ Specimens from Gallon Jug were compared by the author with specimens in the United States National Herbarium.

third most common, were less often used by Red-throats than by Red-crowns. Spanish elder and fever grip branch sparsely and offer few places with both the bottom and the side supports necessary for nests of Red-throats. Palms were rarely used by Red-crowns; a nest in a *Chamaedorea concolor* eventually tilted and tumbled the young bird to the ground. Two nests of Red-throats were set in the most common palm of the undergrowth, the spiny give-and-take (*Cryosophila argentea*); one nest was placed atop two leaves. Three nests were in the wickedly spined *Bactris mexicana*, set on petioles and secured by the proximal two or three pairs of leaflets. The theory of Peck (1910) that the spininess of such palms discourages predators was not confirmed by the fate of these three nests, for all the eggs were stolen soon after they were laid.

Nests of Red-throats were generally lower than those of Red-crowns, in keeping with the lower foraging zone of the former species (Willis, 1960*b*). The highest nest of Red-crowns was 5.7 meters up, the highest nest of Red-throats only 3.7 meters up. The saplings used were from 1.4 to 7.0 meters high, and most of the nests were situated five- to nine-tenths of the way up. However, one nest of Red-throats in a *Bactris mexicana* was only about one-fourth of the way up the leafy cane.

Few nests were placed among crowded twigs and none in dense leaves, perhaps because the birds had some difficulty flying through thick growth and avoided dense tangles most of the time. Before one male Red-throat found a way in to his nestlings, he was turned away on two attempts by the barricade of twigs in which his mate had built the nest. However, shade and concealment were often provided by fallen dead leaves or attached green leaves a few centimeters above nests.

Ant-tanagers nearly always used sites with relatively clear views in one or more directions. Several nests were placed alongside paths or bulldozer trails. Possibly such advantages of exposed positions as the presence of better vantage points and of unobstructed routes for escape outweighed any disadvantage of greater conspicuousness.

The nests were usually in high forest. No nest of Red-crowns was in high second

growth, although some second growth was 15 meters in height and was used in foraging. One nest of Red-crowns, from which the eggs were soon stolen, was placed at the border of a small, recently-cleared cornfield; another was at the edge of low second growth. The latter site was used later in the season by a female Red-throat for her nest; neither nest was successful. Two out of 33 nests of Red-throats were in high second growth, and a third nest was about 10 meters out from the edge of the forest, in shrubby growth less than a year old. Set on a leaf of a sprout of *Coccoloba* sp., this nest was soon torn down by a predator.

The nests of each pair were built within the foraging area and territory of that pair. On a few occasions nests were built near each other. The fourth nest of one pair of Red-throats was built 30 meters northeast of the second nest of another pair while the female of the latter pair was incubating. Two pairs of Red-crowns had occupied nests 120 meters apart in July, whereas the two mates of one male had nests about the same distance apart in July. In May I watched a nest of Red-throats out the front of a blind and kept an eye on a nest of Red-crowns out the left side of the blind; the two nests were about 15 meters apart.

NEST MATERIALS

For birds so alike in appearance as are the species of ant-tanagers, the materials used by the two species (table 2) and the final appearance of their nests (fig. 1) were surprisingly different. The nests of Red-crowned Ant-Tanagers were neat, shallow cups made of slender epiphyte rootlets, rhizomorphs, and plant fibers, and they were so thin that the eggs were sometimes visible in silhouette from underneath. In contrast, nests of Red-throated Ant-Tanagers were loose cups constructed of leaves, vines, and other bulky

TABLE 2
MATERIALS USED IN NESTS OF ANT-TANAGERS

Species: Nest: Body or Lining: MATERIAL:	Red-throats								Red-crowns			
	1		2		3		4		5		6	
	B	L	B	L	B	L	B	L	B	L	B	L
COARSE												
Dead leaves	47	—	13	—	19	—	29	—	2	—	—	—
Palm fragments	9	1	39	—	39	—	33	2	—	—	—	—
Fern pinnae	3	—	—	—	—	—	—	—	—	—	—	—
Moss strip	—	—	—	—	—	1	1	—	—	—	—	—
Thin strips of bark*	9	—	13	3	—	—	1	1	—	—	—	—
Winged seed	—	—	1	—	—	—	—	—	—	—	—	—
Twiglets (2 mm. diam.)	4	—	2	—	—	—	—	—	8	—	1	1
Leaves or twiglets whitened by fungus	3	—	7	—	10	—	—	—	—	—	—	—
MEDIUM (0.5-1.5 mm. diam.)												
Stems of herbs	—	—	3	1	1	1	2	—	5	—	—	—
Vinelets, tendrils, and rootlets of epiphytes	38	—	42	—	27	9	19	5	139	—	165	2
FINE												
Fibers from stems of herbaceous plants	2	—	—	2	—	—	1	—	32	—	—	—
Rhizomorphs	—	61	—	59	—	38	—	37	19	80	14	50
Spider webs	+	—	+	—	+	—	+	—	+	—	+	—
Total of pieces:	115	62	120	65	96	49	86	45	205	80	180	53

Notes: * mostly fragments of bark from saplings of *Bursera simaruba*; + means that material was present, — that it was absent.

material. Such bulky nests resembled the piles of leaves and debris that collected in bushes here and there in the forests at Gallon Jug. Both species lined nests with rhizomorphs or "vegetable horsehairs," the fungal hyphae of *Marasmius*.

In external dimensions, 16 nests of Red-throats averaged 10.7 cm. (standard deviation [s.d.] 0.50 cm.) in width by 6.4 cm. in height (s.d.=1.33 cm.); 11 nests of Red-crowns averaged 9.2 (s.d.=0.26) by 5.5 (s.d.=0.32) cm. in width and height, respectively. The conspicuous white fungus-covered twigs and midribs of leaves (for a photograph of such "decorations" on the nests of other tropical species, see Sick, 1957) on nests of Red-throats, and the few pendent leaves on the nests of both species, often pro-

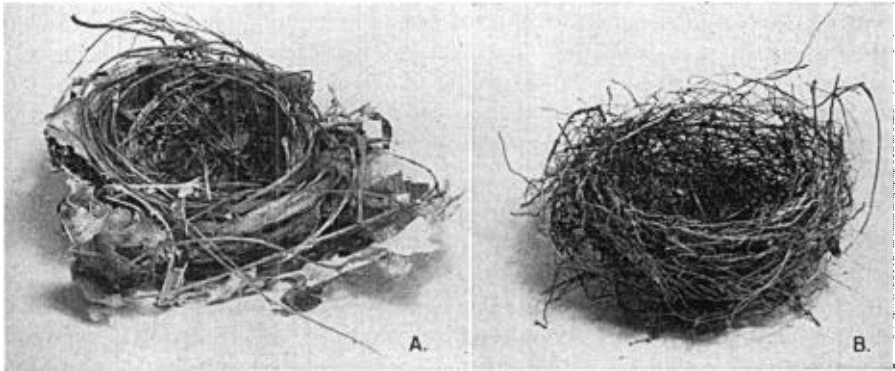


Fig. 1. Nests of ant-tanagers. A, Red-throated Ant-Tanager; B, Red-crowned Ant-Tanager.

jected beyond the nest itself. The inner cups of the same nests averaged 6.7 cm. across by 3.6 cm. deep for Red-throats and 6.1 by 3.0 cm. for Red-crowns. The respective standard deviations are: 0.25; 0.19; 0.18; and 0.19. Female Red-throats average slightly larger in size than female Red-crowns (Willis, 1960*b*), which may explain the larger size of the nest cup in Red-throats.

THE SEARCH FOR MATERIAL

Once I saw a male Red-crown sit briefly on a nest and move strands with his bill. On three other occasions he and another male carried fine strands toward their nests as they followed their mates, but both males dropped their material and darted off with their mates when the latter finished working on the nests. Male Red-throats were never seen to carry material.

Males of both species uttered day songs softly as they followed their busy mates to and from the nests. Occasionally a male inspected the nest before he followed his mate away. Although females searching for material were quiet and scarcely seemed to notice me, their mates were more noisy and evident than usual, and frequently the latter distracted my attention or gave loud notes that caused the females to dart behind the foliage. At other times males drifted off and females visited their nests alone.

The other birds of each family of ant-tanagers were generally less attentive than were adult males, although immature (or adult female) Red-throats often followed nest-building females. Such a group of Red-throats hurrying toward the nest through the undergrowth, the female trailing a long strip of a palm leaf from her bill and crooning a rapid series of faint notes as the male and others followed, was a rather amusing sight. At stops, where all looked around, the immature or immatures foraged briefly as the adult male uttered a few faint songs; then all darted off in the wake of the crooning

female. Immature Red-crowns were less active, and they followed the back-and-forth movements of pairs imprecisely. Female Red-crowns never uttered crooning notes at such times.

At least one nonbreeding bird in one family of Red-throats carried material to and worked on a nest that the female was building. Skutch (1935) has recorded similar "helpers at the nest" for a number of other tropical species.

When a female Red-crown hunted for material, she often visited places where a tangle of branches and vines had fallen to the ground. There she pecked busily at the bark of rotten limbs, pulling and fluttering until the rhizomorph or anchoring root of bromeliad or orchid epiphyte snapped off. Females seldom investigated living trunks and branches, perhaps because rootlets of epiphytes were difficult to remove from live bark. But at times a female went to high limbs and gathered such material as the spider webs used in binding nests to twigs.

Female Red-throats obtained material in similar sites and in several other locations as well. For strips of fronds and fragments of crowns, they visited the tops of various palms. They jerked brown or skeletonized leaves from their mycelial attachments in piles of leaves above the ground and snapped off the birchlike fragments of the bark of gumbolimo (*Bursera simaruba*) in the fashion of flycatchers capturing insects. Females fluttered and clung to tree trunks, tugging actively, to obtain dead stems and tendrils of small vines to bind the nest. The conspicuous white fungus-covered decorations for the nest were obtained from the litter on the ground or from places just above the ground.

One female Red-throat returned again and again to an area 230 to 270 meters from her nest. Ordinarily searches radiated out 50 to 100 meters from the nest and seldom ended closer than 20 meters. Red-crowns looked for material at similar distances. One female returned repeatedly to an area 130 meters from her nest.

CONSTRUCTION OF THE NEST

The interval between the start of building and the laying of the first egg averaged about a week for ten nests of Red-crowns and about six days for fifteen nests of Red-throats. No new material was added to some nests during a period of as much as a week before the eggs were laid; indeed, building was very slow on the fourth and later mornings of nest construction. Periods of about four or five days between the start of nest building and the laying of the first egg, an interval about normal for tanagers in Central America (Skutch, 1954), were definitely noted in a few repeat nestings. The last egg of one pair of Red-throats was destroyed on May 22, and the first egg was laid in a new nest on May 28. The female of another pair, the eggs of which were destroyed June 2, had laid the first egg in a new nest on June 7. A male Red-crown whose first mate was killed by a Ferruginous Owl (*Glaucidium brasilianum*) had a new mate by the next noon. A new nest was under construction on the following morning, and the female laid an egg four days later.

By placing leaves in some nests for the females to throw out or press down if they returned, and by watching during the afternoon at a few other nests, I determined that few visits were made to nests of ant-tanagers in the afternoon. Except for one visit to the nest in the evening by each species, extreme times for visits were 5:15 a.m. and 10:45 a.m. for Red-throats and 6:04 a.m. and 2:19 p.m. for Red-crowns (fig. 2).

Females differed from each other in their hours of greatest activity and from day to day. Typical hourly records of visits for two female Red-crowns, each on the second and busiest day of nest construction, are 2—2—8—15—8—0 (observed from 6:13 a.m. to noon), and 13—14—7—9—2—4—0 (from 6:00 a.m. to 12:30 p.m.). Similar records

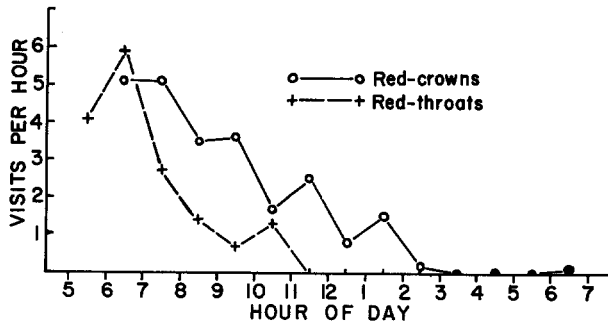


Fig. 2. Diurnal pattern of nest building activity of ant-tanagers.

for two nests of Red-throats on the second or third mornings of nest construction are 0—5—2—3—3—2—0—0 (from 5:50 a.m. to 12:35 p.m.) and 15—4—0—1—1 (from 6:11 a.m. to 11:00 a.m.).

When approaching their nests, female ant-tanagers generally stopped about ten meters away, looked around, and then darted quietly to the edge of the nest. Sometimes female Red-crowns stopped several times closer to the nests, and occasionally hopped up or down to the nests from stops on the nest saplings. Although female Red-crowns might chatter softly as if in answer to the warblings of their mates a few meters away, they were rarely noisy at the nests. Female Red-throats called *sotto voce* at times, but their notes usually were drowned out by the day singing and scolding of the males ten meters or so from the nests.

If I passed while a female Red-throat was on her nest, she froze while the male and other members of the family foraged near me. If I entered the blind, the female resumed slow and quiet activity after a few minutes and finally darted away silently. Female Red-crowns were more likely to dart away while the males chattered near me. If I approached at the same time as did a pair of Red-crowns or Red-throats, the birds flew around and called vigorously until I entered a blind or watched the nest from some distance; then the female slipped cautiously on the nest while the male foraged near me.

Just before the female Red-crown sat down on her nest she placed any material she was carrying beneath her. When the nest still consisted of only a few strands and spider webs looped around some of the supports, she frequently used her bill in pulling a strand from underneath her up over other material or over the nest supports. Then she tucked the strand in on the other side of the material or the support of the nest, thus securing the nest. By the time the female added the first layer of epiphyte rootlets, the nest was a thin disk or cup, depending on the presence or absence of supports underneath. At this stage the female shaped the nest with vigorous movements of her feet. The female sat low on the nest while working and rarely stood up. As she pressed her body down into the forming cup of the nest, she paddled her feet rapidly back and forth. Often her wings and tail were spread out and down with the vigor of her pressing; as she stopped moving her feet, she bounced back up to a sitting or half-standing position, and her tailed closed and rose to some ten or twenty degrees above the horizontal. One female I watched always lifted her yellow crest as she half rose from this pressing and paddling movement. Each female repeated pressing and paddling as many as fifteen times during a visit, turning through a slight angle and tucking loose ends of strands into the nest with her bill. Using her bill, she often arranged the longer strands in a circle around the inside of the nest before rapid movements of her feet matted them into the rest of the

material. Soon the sides of the nest were so thick that the movements of the feet were concealed. During the final stages of building, the material was often deposited on the edge of the nest or on adjacent twigs or leaves before the female settled in the nest. The lining was added with little use of the bill but with much pressing and paddling once she had moved the strands underneath her.

Female Red-throats worked in similar fashion, but they were more energetic than Red-crowns, which worked with finer material. Often the slender sapling quivered with the movements of a female Red-throat. Little use of the bill was required to wind vinelets or spider webs around supports, since nests of Red-throats had supports underneath; but females tucked in loose vinelets or rhizomorphs with their bills. When a female Red-throat brought a leaf to the nest, she occasionally stayed on the nest as little as 20 seconds. When I disturbed one female, she stayed on the nest 30 minutes. The average time for 60 undisturbed visits was one and three-quarters minutes. The interval between visits, although usually over two minutes, was as little as 25 and 30 seconds at a nest where another bird of the family may have been helping the female.

On a few occasions, female Red-crowns merely dropped material and left after a visit of as little as 10 or 20 seconds, although the average for 159 visits was one and three-quarters minutes. Once, when a female stayed on the nest for 11 minutes and 25 seconds, she sat as if incubating. The interval between visits was seldom less than a minute, although I have records of intervals as short as 20 and 25 seconds.

When she departed from the nest, a female Red-crown usually looked around briefly, dropped from the nest, and darted past her mate with a *chauf chauf* or a faint chatter. The pair then moved rapidly away from perch to perch. A female Red-throat usually darted away silently, although chatters drifted back to me from a distance at times.

EGGS

One out of 21 sets of Red-throats was of four eggs, and two were of two eggs; three out of 16 sets of Red-crowns were of two eggs. Other sets consisted of three eggs each. The eggs were laid about dawn on successive mornings. The following description from my notes would serve equally well for either Red-crowns or Red-throats in illustrating behavior connected with laying: "*April 18* (sunrise, 5:42 am)—Two eggs are in the nest at 6:00. At 6:09.30 chatters and rough phrases come from Red-crown pair, and female flies down and settles on nest. Male stays nearby, singing faintly. She looks around occasionally, and finally champs bill a few times. 6:18.15 she rises somewhat, her abdominal feathers puffed out, and turns to face me. Her tail goes up about 20 degrees; then she rearranges her wings and subsides, the process taking about 20 seconds. She sits very high on the nest, blinking now and then as she looks around. She yawns and champs her bill once; then she champs again. Up, off, and down away north she flies silently at 6:30. Three eggs are in the nest."

Eggs of Red-throats were white. Six eggs averaged 25.7 by 17.6 mm.; the extremes were 26.3 by 18.1 and 24.6 by 17.1 mm. On the white background of eggs of Red-crowns were scattered speckles of pale cinnamon, averaging about a millimeter wide except where they coalesced, as they frequently did, in an irregular wreath about the large end; there were also a few superimposed spots of dusky brown of about the same average width, mostly in the wreath. In the one set measured, the first egg was 24.3 by 16.2 mm., the next 24.2 by 17.0 mm., and the third 24.3 by 17.4 mm.

INCUBATION

One female was twice seen to sit on incomplete sets, and once another female sat for 17 minutes during seven hours of observation, a few hours after she had laid the

second egg of a three-egg clutch. However, hatching times for young at a given nest were generally only a few hours apart, and on one occasion the last egg laid in a nest of Red-throats hatched earlier than the first two eggs.

The percentage of time females spent on the nest on Day 0 of incubation, the 24 hours after the last egg was laid, was 69.7 for Red-throats in 32.7 hours of observation and 61.4 for Red-crowns in 21.2 hours (all percentages are calculated by the method outlined by Skutch, 1954). The percentages for daylight incubation for the whole incubation period are 72.1 for Red-throats during 82.6 hours of observation and 68.5 for Red-crowns in 127.2 hours. Skutch (1954) found that many other tanagers incubated about 70 per cent of the hours of daylight.

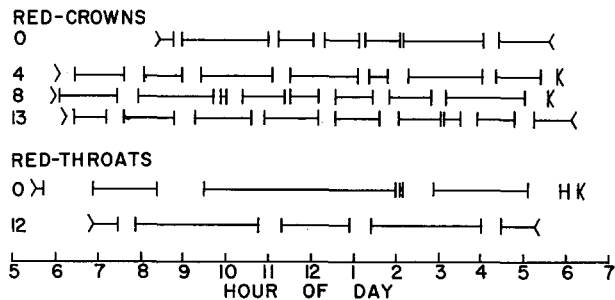


Fig. 3. Periods on and off the nest during incubation at four nests. The three records for the fourth, eighth, and thirteenth days of incubation are from one nest. Periods on the nest are shown by horizontal lines; periods off the nest are shown by blank spaces; > and < mark the beginning and end of a period of observation.

The average time Red-crowns spent on the nest per incubation period was 83.6 minutes for 59 periods; the average for 31 periods for Red-throats was 111.5 minutes. For Red-crowns, the high records were 204 and 188 minutes; for Red-throats, the longest periods were 315 minutes and more than 273 minutes. Skutch (1954) has noted only one longer period for a passerine; this was a record of 365 minutes for *Cyanocompsa cyanooides*, another bird subject to high rates of predation. The usual period for Central American tanagers is 20 to 30 minutes, although Skutch noted average periods of 76.3 minutes for *Eucometis penicillata* and 80 minutes for *Tangara gyrola*. The ant-tanagers spent long periods off their nests, an average of 43.2 minutes for 37 absences of Red-throats and an average of 38.5 minutes for 70 absences of Red-crowns. Consequently a female Red-throat would go to and from her nest only 12 times or so in a 13-hour day and a female Red-crown about 14 times. Infrequent visiting may reduce the possibility that a predator will detect the nest. The daily pattern of periods on and off the nest was variable, even at one nest (fig. 3).

When a shower swept across the forest, a female with eggs or young in the nest always returned to it by the time the first drops reached the undergrowth. She stayed low on her nest, gaping at times as if swallowing rain water, until the dripping slowed down a few minutes after the end of the shower.

A female returned to the nest either as her family foraged past it or after several nestward movements of up to a hundred meters at a time. At stops between such movements the family might forage for a minute or two, or strike out nestward after a brief look around. Near the nest the members of the family foraged in normal fashion. The female was often so inconspicuous that she slipped onto the nest without attracting my

attention. At times she hopped up the sapling and quietly dropped on the nest after a brief look at the eggs. On other occasions she flew directly to the edge of the nest from a few meters away, generally from below the nest. The others of the family foraged on as if the female had not dropped behind.

One female Red-throat called noisily before flying to the nest on several occasions; another called briefly once as she settled on the eggs. I never recorded any notes from female Red-crowns that were settling on the nest.

During incubation female ant-tanagers were quiet, and the slow movements of their heads were the only signs of life much of the time. Now and then a female gaped briefly, as if yawning. Rarely, when a ray of light chanced to illuminate her, I saw the slight quivering of tail and body due to breathing. At intervals her careful scrutiny of every passing bird or other movement was interrupted for a preening session. She half rose, leaving her brood patch open between her drooping ventrolateral feathers, and pecked vigorously at some part of her body as if after a parasite. After a few pokes, alternating with brief scrutinies of her surroundings, she either rocked down over the eggs or looked under her and poked at or between the eggs to turn them before settling. Often she worked her bill as she settled, perhaps removing debris from the edges of it. On the average, female Red-throats turned their eggs four times during each incubation period; the average of 216 intervals before, after, and between turnings was 22.0 minutes. Female Red-crowns turned their eggs twice, and the average of 156 intervals was 28.8 minutes. There was great variation, from turnings only a minutes apart to long incubation periods when the females did not turn their eggs at all. A female occasionally shifted her position on the nest. The tilt of her nest or branches near the nest edge might limit a female to one or two positions; otherwise she sat in several positions.

During the hot hours of midday a female often gaped for long intervals or stood over the eggs for several minutes at a time. Once I noted that the lower eyelid of a female Red-throat winked up over her eye for as much as a half minute. A female Red-crown that closed her eye in similar fashion kept her other eye open; she alternated, closing first one eye and then the other. Such eye-closing ceased abruptly when there was any nearby noise or movement. Mosquitoes occasionally annoyed the incubating birds, as sudden tosses of their heads demonstrated; a mosquito at times alighted on the forehead of an incubating bird and gorged itself.

Female Red-throats seemed more active than did female Red-crowns. The latter turned their heads slowly, a few degrees at a time, whereas female Red-throats more often turned their heads rapidly, through a large angle. Otherwise the two species behaved rather similarly and sat low in their nests with tails tilted slightly above the horizontal and heads held level. Female Red-crowns kept their crests folded to a narrow dark-bordered or dark line.

A family with an incubating female rarely led me anywhere near the nest, but on several occasions a family foraged past as I watched an incubating female from a blind. The male and immatures of a family showed no sign that they realized the female was nearby. On two occasions female Red-crowns darted off their nests past their mates on such visits, but on other visits females of both species stayed on the nest until long after their mates had departed. At times an incubating female rose and turned her eggs, or preened briefly, as her family passed. Rarely she gave a few faint notes, hard to distinguish from the louder calls of the foraging members of the family. Often a female moved her bill while her family passed.

Once an immature came up beside a female Red-throat; the two birds exchanged *wik* notes, the female gaped, and both female and immature left the nest. Once a male

Red-crown visited a female at the nest, spread his wings and tail in a variety of displays, held his bill open, and uttered faint notes. The female gaped and drew her head back but did not leave for another hour.

Each female looked around actively for one to several minutes before leaving the nest. After slipping off the nest the female generally flew below its level for the first few meters, but rose as she disappeared in the undergrowth. Twice I saw that she soon alighted and looked back toward the nest before stretching her wings and defecating. When I approached close to her nest, a female ant-tanager would flutter off through the forest and disappear. If I passed more than two or three meters away and made no moves toward the nest, she might crouch low and stay on the nest.

Female Red-throats when leaving their nests uttered faint *wik* notes as they passed my blinds but gave no louder calls. At some distance from the nests they broke into noisy chatters and rough scolds. On several occasions I was with the male and immatures of a family when such notes broke out some 100 meters distant. The birds immediately stopped foraging and flew higher in the undergrowth, uttering another burst of notes, and the whole group darted toward the commotion. Bursts of scolding, occasional day songs, and chattering drifted back to me. By the time I reached the source of the noise, the reunited family was foraging busily. If a family had been foraging at a swarm of army ants, all returned; for several minutes the tempo of *wik* notes and foraging activity was at a much higher level than before the female had arrived. If other members of a family had been close to the nest when the female left, rapid *waaj-tuk* notes and faint songs from the undergrowth near my blind made it apparent that the female and male joined quickly.

A female Red-crown was quiet in leaving her nest unless her mate were nearby. Then she flew under him with *chauf chauf* notes. Once a pair stayed and foraged near the nest, but more often the male chased the female off through the forest. Such a reunion was much more noisy and active if the female darted past the male at some distance from the nest. After the reunion the female foraged more busily than the male. She might give the *che-e-e* of the precopulatory ceremony now and then as she foraged, but usually she omitted wing fluttering and other actions of the complete ceremony. At times the male flew near his mate or chased her briefly, but I saw no attempt to copulate.

HATCHING OF YOUNG

Young had hatched in one nest of Red-crowns when I arrived at 7 a.m. on the thirteenth morning after the last egg was laid. At another nest of this species young did not hatch until the fourteenth night of incubation. The incubation period for one clutch of Red-throats was less than 12 days and 12 hours. Two young hatched in another nest during the fourteenth night of incubation; the last egg the female laid in this nest hatched after only 13 days and 7 hours. Table 3 lists the incubation periods of the two species.

Females were nearly always on their nests at the time eggs hatched. At three nests of Red-throats and at one nest of Red-crowns, females stayed on the nests for 210, 206, 159, and 222 minutes, respectively; but, at seven other hatchings of Red-crowns, females stayed on the nests for normal incubation periods and left between hatchings. A female might rise every few minutes to poke or peck at the eggs with great vigor, as did one female Red-crown, or be unusually quiet, as was a female Red-throat that made no noticeable move for an hour and a half.

After the young had hatched, the female pecked into the nest and swallowed small fragments of the shell. Occasionally she lifted her head and gulped down a large fragment after she had flattened it into a strip with her bill. Eating eggshells eliminates the necessity for special trips to carry them away, trips that might attract the attention of

TABLE 3
INCUBATION PERIODS FOR ANT-TANAGERS¹

Species	First young	Second young	Third young
Red-crowned Ant-Tanager	13 days 7 hours	13 days 12 hours	Egg infertile
	?	13 7	?
	13 4	13 5	13 days 10 hours
	13 4	13 8	13 9
	?	?	13 12
Red-throated Ant-Tanager	12 5	12 6	Egg infertile
	13 7	13 8	13 10

¹ From hour of laying of third egg to hour of hatching of the young specified.

predators. Ordinarily the female remained on the nest for some time after eating the eggshells.

FEEDING THE NESTLINGS

One male Red-throat brought food twice to a nest while it was being built, but males were never seen to visit their nests while the young were hatching. Direct sight of the young was not necessary for one male Red-throat to start bringing food, for I recorded the following sequence some 15 minutes after the female first departed from the newly hatched young: "12:05 there is much noise moving up to 15 meters west of nest, with loud chatters and scolds. As female darts past me to the edge of the nest, the other three birds of the family perch around my blind and utter *wik* and *waij* frequently. The male sits with his body and tail feathers spread, food in his bill, on a stem in front of the blind; he looks around and toward female. She croons a soft warble, feeds young, spreads her abdominal feathers, and settles over the nestlings. But the male is insistent in his calling; she flies off at 12:05.55 and utters a few faint scolds as she passes her mate. He flies toward nest and . . . finally stretches down to young at 12:06.10."

Generally males were not so quick to feed their young as was this male. At one nest the male Red-crown was never seen to feed the young, although he visited them a few times and fed young in a later nest. Of 397 feedings of Red-throats, 131, or 33 per cent, were made by males; of 469 feedings by Red-crowns, 69, or 14.7 per cent, were made by males.

Eighteen successful feedings of young Red-throats, or 4.5 per cent, were made by immatures or by adult females other than the female parent; all records but one were at one nest. The immature at the latter nest fed the young at least as early as their fifth day in the nest and by their ninth day was feeding them at about the same rate as were the male and female.

The first meals for three young Red-throats in different nests came 40, 57, and 100 minutes after the females ate the eggshells; the first meals for three young Red-crowns came after 74, 130, and 170 minutes. On several occasions the tiny young was seen to gape when the female rose and poked downward into the nest a short time before leaving briefly to obtain food.

Very young nestlings were fed infrequently, but the rate of feeding increased as they grew older (fig. 4A). The average interval between feedings was 29.6 minutes for Red-crowns (417 intervals) and 21.2 minutes for Red-throats (366 intervals). The great activity of male Red-throats accounts for part of the difference between the two species.

When only one young was in a nest, the intervals between feedings were shorter than when two young were in a nest; when three young were present the intervals between

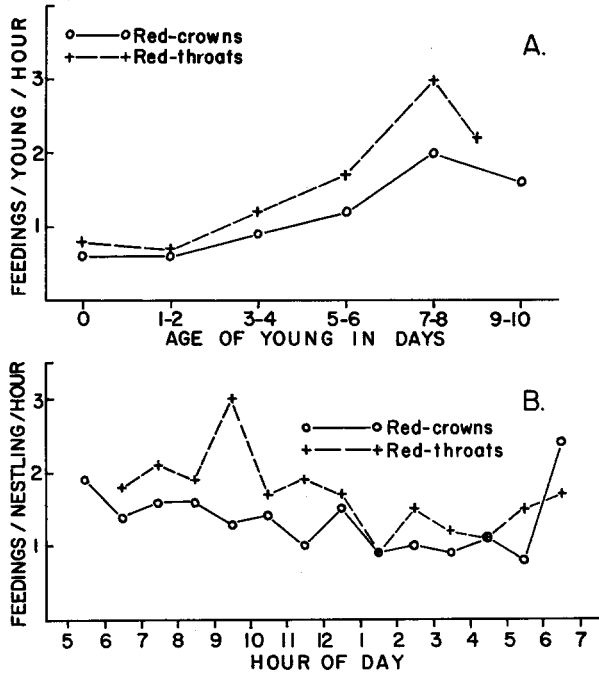


Fig. 4. A, changes in the rate of feeding as nestlings grew; B, rate of feeding young during the day.

feedings were the shortest. However, most of my records for only one young in a nest were in the late days of the nestling period, after the disappearance or departure of one or more nestlings, at a time when feedings were normally more rapid (fig. 4A). If the bias thus introduced is offset by recalculation (for example, from fig. 4A the feeding rate for Red-crowns on the eighth day is 3.2 times the rate on the first day; hence each interval for Red-crowns on the eighth day is multiplied by 3.2), the ratio between intervals for one, two, and three young becomes 2.4: 1.6: 1 for Red-crowns and 2.0: 1.6: 1 for Red-throats. These ratios are not the 3: 2: 1 ratio that might be expected, but are in agreement with the observations of Moreau (1947) that the rate of feeding is higher in larger broods but not in direct proportion to the number of young.

The rate of feeding was slightly less rapid in the afternoon than in the morning (fig. 4B), but the assertion of some authors that tropical birds stop feeding their young in midday because of the heat was not true for the ant-tanagers at Gallon Jug. The variability in feeding rates from hour to hour at six nests is indicated in table 4.

The female ant-tanager held food nearly hidden in her bill as she approached the nest. At each stop she looked around carefully. The brief passage of a breeze through the undergrowth, which rustled leaves and made other movement hard to detect, often coincided with the female's flight up into the nest sapling. If the nest were low, the female generally flew directly to its edge; but a few females, particularly those at two successful nests of Red-crowns, often halted for as much as half a minute in rigid poses on limbs below the nests. If the young had gaped when the female landed below the nest, they generally settled back and were quiet when the female finally ascended to the nest. But in the days just before departure of the young birds, particularly if two or three

TABLE 4
VISITS OF ANT-TANAGERS WHILE FEEDING YOUNG

Hour of day:	6	7	8	9	10	11	12	1	2	3	4	5	6
Red-crowns													
2 young, 0 days old (May 20, 2:53-6:18)										-	3	2	1 2
3 young, 5 days old (July 18, 11:55-6:30)							1	-	3	5	2	5	4 4
2 young, 9 days old (July 4, 6:08-6:25)	6	4	4	2	1	3	3	1	1	1	3	4	1
Red-throats													
2 young, 1 day old (June 15, 8:20-3:30)				-	4	-	1	3	-	2	-		
3 young, 5 days old (July 6, 9:19-6:11)					2	4	14	7	4	3	5	5	8 1
3 young, 9 days old (July 20, 6:03-4:25)	5	5	2	5	5	3	15	3	1	1	3		

were in the nest, their importunate gaping and squeaking left the female no choice but to break her stop off short.

As they approached their nests, female Red-crowns were ordinarily silent; but some female Red-throats gave every few seconds the faint calls normally used in foraging. If I was out of the blind when the female approached the nest, she called noisily, flew about, and turned back and forth on her perch. She did not drop or eat her food but refused to go to the nest while I was near it.

Male Red-crowns often warbled a liquid and irregular song and quivered their wings as they approached nests. Female Red-crowns accompanied by warbling males, or by day-singing and chattering males without food, often gave *chook* notes or faint chatters until they were only a few meters from their nests. As a female fed the young, the warbling of a male with food grew louder, more rapid, and more irregular; her movements became quicker, and finally she darted past the male with a faint *chauf chauf*, to forage and chatter nearby as the male, suddenly silent, darted to the nest. When a male arrived and found the female brooding, he warbled until she darted off past him after a few seconds of looking around and poking the young. Occasionally a male warbled near the nest for several minutes even when no female was present. Male Red-throats alternated low and deliberate day songs with faint *wik* notes until the females left the nests. However, females at times offset this comparative restraint by uttering a rapid stream of notes as they flew nestward ahead of their mates or as they flew past the males when leaving. Although males of both species often spread their body feathers and tail while singing, they compressed their feathers as soon as they flew to the nests. I never saw a male display his bright crest during a visit.

On the occasions when young were fed as a foraging family wandered past the nest, perhaps in company with the many other insectivores of a wandering forest flock, the usual calling and foraging activity was interrupted only by the ant-tanager that went to the nest.

Ordinarily the first downward poke with food, usually within a second after the adult reached the edge of the nest, resulted in the gulping movements of a young bird swallowing food. But when a parent Red-crown brought a large arthropod, the young generally had trouble eating it. Into one open gape after another the parent placed the food, crushed-end foremost. Retrieving the arthropod quickly if it did not go down im-

TABLE 5
TIME REQUIRED TO FEED YOUNG

	Red-crowns	Red-throats
Feeding immediate	318 visits (68.5 per cent)	323 visits (82.2 per cent)
Feeding difficult (2+ seconds)	146 visits (31.5)	70 visits (17.8)
Average time to feed young	52 seconds	8 seconds

mediately, the parent crushed it still more by moving it back and forth in its bill. A low *chuk*, seemingly a soft version of the normal foraging call, usually stimulated one or more young to gape again. But after several attempted feedings the young became sluggish, and the *chuk* notes came louder and faster. A male might resume warbling and fluttering as he looked for open gapes; if he found none, he ate the food himself before departing. A female soon would settle over the young. At intervals she rose and crushed the food still more as she uttered the *chuk* note rapidly. One female finally fed a young bird an hour after she arrived. On a few occasions the female ate the food herself. Skutch (1954) found that Red-crowned Ant-Tanagers in Costa Rica had similar troubles feeding their young large arthropods.

Pairs of Red-throated Ant-Tanagers seldom (table 5) had as much difficulty feeding their young, perhaps because they generally brought smaller particles of food. The note corresponding to the *chuk* of Red-crowns was a faint *wik*, much like the ordinary call of Red-throats.

As soon as the young bird grasped the food, the adult ant-tanager champed its bill and looked around briefly. If the young began to swallow the food, the adult repeated champing as it looked at the young with one eye and then with the other. After 40.4 per cent of 463 feedings of Red-crowns and 38.8 per cent of 379 feedings of Red-throats, the young lifted its tail and emitted a fecal sac. The parent either ate the sac or flew off with it (fig. 5). Eating fecal sacs probably reduced the conspicuousness of the departure of the parent and, when the female stayed to brood, made it unnecessary for her to leave the nest.

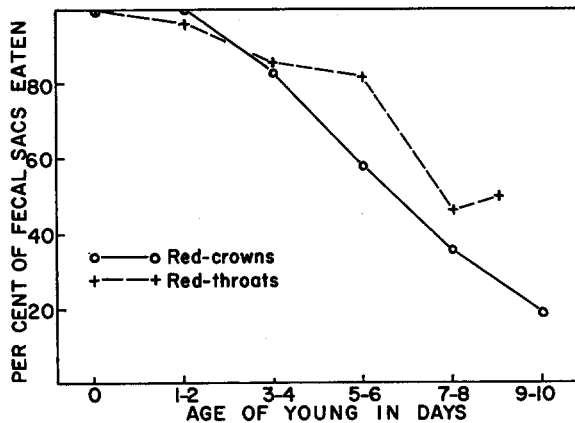


Fig. 5. Percentage of fecal sacs eaten by parent ant-tanagers.

A female often remained for some time after she fed the young. She looked at the young and the lining of the nest carefully between periods of scrutinizing the rest of her surroundings. Now and then she tapped lightly down into the nest, or pulled and pecked

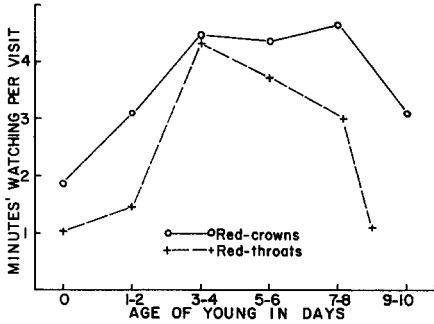


Fig. 6. Time spent by female ant-tanagers watching young after each feeding.

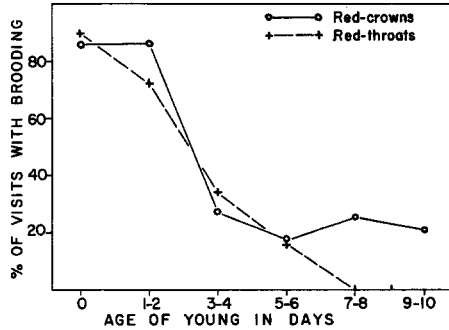


Fig. 7. Percentage of visits to nests by female ant-tanagers followed by brooding periods.

vigorously. Often she worked her bill after such sessions, which apparently were devoted to removing and eating tiny parasites, bits of food, fecal matter, debris, and fragments of the sheaths of feathers. One female Red-throat pecked at a dead young at intervals for several hours before she carried it away from the nest in her bill. Occasionally females of either species captured and ate one of the mosquitoes that hovered persistently around the young. When the young began to gape and call, the female left the nest.

The average time between feeding and departure from the nest or resumption of brooding was 3.6 minutes for female Red-crowns and 2.8 minutes for female Red-throats (fig. 6). The period of watching the young was often interrupted by the arrival of the male with food. Males seldom stayed and peered into the nest. Occasionally males of either species stayed as much as four minutes, but the average length of time the male remained at the nest was 40 seconds. Immature Red-throats usually waited only for fecal sacs: their average stay at the nest after feeding was 27 seconds.

After watching the young, a female of either species often lowered her abdominal feathers and hopped forward over the brood. A brooding female differed from an incubating female in her higher position, her more frequent shifting, and her behavior during her more frequent periods of standing. During such periods she often tapped at the

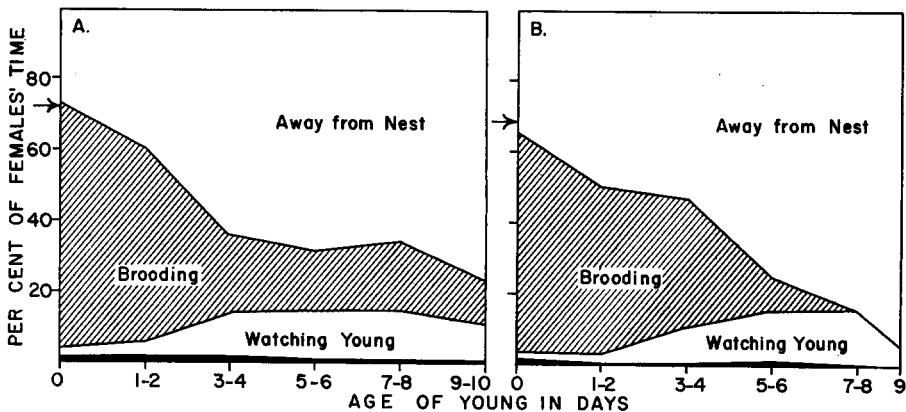


Fig. 8. Disposition of time by female Red-crowns (A) and Red-throats (B) during the hours of daylight. The arrows indicate the percentage of the daylight hours spent in incubating. The black areas indicate the time spent feeding young.

young or picked up bits of debris. If the young gaped before she settled, faint peeping notes continued under her. Large young thrust their heads through her feathers at such times and called and gaped whenever she moved. The increased activity of large young did not cause the average period of brooding to become shorter; instead, the per cent of visits that were followed by brooding periods became less (fig. 7) as the young grew older. Brooding periods were partly replaced by periods when a female watched young from the edge of the nest as they grew older (fig. 8).

The average brooding period for Red-throats was 34.8 minutes, and 59 records varied from 1.5 to 116.5 minutes; for Red-crowns, the average was 31.6 minutes, and 127 periods ranged from 15 seconds to 131.7 minutes. The average brooding period was much shorter than the average incubation period, even though brooding took nearly as much of the time of the females at first as had incubation (fig. 8). The average for 15 brooding periods of Red-throats on Day 0 (the period from hatching to the first dawn after hatching), was 23.9 minutes; for 50 periods for Red-crowns, the average was 34.4 minutes. The visits of males with food, and the gaping of young when females rose and pecked at them, interrupted periods of brooding. Occasionally females returned to nests and brooded without feeding young birds.

Before leaving the nest, an ant-tanager of either sex generally looked around carefully. Often the bird dropped in shrike fashion as it flew away. On a few occasions, I saw the adult stop ten to thirty meters away from the nest and look back toward it before flying on. Less often a parent hopped up or down in the nest sapling and paused for as much as several minutes before darting away.

GROWTH OF THE YOUNG

Young Red-crowns and Red-throats proved similar in their development. Because of extreme predation, few young could be examined, but the following notes should help future workers in determining the ages of nestling ant-tanagers to within two or three days.

In table 6 feather growth has been divided into five stages, which are represented by the letters D, W, P, B, and V: first, invaginations into the skin formed, but were noticeable only on a few tracts; dusky dots (D) soon formed at the bases of invaginations; the dots elongated into wedges (W) inside the feather follicles; pinfeathers (P) then projected as metallic-blue shafts; eventually the shaft tips acquired greenish pigment and split until they were like tiny camel's-hair brushes (B); soon the brushes expanded into vanes (V) as barbs separated from the central axes closer and closer to the bases of feathers. Lengths of feathers (in millimeters; or "short," "medium," or "long"—S, M, or L) and of the part of the length of each feather with open vanes (decimal preceding a "V") represent measurements from the points where feathers emerged from the follicles, not from points at the true bases of the feathers beneath the skin.

Newly hatched young had buffy brown down on several tracts: coronal, occipital, scapular, femoral, posterior dorsal, extreme posterior abdominal, greater secondary covert, and median secondary covert. The down was most conspicuous on the coronal lines, but it reached 9 mm. in length only on the dorsal tract. Slender filaments up to a millimeter in length became visible on the rectrices and on additional feathers of the abdominal tract as the down was pushed out on the tips of the pinfeathers. Although a few feathers of the wing of one well-fed young Red-throat were opening on Day 5, most feather debris was shed after Day 6. Since the debris remained in the lining of the nest, it was easy to tell from examination of an empty nest whether or not young had reached the age of seven days. The feathers opened serially from outermost to innermost in the secondaries, greater secondary coverts, and alulars; primaries opened in the reverse

direction, that is from 1 to 9. The greater primary coverts opened 5-4-3 and so on. The left and right wings of an individual often differed in the number of feathers open at any one time, although the order of opening of feathers was constant.

The gapes of young Red-crowns were red or orange, as is usual in the Thraupidae (Skutch, 1954); the gapes of young Red-throats were yellow at first but gradually became reddish. On Day 0 the bills of all nestlings were stubby and mottled pink. On Day 2 bills were becoming dusky; by Day 7 the mottling was nearly obscured by dusky pigment. The yellowish white angles of the gapes were retained, but the remainder of the bill became dark as it grew in size. The orange and fleshy feet anteriorly developed tarsal scutellation and a horn-pink color by Day 2. By Day 9 the legs were dusky in front, pink on the sides, and pale flesh-color behind; the claws were dark above but remained whitish below. Gradually the feet became as dusky as the feet of adults.

TABLE 6
FEATHER GROWTH IN YOUNG ANT-TANAGERS

	Age in days									
	2	3	4	5	6	7	8	9	10	
WING FEATHERS										
Primary	LW	P	P	B	B	B	0.25 V	0.5 V	0.7 V	
Longest (no. 4 or 5)		2-5	5-11	9-18	15-20	23-25	26-39	35-39	48	
Secondary	LW	P	P	B	B	V	0.25 V	0.6 V	0.7 V	
Longest (no. 1)				7-15	12-18	23-24	34-36	36-37	48	
Greater covert	SW	P	P	B	B	V	0.25 V	0.6 V	0.7 V	
Longest		2	4-6	7-11	8-15	17-18	19-25	18-25	20	
Marginal	Few D	D	SW	W	P	SB	B-V	V	V	
Alular	D-MW	P	P	P	SB	B-V	V	V	V	
Longest		1.5-3	4-6	5-10	8-15	14-15	15-20	18-24	20	
HEAD FEATHERS										
Frontal-coronal	D	D-SW	MW	LW	SP	MP	P	P	P-B	
Occipital	D	D-SW	MW	LW	SP	MP	P	P-B	SV	
Auricular	—	—	D	D	SW	P	P	P	P-B	
Malar	—	—	D	D	SW	SP	SP	MP	P-B	
Throat	—	—	—	—	D	D-W	D-P	D-P	D-B	
BACK AND LEG FEATHERS										
Dorsal										
Cervical	D	SW	LW	SP	P	P	V	V	V	
Mid-dorsal	D-W	MW	P	P (3)	P (5)	B	V	LV	LV	
Pelvic	—	D	SW	LW	SP	P	SV	V	V	
Scapular	D	D	D-SW	P (3)	P (5)	B	V	LV	LV	
Femoral	D	D	MW	P (3)	P (4)	B	V	V	V	
Crural	—	D	SW	MW	P (1)	B	V	V	V	
Tail	—	—	—	D	MW	P (1)	P	P-B	SV	
VENTRAL FEATHERS										
Breast	D	MW	LW-P	P	B (5)	V	LV	LV	LV	
Abdominal	D	D	MW	P	P (3)	B	V	V	V	
Anal cirlet	—	—	—	D	W	P	SV	SV	SV	
Undertail covert	—	—	D	D	W	B	SV	SV	SV	
YOUNG EXAMINED IN DETAIL										
Red-crown	1	1	2	1	2	2	1	1	2	
Red-throat	2	2	2	2	1	1	1	2	0	

Nine young Red-throats from 5 nests and 6 young Red-crowns from 4 nests were examined. Young 0 days old showed no feathers; short wedges were on the primary, secondary, and covert tracts on Day 1. Lesser and median wing coverts were intermediate between marginals and greater coverts. For explanation of symbols see text, p. 494.

By Day 2 the formerly united eyelids were separated by slits up to a millimeter in length. On Day 4 the eye slits were nearly complete, and young opened their eyes at times. On Day 6, young kept their eyes open during their extended periods of preening and movement each time the female stayed after a feeding.

Newly hatched young were barely able to right themselves when inverted. On Day 2, young could right themselves readily, hold their wings and legs close to their bodies, and loosely grasp a stick or my finger. At this age young no longer gaped or peeped in the hand when I moved or blew upon them. On Day 3 and thereafter young commonly excreted when removed from the nest. On Day 4 and thereafter young clutched the nest when captured and huddled when in my hand; some yelled *weeah!* when taken from the nest. Young five days old or older gaped in my direction and cowered in the nest when I extended my hand toward them.

From a *peep* much like the call of many young birds, the notes of ant-tanagers became a brief *chee* or *chee-e-e-e* by the third day of life in the nest. Young squeaked variants of such notes rapidly during feedings. Loud *chut-chut-chip!* or "nest-leaving" calls were first uttered on the day before the first young bird left the nest and were given frequently when the parents were foraging nearby in the days that followed. Whenever the calls were uttered while the parents were out of sight, as on occasions when I held a fledgling inside my blind, both parents darted toward the calls at once. Possibly the calls may have served to keep the parents near the young during the critical period of departure from the nest. From Day 15 to Day 20 notes intermediate between the chatters of adults and the nest-leaving calls of young were heard from fledglings of both species. Young Red-throats gave calls intermediate between the *chee* and the scold of adults as early as Day 11; on Day 18 the scolds were still weak but like those of adults in other respects. From Day 18 to Day 36 a loud *chiat!*, intermediate in quality between the scold and the *chee* but more like the former in amplitude, was repeated rapidly by the juvenile as it followed its parent. Young Red-crowns, which usually sat hidden in leaves or vines three to ten meters above the ground waiting for parents to return, gave a faint *chie* as a location call from Day 10 to about Day 35. The *wik* of adult Red-throats was but a slight modification of the *chee* of the nestling, but the origin of the *chook* of adult Red-crowns is uncertain. The *chook* was first heard from a fledgling Red-crown on Day 27. Songs and calls of adult ant-tanagers are described in Willis, 1960a.

On Day 7, young Red-throats occasionally detected approaching parents by their *wik* calls and gaped while the parents were distant from the nest. At times a young bird uttered a nest-leaving call. The young preened actively, climbed over each other, and pecked or gaped at one another more and more frequently on days 8 and 9. Four young left two nests on Day 8. I caused the departure of two; the other two may have been ousted by a predator. Five young Red-throats left on Day 9. Young Red-crowns were similar to young Red-throats in feather development, but the former did not utter nest-leaving calls or start active movement in the nest until Day 9. They left the nest only on Day 10.

Young Red-throats and Red-crowns rarely fluttered their wings in the nest. Young which fell out of nests of Red-crowns on Day 7 refused to move when pushed. Young Red-throats eight or nine days old could barely hop and rested for long periods. On days 10 and 11 young of both species hopped and fluttered along the ground for longer periods and took shorter rests. On Day 13 a fledgling Red-crown fluttered as much as six meters after its parents, but it usually had to flap its wings and pull itself up to the top of a limb with its bill and neck when it alighted. On Day 18, fledgling Red-throats whirred directly and rapidly from limb to limb, and by days 20 to 25, young of both species flew fairly well.

During feedings, fledglings usually gaped and fluttered the tips of their wings but rarely squeaked. The competition among nestlings probably caused the vigorous squeaking in the nest after Day 3. Three nestlings in a nest were far more noisy when fed than were two nestlings, and a single nestling was quiet unless the parent hesitated before a feeding or had been gone a long time. Once, when a female tapped the gape of a 13-day-old Red-crown and pushed an insect down its throat with scarcely a break in her chattering at me, the young bird did not even move its wings.

A Red-throat about three weeks old visited a nest when the nestlings were in their fifth day and begged silently from the pair feeding them. This bird pointed its gape at the food, even when the morsel was in the beak of a nestling after the adult had departed. The female which accompanied this fledgling on following days may have been a second mate of the male at this nest.

The earliest that a young Red-crown was seen to dart after an insect was Day 27. On days 32 and 36 this bird was obtaining most of its own food, although it lacked the grace and agility of its parents. Immature Red-throats apparently became independent at approximately the same age. None was seen to be fed after Day 30, although one begged from a female on Day 39.

Bare shafts and gaps still showed in the wings of young ant-tanagers on days 10 and 11. At this age the dorsal and scapular feathers covered most of the back of the bird when it hunched in the normal sitting position. However, the head was bare except for a few areas of pinfeathers and small feathers, the midventral apterium was exposed from breast to anal circlet, and the flanks, the sides of the neck, and the thighs were bare. On Day 18 the faces of young birds still lacked covering. The heads of young Red-throats seemed shaggy and small until the postjuvinal molt, but young Red-crowns resembled the adult female in the feathering of the head long before the molt.

The length of the tail beyond the upper tail coverts was in the field the best indication of the age of a fledgling. The tail of each young first showed beyond the upper tail coverts about Day 13; on Day 22 the tail was about 30 per cent as long as the tail of a female parent; about Day 29, the tail was about 80 per cent as long as that of the adult bird, and on Day 36 it was as long as that of the adult bird, namely 50 mm.

The drab, brown plumage of one young Red-throat was unkempt on Day 52, as if it were molting. On Day 72, August 1, the throat of this bird was yellow, as is true of young in their first winter plumage. The brown color of the rest of the body had been partly replaced by the lighter shade of the first winter plumage. Fledgling Red-crowns had throats that were yellower than the throats of fledgling Red-throats or of female Red-crowns; but in several young Red-crowns, which were two months old in late July, I detected molt not by changes in the color of the plumage but by the ragged state of the plumage.

DEPARTURE FROM THE NEST

Young ant-tanagers are no better feathered when they leave the nest than are the nestlings of other tanagers several days before leaving. The early departure of young ant-tanagers may be a behavioral adaptation to predation. The noisy competition of the young for food as they grow older and the repeated visits of their parents to the same spot increase the chances that a predator will find the nest and capture the whole brood at once. But, as soon as young leave the nest, they can be secreted in separate spots and these hiding places changed at intervals. A hopping fledgling might be conspicuous during infrequent intervals of movement, but it is not much more conspicuous than several young preening actively in one nest. Covering the young during the relatively cool rains or nights in the tropics may be a problem with such early departure

from the nest, however. Two young Red-throats were secreted 20 meters apart after leaving one nest. But the sibling Red-crowns out of the nest were perched only a few meters apart on two occasions. Moreover, the tolerances of unfeathered fledglings to rain and chilling may be greater than one would suppose. It is not the danger of chilling but the inability of birds younger than eight days old to move about that probably sets the lower limit for the age of fledging.

When young left the nest, the female was always calling nearby. Otherwise the details of departure varied considerably. One female Red-throat found me examining a young bird. As soon as I had replaced the young bird and entered the blind she stopped her displays and darted to the edge of the nest; a few notes and a peck under the two huddling, silent nestlings stimulated them to give a few nest-leaving calls and hop over the edge of the nest. A female Red-crown watched her actively preening young for three minutes after a seven-minute brooding period; then she hopped off into the nearby limbs and started calling *chuk*, the usual feeding call, as she looked at the nestlings. Soon one fledgling hopped out. After it was led away the female and male returned, and I recorded: "Female calls frequently from bush about 3 meters SE of nest. Young calls *chee* and *chip*. Finally young stops preening and turns toward female, answering each *chuk* with faint *chee* notes as it looks back and forth for way up onto nest edge. Once young tries ascent; flutters as falls back into nest. Young looks again, finally hops on edge at 9:37. Female turns her tail toward it, calls *chuk* less often. Young looks for place to land. 9:38.45 it jumps and flutters down, clinging for a moment to the tip of a palm leaf before it drops to the ground, 3 meters below the nest. Parents lead young bird away, as before."

At two other nests of one pair of Red-crowns, the young birds fell out of the nest when seven days old. One nest was knocked down by a heavy rain. The rim of the second nest was so low on one side that the young bird may have fallen out when it backed up to the edge of the nest to emit a fecal sac. Both young birds were fed on the ground. When they were replaced, the female fed them in the nests after looking for them on the ground. At one nest of Red-throats one young bird and at another nest three young in succession left by jumping out of the nest as soon as the females flew to nearby trees after feedings.

After young ant-tanagers left the nest they were led away by their parents. The female fluttered back and forth from twig to twig just ahead of a fledgling, fluttering from one side of it to the other in a kind of "shielding flight" (Skutch, 1955) every time it moved. Female Red-crowns kept up a stream of faint feeding calls and other notes; female Red-throats gave *wik* calls, faint scolds, and other sounds. The male usually flew from branch to branch ahead of and above the female and called occasionally as he looked around. Once an immature Red-throat joined such a caravan and flew back and forth ahead of the male. At another nest of Red-throats a second female left her well-grown immature and led off one of the young while the parents were leading the other two away. Young of either species, if over eight days old and able to climb, were enticed up on twigs or vines arising at an angle from the ground.

If I came near one of these young and then retired to a distance, it was soon led off to another perch. When I emerged from a blind and captured a fledgling, I encountered the first distraction displays recorded for any members of the tanager family (Skutch, *in litt.*). At the first squawk of the young bird the female uttered a loud chatter as she darted past my hand. Then she hopped rapidly over the ground and low twigs nearby, her wings held up or down or one up and one down. Her tail was spread fully and dragged the ground or was held high. Red-throats gave prolonged scolds, while Red-crowns typi-

cally uttered falsetto chatters. If the male were present, he displayed as vigorously as the female. Once an immature Red-throat joined a pair, and three birds displayed around me. Each call from the young bird inspired a fresh display, but eventually the parents stopped and watched me from nearby limbs, where they turned rapidly from side to side and called noisily.

Some parents hardly displayed at all. Others added variations to the displays just mentioned. Two different male Red-throats were seen to fall to the ground from about two meters up, give a loud call as they hit, and hop away from me while performing the usual display. Once a female Red-throat drooped her body and tail feathers, quivered her lowered wings, and turned her head listlessly as she looked toward her toes. Such displays made the parent seem crippled or sick.

The use of these displays only at a time when the fledglings were near or on the ground, which few other young tanagers ever reach, fits in well with the observation of other authors that most such displays are performed by ground-nesting birds. Later, when the young were higher in the undergrowth, I did not note distraction displays.

Young Red-throats over 18 days old were led through the forest in a characteristic fashion by their parents. As the male scolded, the female uttered a series of rapid *week* notes and low scolds until the less wary young bird followed. As soon as it took wing, one or both parents crisscrossed its path in a shielding flight so effective that I rarely saw the young alight even on a few occasions when it alighted in plain sight. My eye was attracted by one parent or the other, which alighted in full view before the young alighted at all. Once the young bird started moving, it and the rest of the family moved so rapidly that I detected the birds for minutes at a time only by a stream of faint notes from the distant undergrowth. Young Red-crowns of about this age sat quietly and were led away only after I retired to some distance. They were ordinarily secreted farther above the ground when I found them than were young Red-throats, in keeping with the generally higher foraging range of Red-crowns (Willis, 1960*b*).

The male Red-throat from a territory near one nest repeatedly brought food to two fledglings, although it was persistently driven away by the male parent.

PREDATION, RENESTING, AND CLUTCH SIZE

Destruction of the eggs and young of ant-tanagers was as great as has been reported by several authors (see Moreau, 1940; Skutch, 1945) for other birds of the tropical forests. Of 53 nests of ant-tanagers, only 8 or 15.1 per cent produced one or more fledglings. Only 16 young were fledged from at least 147 eggs laid, for 10.9 per cent success. One nest was knocked down by a heavy rain, one by a falling limb; the other unsuccessful nests were robbed by predators. The disappearance of eggs and young from nests of other species on the study area was similarly frequent. Since on an adjacent area that I rarely visited, three out of three nests of ant-tanagers were successful, it may be that my intensive observations of nests on the study area attracted the attention of predators.

In over 530 hours of watching nests of ant-tanagers from blinds, I never saw a predator take the eggs or young. Possibly much of the predation came at night, but perhaps predators were inhibited from going to a nest by my presence.

Skutch (1945) thinks snakes are the major predators. Once a pair of Red-crowns chattered long and violently at a snake (*Oxybelis*), and the female left her nest to join in the chatter. Whenever ant-tanagers and the small birds of a wandering flock encountered such snakes, they scolded for minutes at a time. Undoubtedly various mammals and birds rob nests at times. Motmots (*Momotus momota*) approaching close to nests aroused ant-tanagers to more violent reactions than did any other species except such

a hawk as *Micrastur ruficollis*. Reactions of one pair of Red-crowns and of one family of Red-throats to motmots were as follows:

"June 3—[3 eggs in nest of Red-crowns]—One motmot flies down to a perch about one meter on the other side of the nest from me. Female ant-tanager hops off eggs and flutters along nest limb with wings down and tail spread. Male flies up; both yell, and finally attack and drive motmot off.

"June 23—[2 small young in nest of Red-throats]—3:51 two motmots fly up near nest, and female ant-tanager flattens out and becomes motionless . . . she presses wings flat on rim of nest and lowers her head and body as much as possible . . . At 4:40 scolds and faint day songs approach from northwest. The male and one immature ant-tanager fly up above my blind, scolding noisily, at 4:47. Female has not moved noticeably since 3:51. At 4:52 male and immature flutter around one motmot and drive it off southeast. Then two come back and scold near other motmot. At 4:54 they drive it off southeast. Male and immature fly back and give *wik* calls near the nest as the female rises and looks down at the young for the first time in over an hour." [The young were gone the next day.]

Whatever the sources of destruction of nests may be, it is probable that the nesting activities of ant-tanagers are adjusted to them. The great caution ant-tanagers ordinarily displayed in approaching and leaving their nests has been noted in discussions of incubation and the feeding of young. The wide spacing of feedings, and the unusually long periods on and off the nest during incubation, may have resulted from the danger to the young or eggs posed by frequent visits, as Skutch (1949) suggests. He has noted that many other tropical birds visit their young infrequently and bring large food items on such visits. However, factors other than predation may have caused this slow feeding rate. Ant-tanagers probably spent much time traveling to and from their nests over their large territories except when the young were ready to leave and food was obtained near the nests. It may be that tropical birds have a more difficult time finding food than non-tropical birds. Even though northern birds go to the tropics when northern woods do not provide enough food, the great number of species in such a forest as that at Gallon Jug may mean that the available supply of food for each species is reduced.

The rapidity of the renesting of ant-tanagers may be a response to predation. Averages of less than a week for nest construction, of 15 or 16 days for egg laying and incubation, and of 9 to 10 days for feeding nestlings add up to an extremely brief period of nesting. Young of other species of tanagers use their nests at least two days longer (Skutch, 1954). A complete nesting of Red-throats required only a month. Red-throats ordinarily started building a new nest only one or two days after the destruction of the contents of an old one, although most Red-crowns and some Red-throats delayed up to a week or two between nestings. One female Red-throat attempted five nestings between April 25 and June 17; I inferred at least two more from her behavior before I left on August 2. Other females were less prolific because some of their nests lasted more than a few days. Several females evidently attempted at least five nestings.

Despite constant renesting from April to August, only two out of the ten pairs of Red-crowns in the central part of my study area had a surviving fledgling when I left. Only two out of eleven families of Red-throats had young out of the nest after three months of nesting. One of the latter families produced two broods; two young from one nesting were about 60 days old on July 31, and one from a later nesting was about 38 days old. The two broods were probably the offspring of two females. A similar case of two broods from a family outside my study area has been noted in the discussion of the care and feeding of young. The 32-day old young bird of the second pair of Red-throats on my study area followed the male on July 27 while the female incubated two eggs of the next brood. No Red-crowns on the study area reared two broods; but a pair on an adjacent area had a juvenile about 40 days old with them on August 1, the day when two young left the nest. High rates of predation, and the low clutch sizes of tropical

species, probably account for the finding of Davis (1946), corroborated by my observations at Gallon Jug, that "the number of young birds in the tropics does not at any time reach the high levels of the temperate regions." The predation-induced slow recruitment of young birds may insure that the food supply in summer is not over utilized by a large crop of young in a restricted period.

Although it may be theoretically advantageous for young ant-tanagers to leave the nest at an early age for reasons already noted, mortality of young out of the nest was rather high. When I left, only four out of seven young Red-crowns to leave the nest on my study area and elsewhere were still alive (average age of survivors, 19 days); only two out of nine young Red-throats were still alive, at ages of 19 and 73 days. Most of the young that disappeared did so within a few days after leaving the nest.

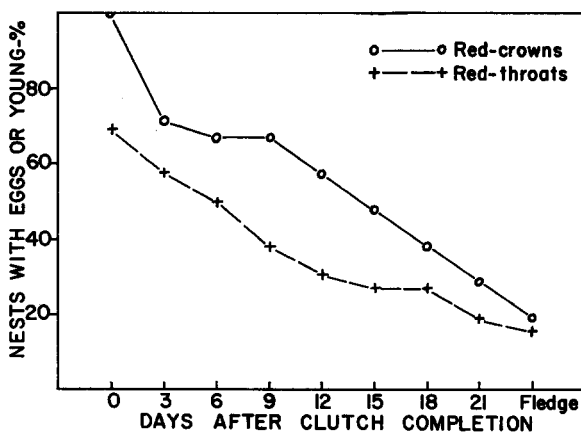


Fig. 9. Percentage of nests of ant-tanagers still containing eggs or young at various times after completion of clutches; figures are based on 21 nests of Red-crowns and 26 nests of Red-throats. Young hatched 12 to 14 days after completion of clutches and left the nest 21 to 24 days after completion of clutches.

Eggs of Red-crowns were lightly speckled, and eggs of Red-throats were white. Ever since it was first observed that most birds that nest where their eggs are hidden lay eggs lacking pigment while most birds that nest where eggs are uncovered on leaving the nest lay colored eggs, it has been repeated that pigments make eggs less conspicuous. Why should ant-tanagers lay "conspicuous" eggs? It may be that, if a nest is situated on a predator "route," it is an advantage to an ant-tanager to have the set of eggs destroyed early, thus giving more time for a renesting that may be off the predator routes, rather than after several weeks of effort have been expended raising doomed young. Figure 9 gives some support for this hypothesis, since the main destruction of the eggs of ant-tanagers may be seen to fall within the period of egg laying and the three days thereafter. It is to the advantage of a repeatedly nesting species to show a low curve on such a graph, granted that the end point is as high as possible.

The eggs disappeared from eight nests of Red-throats. At some nests eggs were destroyed on the day of laying. A female Red-throat never incubated the remaining eggs of a clutch in which even one egg had been destroyed; she laid the other eggs of the clutch and then deserted the set, which at times remained in the nest several days before a predator took it.

SUMMARY

At Gallon Jug, British Honduras, each pair of Red-crowned Ant-Tanagers (*Habia rubica*) under observation nested from late March to August or later in 1957; Red-throated Ant-Tanagers (*Habia gutturalis*) began nesting in late April.

Nests of Red-throats were loose and leafy structures which needed support underneath. The thin but compact nests of Red-crowns, woven of epiphyte rootlets, rhizomorphs, and similar materials, were sometimes pensile.

Females of the two species differed less in their methods of hunting for material and of working on nests than in their choices of materials. Once a nonbreeding bird of a family of Red-throats helped the female build a nest. Nests were nearly complete after three mornings of work. The interval between the start of building and the laying of the first egg averaged seven days for Red-crowns and six days for Red-throats.

Three eggs, laid on successive mornings, formed the usual clutch. Females incubated about 70 per cent of the hours of daylight during incubation periods of 12 to 14 days. Thereafter the time spent brooding decreased rapidly from the level of 70 per cent.

Of the feedings of Red-throats, 33 per cent were made by males; but only 14.7 per cent of the feedings of Red-crowns were made by males. Nonbreeding birds in two families of Red-throats helped feed young. The rate of feeding increased as young grew older. The rate was faster in larger broods, but not in direct proportion to the number of young. Feeding was only slightly less frequent during the afternoon hours than in the morning.

Young of Red-crowns and Red-throats were quite similar in growth of feathers, even though Red-crowns left the nest when ten days old and Red-throats left when eight or nine days old. Young of both species were small and poorly feathered after leaving the nest and could barely fly for two or three days thereafter. Adults gave distraction displays when fledglings were approached. Juveniles attained full tail length about four weeks after leaving the nest.

One pair of Red-crowns apparently raised two broods, and one pair of Red-throats had eggs in one nest while the male fed a young bird out of the nest. Two families of Red-throats raised two broods each, but in these cases each male was probably bigamous. One male Red-crown had two mates and two nests at the same time. However, most pairs did not raise even one brood, even though several pairs probably nested more than five times during the three or four months in which I observed breeding. Unknown predators robbed 43 of 53 nests of ant-tanagers.

Probably many aspects of the nesting of ant-tanagers are influenced by the high danger of predation in tropical forests. Very long attentive periods alternated with long breaks and thus reduced the number of arrivals and departures per day. Females and their mates tended to approach nests very carefully. Eggshells and fecal sacs were eaten, at least when young were small. Such behavior eliminated the necessity of carrying away conspicuous objects or of making special trips to do so. Young Red-crowns were fed large arthropods, which the younger nestlings had trouble swallowing; but the large size of food particles may have made frequent feeding unnecessary. Perhaps the premature departure of nestlings reduces their vulnerability to predators, but there was rather high mortality of young out of the nest in this study. It seems likely that the short length of each nesting cycle makes it possible for ant-tanagers to produce young birds despite frequent destruction of nests.

Some aspects of the nesting of ant-tanagers seem inadaptive. Ant-tanagers used cup-shaped nests, not covered nests; the latter would perhaps take much time to build, thereby decreasing the number of nestings possible in a season. Ant-tanagers placed nests in

open sites, not in dense growth; but open sites far outnumber dense tangles in the high forest favored by ant-tanagers over dense second growth. Moreover, while foraging as well as while nesting, ant-tanagers kept out of dense tangles, perhaps because dense growth restricted their movements and made them more vulnerable to predators.

Possibly predation and low clutch sizes account for the slow recruitment of young into tropical populations.

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