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VOICE, COURTSHIP, AND TERRITORIAL BEHAVIOR OF ANT-TANAGERS IN BRITISH HONDURAS

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From February to August, 1957, I studied Red-crowned and Red-throated ant-tanagers (*Habia rubica* and *Habia gutturalis*) at Gallón Jug, British Honduras. This report compares the calls and songs, "courtship," and territorial behavior of these sibling species.

I am indebted to the National Science Foundation for fellowships supporting this study, to the United Fruit Company for transportation to Belize, British Honduras, and to the Belize Estates and Produce Company and the many generous people of that organization for their help in many ways at their camp at Gallón Jug. Peter Marler and the Department of Zoology of the University of California made audiospectrographic equipment available. L. Irby Davis and the Cornell University Library of Natural Sounds provided several ant-tanager recordings for analysis. The American Museum of Natural History and the United States National Museum loaned specimens for examination of crest development and other features. S. M. Russell, P. A. Daigre, and the Museum of Natural Science at Louisiana State University provided mounted specimens for tests. R. J. Newman of that Museum has taken time to examine the manuscript critically; and G. H. Lowery, Jr., directed the study.

CALL NOTES

Red-throated Ant-Tanagers.—The note most often used by Red-throats was an extremely rough, low-pitched call, commonly given at the rate of two or three per second in groups of two or three. Such notes resembled in quality the growls of an old car being started on a cold morning. Other ornithologists have referred to such noises as "wren-like" and "like tearing paper." I represented them as *waij jaij jaij*, or called them "scolds."

When Red-throats were greatly excited, as when they dashed away after I began to follow them, they occasionally gave staccato notes that resembled in quality the *scack-ack-ack!* of the Catbird (*Dumetella carolinensis*). The "chatter" of each Red-throat commonly included two to four notes, given at the rate of about six notes per second; at times several chatters were given in rapid succession. Males uttered such loud chatters more often than did females. Once a fledgling Red-throat gave a weak form of this chatter as a continuation of its *chut-chut-chip!* nest-leaving call.

The third common note of Red-throats was a low call barely audible at ten meters. I represented this note by *wik*.

Red-crowned Ant-Tanagers.—Although Red-crowns had a greater variety of notes than did Red-throats, they seemed to lack calls comparable to the scolds of the latter. Instead, the most frequent call of Red-crowns was a rapid series of as many as fifty (commonly five to fifteen) staccato notes, given at the rate of about six per second. At times the pitch and/or quality changed one or more times, as *chit chit cheut cheut cheut*, during a "chatter." Chatters were definitely modifications of *chut-chut-chip* calls, as young birds 15 to 20 days after hatching had calls intermediate between the two sound types. Males were less prone to chatter than were females.

A low-pitched *chook*, resembling the call of the Hermit Thrush (*Hylocichla guttata*), roughly corresponded to the *wik* of Red-throats.

There were many other faint notes that Red-crowns uttered: a soft, musical *ch'ree* (mainly from males); a low *ch'r*; a *wreed reed reed*; and so on. The many calls I recorded can be arranged in a number of intergrading series, and the more musical were hard to distinguish from songs.

A male observed eight kilometers northeast of San Blas, Nayarit, México, on December 28, 1959, had similar calls; but the chatters and *ch'ree* were rougher and more nasal.

SONGS AND SINGING BEHAVIOR

Each species of ant-tanager had two distinct major songs, which I shall call "day songs" and "dawn songs," although the implications of these names are correct only for Red-crowned Ant-Tanagers.

Red-crowned Ant-Tanager.—Rough chatters graded into the somewhat burry *cheer cheer cheer cheer* (fig. 1C) of the simplest day song merely by a slowing of the tempo from more than four to about two or three notes per second and, apparently, by an elision of some of the tones so that the rough noise became a fairly pure whistle. In all the variants of the *cheer* type of day song each slur or couplet descended in pitch; a type of day song in which each slur or couplet rose in pitch was nearly as common. The males seemed to say *pirtee pirtee pirtee pirtee* in the latter type of day song. Variants and combinations of the two song types were numerous.

Day songs varied in the number of notes (one to ten, but usually three or four), in force, and in frequency of delivery. As the singing male turned his head the volume of

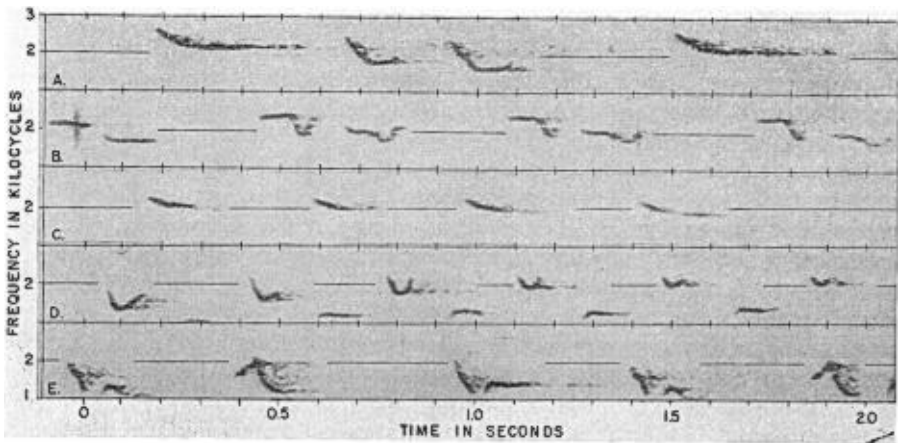


Fig. 1. Narrow-band audiospectrographs of ant-tanager songs. A, *peer, p'yerk pewk, peer*, dawn song of Red-crown from 10 miles south of San José del Carmen, Veracruz, México. B, *purtor, peter, peter, peter*, dawn song of Red-crown from Gallon Jug. C, the *cheer, cheer, cheer, cheer* day song of same male as in B. D, *purtor purter pur tirpee tirpee tirpee*, day song of a Red-throat from mountains above Tuxtla Gutiérrez, Chiapas, México. E, *ch'bewk, whewk, ch'berk, ch'bewk, whew*, fragment from dawn song about three times this length, from male Red-throat near Coatzacoalcos, Veracruz, México. (A, D, E by Irby Davis.)

the song waxed and waned, suggesting that the whistles were directional in nature. Figure 2 shows the variation in the frequency of one male's songs at a time of day when songs were most regular. When a male was singing uninterruptedly, some ten to twelve songs were uttered per minute; pauses between songs were as long to twice as long as each song.

Singing males often foraged, chased females, disputed along a territorial boundary, or occupied themselves with other activities. The males adopted no special postures; only the opening of a bill, a slight downbeat of the tail with each slur or couplet, and a pulsing of throat feathers as a male looked around showed the origin of a voice. Occasionally males sang in flight or when eating, but consuming large insects or fruit usually halted singing temporarily.

Day singing began in 1957 in late February, about a month before the females began building nests. For a time song was infrequent, but by the end of March all the adult males were singing, especially in the two or three hours after sunrise. Red-crowns were still singing when I left in early August, but the song periods were as short and infrequent as in early March.

In contrast to day songs, dawn songs varied detectably between individuals, and each individual rarely had more than one type. The simplest type of dawn song, a flute-like *peter peter peter*, was seemingly a strong and deliberate day song. Only 11 out of 24 males I heard at Gallon Jug had dawn songs audibly different (fig. 1B) from this type. Songs recorded by L. Irby Davis in Veracruz (fig. 1A) differ no more from songs I heard in British Honduras than some of the songs at Gallon Jug differed from each other.

The dawn song of the immature male of one family, first heard on May 24 in a whispered version, had by July become indistinguishable from the dawn song of the adult male of that family. The adult males on two adjacent territories had a similar song type, but the adult males on two other adjacent territories used the simple *peter peter peter peter* type.

The three-quarters of an hour before the sun broke through the low dawn clouds over the ridge east of the study area was the usual dawn-song period (fig. 3).

Unlike day singing, dawn singing was seldom interrupted by other activities. The first few songs, as each male moved from back in the forest toward his dawn-singing area, were often short and somewhat irregular in frequency of utterance. But as each male reached his song area, dawn songs came with clocklike regularity; he even sang in flight as he ascended from perch to perch toward his station.

Individuals differed in their singing rates, for some averaged only 8 songs per minute while others averaged up to 12. The full-length songs of the main period of song came about the same number of times per minute as the short versions of the beginning and end of the period. None of the birds at Gallon Jug gave more than six slurs or couplets per song; but on the Pacific slope near Colomba, Guatemala, Skutch (1954) heard Red-crowns giving seven to nine notes in their dawn songs. Males near Skutch's home at El General, Costa Rica, chanted monotonously, somewhat in the fashion of the dawn singing of Red-throats. No Red-throated Ant-Tanagers occur in that part of Costa Rica.

Most males on my study area (fig. 5A) sang from the edge of the forest, on a road or beside a plantation or patch of second growth. Males with territories which did not border on such areas sang in isolated treetops rising above the level of the surrounding forest. The dawn-singing station generally lay near the edge of each territory, not in the center. This might have been because the open areas were generally at the edges of the ant-tanager territories mapped here rather than within them. Whether there is any tendency for territories to radiate from open areas within the main forest is not known. Nor do I know whether the song areas tend to be on the peripheries of territories in less broken woods than those of the study area. Commonly two or three males sang near each other, even in areas of unbroken forest.

The favored perches were most often below the tops of song trees, on bare branches near the centers of the trees rather than in dense peripheral foliage. Hence the males sang from perches quite different from their usual foraging perches in the undergrowth.

Often males that sang close to the ground became nervous as I approached, turning back and forth and hopping about. If I moved closer, they flew to other perches. One such male moved from one perch to another around a small cornfield when I entered it, once singing from a log on the ground. The birds that sang 25 meters or more up rarely moved more than a meter while I watched.

The dawn-song period was the only time that the brilliant scarlet of the Red-crown crests was consistently displayed. Every bird I saw seemed capped by a crown of fire

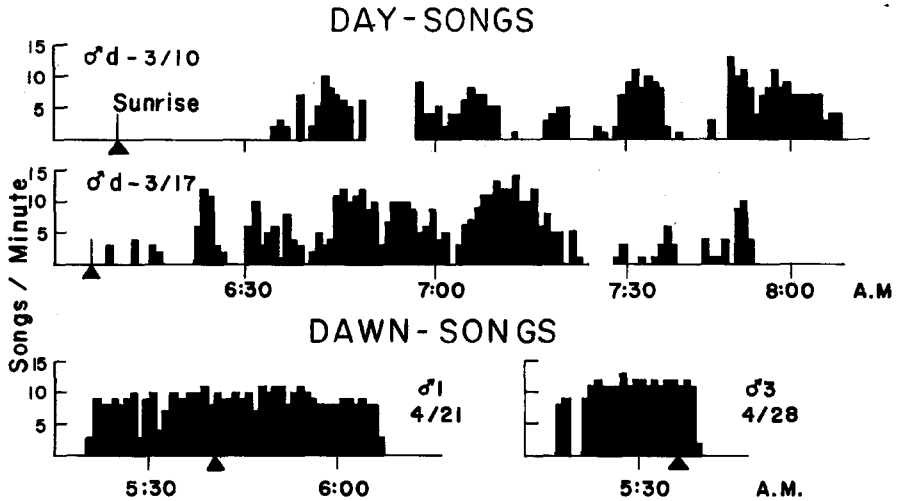


Fig. 2. Timing of day songs and dawn songs of Red-crowns.

during the whole period. Even later in the day, on the few occasions when one uttered dawn songs in boundary disputes, each repetition of the song brought a lifting of the crest, followed by a drop before the next song. Some adjoining dawn-singing males may have been able to see each other, but most males probably could not; however, the females wandering about nearby undoubtedly could see their fire-crowned mates at times.

During most of the dawn-song period a singer typically held his tail and body in line, little inclined above the horizontal. His body plumage was seldom fluffed out although his tail was often partly spread. His looking around was interrupted only for a song, which he usually gave with beak in line with the body, throat pulsating, beak moderately open, body quivering slightly, and the tail jerking a little at each slur or couplet. Less often the singer sat with tail down like a flycatcher or singing finch, or hopped along the limb as he sang.

As the sun broke through the morning clouds the chatters of the female and other members of the family came now and again from the nearest forest edge or below the male, and he began to move about more actively. Eventually he flexed both wings, looked around, and dropped shrike-fashion to about two meters above the ground before leveling off to streak away toward his family. At times the drop was made in steps, with a song or two at each stop; on a few occasions a last song or two drifted back from the interior of the forest after the male's descent, or irregular singing persisted there for several minutes. But more often a silent descent was followed within a minute by an

outbreak of chatters and *chauf chauf* notes as the male chased his mate about. Then the first day songs began, and the family went off to the affairs of the day.

When bringing food to young in the nest, engaging in territorial disputes, or shaking vigorously after bathing, the Red-crown males poured forth at times what Skutch (1954) has aptly described as a "softly warbled refrain of singular beauty." Often the singer quivered with his warbling, fluttering his wings rapidly and raising his tail in the manner of a female in the precopulatory display. Among the commonest sounds of the

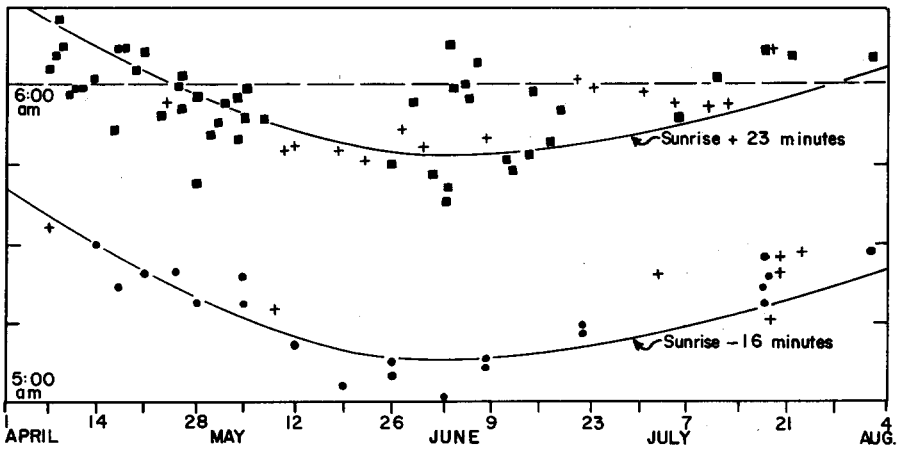


Fig. 3. Times of beginning (dots) and end (squares) of dawn songs of Red-crowns. Crosses indicate singing was in progress.

warbling were two that may be represented as *turree-e-e-e* and *kiss'l*. At territorial encounters, but rarely at other times, rough and low chatters and sometimes a day song or two were intermixed with the warbling.

Red-throated Ant-Tanager.—The day song of Red-throats was a rapid series of whistles that bore no resemblance to their harsh scolds. In its alternation of two kinds of notes on a rising scale (fig. 1D), this song was quite different from any song of Red-crowned Ant-Tanagers. The song may be represented as *pur'-tor-pur'-ter-pir'-tir-pee'-tir-pee'*.

The day songs of Red-throats averaged 11 to 15 notes in length. The speed varied considerably, averaging five notes per second. Amplitude ranged from soft to loud within a single song. At the nest, songs were barely audible at ten meters, although the loudest songs were audible through the undergrowth at over 100 meters. I could never detect differences between individual males, although from one song to the next a singer often varied his songs. At times a low squawk ended a song, or the first few notes of a song were repeated as a low-pitched ending.

There were often long intervals between day songs. About four songs per minute were usual during uninterrupted singing, and there were rarely more than seven per minute.

The peak of day singing came in the hours from 5:30 to 9:30 a.m. (fig. 4). I never heard the day song before civil twilight in the morning nor after sunset in the evening. Day singing was at its height during the nesting season, although for a month before nesting this song could be heard nearly every day. In the rainy season, as other forest

birds became quiet, Red-throat singing slacked off abruptly; and after July 21 day songs were rare, although Red-throats were still nesting.

While singing, Red-throat males looked around as if foraging, tails no more spread and bodies no more fluffed than usual. Although I never saw a male eat during a song, in the way that Red-crowns did, Red-throat singers occasionally interrupted singing and captured an insect or other arthropod.

The dawn songs of Red-throated Ant-Tanagers were deliberate chants, strikingly different from the dawn songs of Red-crowned Ant-Tanagers. In its simplest form at

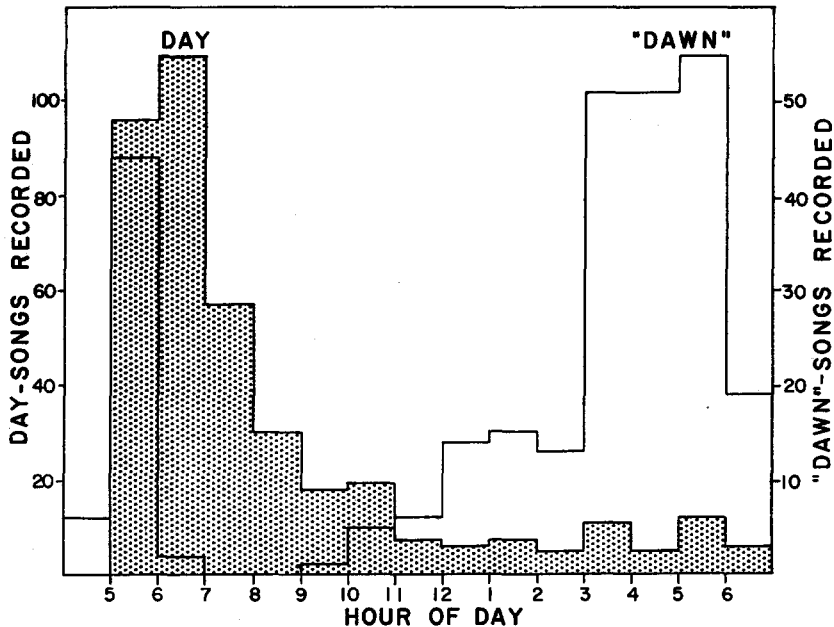


Fig. 4. Hourly record of day songs and "dawn" songs of Red-throats.

Gallon Jug the dawn song of the Red-throat was a measured chant of two or more (commonly 12 to 15) staccato notes in phrases of three: *chuk, per, chick, chuk, per, chick, chuk* and so on. Four out of 14 males on my study area used such a song. The most complex of the variants used by the other males were the closely similar songs of adjoining males XI and IX (fig. 5B); *pee-oh, perk, chork, p'ree, cherk-puk-peeoh, perk, chork, p'ree, pee-oh, perk* and so on. Figure 1E is an audiospectrograph of a song recorded by L. Irby Davis near Coatzacoalcos, Veracruz, México; it differs little to my ear from songs at Gallon Jug.

Dawn songs were given at a steady pace of about two notes per second. Exact repetition of phrases was not the rule; one or two notes in a phrase might be varied or omitted. The songs began and ended on any note of a phrase, giving the songs an incomplete sound when the ending did not correspond with the end of a phrase. Usually five or six songs were given per minute during uninterrupted singing, rarely as many as nine. Neighboring singers often had similar songs, as did Red-crown neighbors. An occasional male Red-throat used a dawn song similar to that of a neighbor when the neighbor was singing, whereas he used a different song at other times.

Dawn singing was mainly restricted to the actual nesting period, which started in

early April in Red-crowns and in late April in Red-throats. At times of noisy scolding at dawn and dusk, I heard a dawn song of a Red-throat once in February and once in March.

Unlike the dawn singing of Red-crowns, the dawn singing of Red-throats was not restricted to the hour of dawn: I have heard these songs at every time of day except the period from 5:45 to 9:15 a.m. (fig. 4). The two early records for Red-throat dawn singing are 4:43 a.m. on May 26, 18 minutes before civil twilight, and 4:56 a.m. on June 3, 5 minutes before civil twilight. The late record is for 6:50 p.m. on July 10, ten

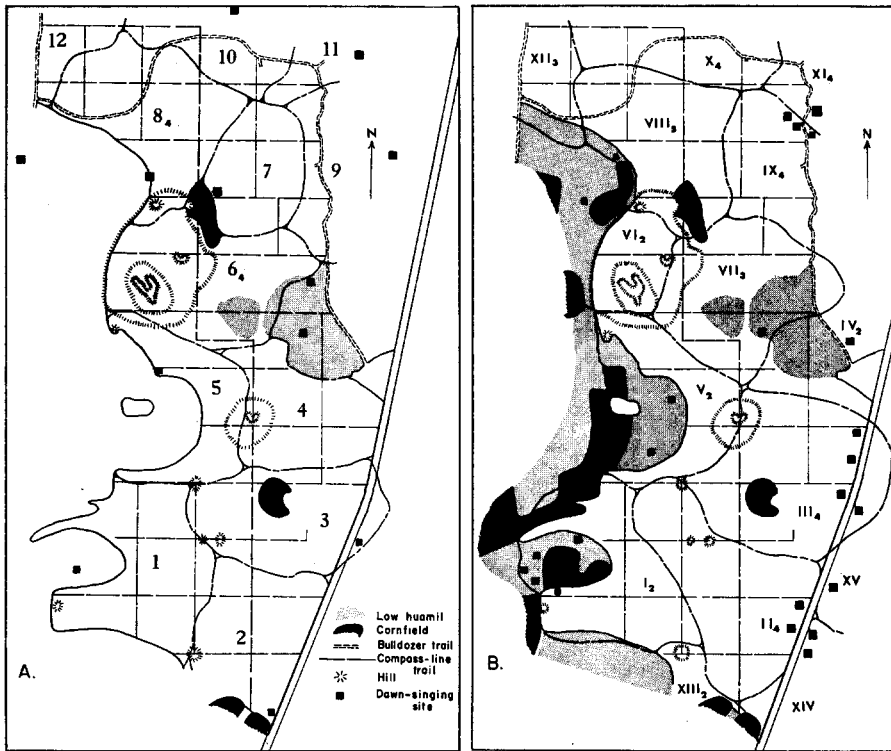


Fig. 5. Territories of pairs and families of ant-tanagers on study area at Gallon Jug. Length of arrow represents 100 meters. A subscript to a territory number indicates number of birds occupying that territory. A, Red-crowns; B, Red-throats.

minutes after sunset. The dawn songs of Red-throats came sporadically at times, broken by long pauses or short periods of day singing. But at other times two males sang in alternation, or both chanted nearly continuously.

The end of singing occasionally came long before nearby Red-crowns finished dawn singing, but at times it ended only a few minutes before the Red-crowns stopped. One Red-throat male consistently sang late, up to 15 minutes past sunrise, even after an adjacent male Red-throat started his day songs.

The dawn-singing areas of Red-throat males were less restricted than those of Red-crown males; male I (fig. 5B) was heard singing at one time or another over the whole western half of his territory. Commonly the areas used by Red-throat males were patches of thick second growth a year or two old or the dense edges of the forest along a road,

trail, or cornfield. While singing, the males moved now and then, often with a chatter in changing perches. I was unable to creep up on them through such thickets, but fortunately happened to see a singing male once while I was sitting in a blind: "July 9—5:07–5:10 p.m. male sings near Red-crown nest. His crest is compressed, not displayed, and he is not particularly fluffed out. He sits with tail down (not spread) in finchlike pose, the only movements those of his head. To chant he merely turns his bill forward, and bill and throat feathers move slightly. Finally he turns around, leans forward into a more tanagerlike pose, and flies off a few meters to resume singing."

It is perhaps noteworthy that his crest was definitely concealed under his crown feathers. Except for one time when a male was giving a chattering and scolding series near an ant swarm, I have seen male Red-throats display their crests only during preening; I wonder if their crests are functional. Certainly, in the three species of the genus *Habia* only the crests of Central American members of the *Habia gutturalis* complex are short and rather dull in males and undifferentiated from other parts of the crown in females. *Habia gutturalis gutturalis* of Colombia, in which both sexes have long and bright red crests set off vividly by dusky bodies, is possibly a different species from the Central American members of the complex, as Eisenmann (1955) has suggested. Males of *Habia rubica* have bright and fairly long crests with contrasting dusky borders, although their females have yellow crests that are much less striking than the red crests of females of *H. g. gutturalis*. *Habia cristata* of the Colombian Andes has a longer crest than *H. g. gutturalis*.

Since dawn-singing Red-throat males sang far apart in dense undergrowth, and since their dawn songs were generally given while females were on their nests, probably crest raising could serve no communicatory function in a dawn-singing situation. But Red-crown males, which consistently raised their crests during dawn singing, often sang from conspicuous perches while their mates were nearby.

COURTSHIP AND MATING

The *chauf* notes of Red-crowned Ant-Tanagers consisted of one to several very rough, low notes that in quality approached some scolds of the Red-throat. Male Red-crowns at times used such notes, especially when chased by another bird of the family in a food dispute. Frequently while the female of one Red-crown family was on the nest, the adult male chased the immature of the family. The immature gave *chauf* notes each time, but my supposition that it was a female was proven wrong when the young bird started acquiring red male feathers in July. However, the *chauf* notes were most often uttered by females being chased by their mates. These notes were among those frequently used when a female flew past her mate on leaving the nest; he chased her if he did not have food for the young. Although the immediate effect of such *chauf* notes was to break off a chase abruptly, the male often chased his mate again after a brief pause.

Female Red-throated Ant-Tanagers had, instead of special "chase" notes, outbursts that were generally associated with the day songs of their mates. Such outbursts consisted of light scolds interspersed with rapid conversational notes; I represented one such series as *waaj-tuk-tuk-waaj-tuk-tuk-tuk-waaj-waaj-waaj-waaj*. The effect can be approximated by whispering the word "agitate" very rapidly, with emphasis on the "ag" parts. The first time I heard day songs and such female outbursts was on March 23, when, in one of the first territorial disputes I witnessed, one female started these calls during day singing of the males and both males started chasing her. This was the only time when male Red-throats were seen to chase a female. Either the start of the female's outbursts set the male off on each day song or she detected when he was about to start, for her outburst rose in speed and volume a second or so before his song and continued

at a high level during it. The male usually sat calmly as he sang, but the female turned from side to side and dashed about rapidly. The *waaj-tuk* outbursts were among the notes used by females leaving the nests when their mates arrived with food for the young, a situation in which the males usually gave day songs.

The precopulatory displays of female ant-tanagers of the two species were similar in several respects. As a female of either species fluttered her spread wings through a small arc, she lifted her tail like a Hermit Thrush in slow motion. The latter action revealed her anal circlet as her abdominal feathers drooped nearly to the perch on which she stood. At times the female tilted far forward in her displaying and in returning to a more normal position went into an "upwards" position (a rather similar posture is illustrated for thrushes by Dilger, 1956) with bill up and throat prominent. At low intensities of display, when the precopulatory notes were uttered briefly, only slight quivering of the wing tips was retained from this behavior pattern. Even following copulation a female might repeat the performance over and over, with brief pauses when she looked around for food or preened busily. Displays were usually given at normal foraging heights. Once I saw a female Red-throat display on the ground in a bulldozer trail, but horizontal limbs and twigs were the usual places selected.

One difference between displaying female ant-tanagers of the two species was in the notes they gave. The notes of Red-crowns were *che* notes given so rapidly that the series sounded like *che-e-e-e-e-e-e* to me. The notes of female Red-throats were slower and more variable, a *chee cheu chee cheu cheu cheu* like the peeping of a flock of baby chicks, averaging some six notes per second. Another difference between female Red-crowns and female Red-throats was in the spread of their crests. The crest of each female Red-crown was ruffed up and showed its yellow center as at no other time, whereas female Red-throats, which lack such a decorative center, barely raised their crown feathers. It was my impression that female Red-throats looked around with bills pointing up more than did female Red-crowns; the bright yellow bibs of the former were made conspicuous by this movement. Although female Red-throats spread their fluttering wings up, out, or down, I never saw a female Red-crown spread her wings in any direction but slightly above horizontal.

Males of the two species differed little in their precopulatory behavior. Both hopped or fluttered toward their females with tails down and spread, the feathers perhaps fluffed a little. On some occasions male Red-crowns held their wings upstretched for the brief moments they were on the limbs beside their females, both before and after copulations. Once a male Red-crown uttered a loud series of *jee* notes when he flew to the female, and at times a few faint notes preceded the copulations of either species, but usually actual coitus was silent. The females were nearly always concealed from my view in fairly dense foliage when the males went to them. Copulations were sometimes followed by bathing or preening sessions. Rarely an immature bird came up near a displaying female, and one immature Red-throat crowded the female off her perch; but I never saw an immature attempt copulation.

The precopulatory calls of female Red-crowns were given at all stages of nesting except for periods when a female was searching for a nest site. But I noted high-intensity displays and actual copulation only during nest building and egg laying. Red-throat females limited their displays in the main to the two latter periods.

Although in voice and behavior of both sexes there are many interspecific differences that may reduce the possibility that mixed pairs of ant-tanagers could form, persist, and give rise to interspecific hybrids, the important process of pair formation is as yet unknown for these birds. All the males on my study area had mates when I arrived, and they probably stay mated all year. Unfortunately, I did not see how one male obtained

a new female when his mate was killed by a Ferruginous Owl (*Glaucidium brasilianum*) as she returned to her nest with food for her young at noon on May 26. The next noon this male had a new mate, which he chased with great vigor and persistence; a *chauf* series came from the female each time he chased her. The new female began a new nest the following morning.

DISPLAYS AND TERRITORIALITY

The two species of ant-tanagers held territories overlapping interspecifically but not intraspecifically (fig. 5), which implies that each species could somehow distinguish its own species from the other. The ability of the birds to recognize their own species by voice was obvious. The sound of distant song and chatters of Red-crowns brought eventual investigation by a male Red-crown whereas it would leave nearby Red-throats unmoved. When I whistled Red-crown day songs in the forest, only Red-crowns came up and investigated. A distant song or scold of a Red-throat never brought any response from a Red-crown pair, but it often brought forth a song or two from accompanying Red-throats, with perhaps rapid movement toward the intruders.

Some experiments were performed to test whether the two species can tell each other apart when one or both are quiet. Dilger (1956) tested five species of thrushes of the genus *Hylocichla* with painted models and found that all models were attacked indiscriminately unless he played back a recording of the voice of another species when he presented the models. To see if the ant-tanagers were unable to tell their own species from another by sight alone, I placed before them mounted specimens kindly prepared by P. A. Daigre. These were employed in about the same manner in which Dilger used his painted models before he played recordings. Since the mounted birds could not give vocal or behavioral cues, any recognition by the ant-tanagers would be based on appearance of the mounts alone.

On the five occasions when the mounted male Red-throat was set up within two to seven meters of different Red-throat nests, the resident male at each nest attacked it violently on his first return, although not on later visits. Five times when a mounted male Red-crown was set up in similar positions it was ignored; the models were left up for two to four hours on each occasion. On another occasion, when I set the male Red-crown up so that its left eye was oriented directly toward the Red-throat nest and about five meters from it, this reaction ensued: "May 27—(female, male, and immature just back to nest; female with material). Immature flies over my blind to the tree on the other side of the nest, scolding noisily, with tail spread. Female freezes on nest, and male comes up and looks at *Habia rubica* mount. He sits with tail spread and breast ruffed out. Then he hops around in front of mount and starts a very faint irregular growl, holding his bill open and tail spread. Female resumes work on nest, but her movements are slow and inconspicuous, and she sits very still for long periods. Finally male flies away with immature, one of two scolding; and soon female follows." On the preceding day the local male Red-crown had been greeted by a similar display when he came near this nest; his reaction had been to retire a few meters and resume foraging. On only one occasion was the Red-crown mount attacked violently by a male Red-throat; but the attack was not as violent as that on the Red-throat mount I had just removed from the spot.

Twice when I put up a male Red-crown mount near a Red-crown nest, the male attacked it violently on his first visit. Twice when I put up the male Red-throat for two to three hours near nests that were being visited every few minutes by the pairs, there was no reaction. On a third occasion I set the male Red-throat only two meters from the base of the sapling in which Red-crowns were building their nest, and I obtained this

reaction: "June 13 (second visit of pair after start of test)—7:38.15 to 7:38.40 a.m. Female flies to nest from east with nest material and works as male flies to limb near her and looks down toward Red-throat mount. Tail down and spread, body fluffed, he flutters down past the mount, tilting it slightly. He fluffs out again as he perches under it, but then looks up and seems to lose interest, compressing feathers and flying off nearby." The crests of ant-tanager specimens show more conspicuously than the crests of live birds; when viewed from above, this mount showed a crest nearly as conspicuous as that of a male Red-crown in partial dawn-singing display.

The male Red-crown that reacted to the Red-throat mount had not helped his female at her first nest, but when I set up the mounts at this nest I obtained interesting reactions, one being the only reaction I ever obtained from a male bird distant from his nest. "May 3 at 8:12 a.m. I set up the mounted male Red-throat. At 8:19 male Red-throat I suddenly appeared on the log beside the mount. He looked, puffed out his abdominal feathers until they covered his legs, and kept his tail down and slightly spread. He hopped along the log silently, once stretching his bill and head upward. Then he flew at the mount, alighting on top of it, his wings up and fluttering. The mount tilted forward, and the male flew to a nearby bush. He looked back toward the upside-down mount and ruffed his body feathers again; but his head and crest feathers were compressed, giving him a small-headed look. He flew to the limb above the mount and pecked down several times at a pin sticking from its right wing. He fluffed out again, and flew off to another perch. Back to the mount he flew, pecking it a few more times. Then he departed silently, about 8:22 a.m. His tail was never spread much, nor his head and neck feathers." When I put up the male Red-crown at the same spot later that day, the female Red-crown behaved as if it were her inattentive mate. During both periods when I set the mount up she flew past it on leaving with *chauf chauf* calls followed by chatters and gave a few soft notes each time she approached the mount and the nest; but during an intervening period when I removed the mount her visits were as quiet as usual.

Hence it seems likely that the ant-tanagers were able to detect the slight differences between the two ant-tanager species on sight, although more tests are needed to be certain. What morphological cues are important in such recognition, and whether this ability is characteristic of the two species in areas where the two do not occur together, are also interesting questions for further investigation.

Meetings of two families of the same species near the common edge of their breeding territories were occasional in February and March; the groups foraged together peacefully for varying lengths of time before the trespassing group returned to its own area. But as the day songs of the males began, this camaraderie waned, and by the beginning of nesting each group had only one adult male, who tolerated no adult male intruders of his species on his territory. Now the females and immatures might chatter or scold as they foraged together with little sign of animosity, but their males disputed busily as the two groups moved along the boundary line between the two territories.

Although I was able to view the wary Red-throats at boundary disputes on rather few occasions, my observations are consistent in indicating that boundary displays are reduced to a minimum in this species. Crest and head feathers were sleeked down, but body and tail feathers were spread to varying degrees, as opposing males hopped along and looked toward each other. Ritualized movements were few and irregular; the only distinct one was an "upward wigwag," with beak pointed upward stiffly as the displayer turned back and forth in a wigwag or sparring motion. At times one bird opened its beak slightly, but no sounds emerged. Suddenly one male would dart at the other, which would retreat a few meters; or there might be no attack. Usually the pair I had been following moved back into its territory on a new course after a few seconds of such display. At

times a few day songs were exchanged as the pairs separated. Once I saw a male come back past his female after a rapid chase of another male down a boundary line. The body plumage of the returning male was puffed out as he fluttered along like an Eastern Kingbird (*Tyrannus tyrannus*) and gave a stream of *scack-ack-ack* chatters. Such loud chatters often burst from a male as he left after a violent attack on a mounted male.

Territorial displays of Red-crowns were more complex than those of Red-throats, although they were highly irregular compared to the stereotyped patterns of display of many birds. In Red-crown territorial disputes, songs played a major part. At times two males sang back and forth for some time without coming into sight of each other. But if a rival persisted in singing while foraging along or across the boundary between territories, the resident male sat with tail down for a minute or two and then darted through the forest toward the intruder. As the two males approached and faced each other, they uttered a varied assortment of day songs, chatters, warblings, and other notes. The louder songs were more frequently used when the males were far apart, whereas softer songs prevailed at close range; but loud *p'ree p'ree p'ree* songs occasionally poured out as two males foraged scarcely two meters apart. Otherwise the varied vocabulary fell into no consistent patterns.

Frequently a male picked off an insect or a berry and sang between gulps as he ate it. Because the males made a great show of foraging, a casual observer of a boundary dispute might think that the two families were foraging along peacefully together were it not for the varied songs and occasional displays.

Movements of the males such as their frequent bill wiping and looking at their feet may have had display significance. Occasionally bouts of spasmodic preening interrupted the more protracted disputes. The two males seemed to avoid looking at each other, but even when one foraged within a meter of the other each stayed on his own side. Crest and head feathers were usually sleeked down, so that the dark edges of the crown formed a zigzag seam that completely concealed the scarlet crest; but the tail and body feathers tended to be somewhat spread.

The only distinct display besides the wing quivering during warbling was the upward wigwag display. Unusual postures, some with wings outstretched, were used by males in attacking mounts, but not in boundary disputes.

Supplanting and chasing was uncommon. On the few occasions when a trespassing male had wandered some distance inside the owner's territory before the latter arrived, the owner sat quietly for an instant with tail down and spread. With no other posturing, he darted suddenly at his singing rival, which dropped backward off the perch after gaping briefly. At times there were two or three such attacks before the intruder was near enough to the boundary that the usual singing and foraging began once more. A bird attacking a mounted bird pecked at it as he hit it and knocked it over.

One immature was an active participant in boundary disputes. The adult male of the family never displayed against his immature, which was developing dawn song and day song while I was there, and the immature came to help him in boundary disputes with adjacent males. As early as April 17, when the immature was singing infrequently, it helped the adult male in a dispute with another male; the latter directed a supplanting attack at the immature even though the adult male sat singing nearby. By July, when the immature male obtained his first red feathers, he was even more eager for battle than his adult male. The immature then engaged in warbling and display duels with rival males while the adult male sang day songs out of sight some 30 or 40 meters from the boundary. Why did the adult male not react to his immature's songs in the same way that other males did?

Territorial disputes were most frequent on boundaries in parts of the forest where

the undergrowth was sparse. As Red-crowns spent much of their time foraging in such areas, this might have been expected; but other boundary lines in similarly sparse undergrowth rarely were defended. Certain males argued frequently along certain boundaries and hardly ever disputed with other males on other boundaries of their territories.

Territorial disputes of Red-crowns were often prolonged. One dispute between three males lasted at least 65 minutes before the males separated. The average length for 52 disputes was about 17 minutes.

Six territories of Red-throats averaged about 5.7 hectares (15 acres) in extent while eight Red-crown territories averaged about 4.5 hectares (about 12 acres). When one male Red-crown disappeared, seven males occupied 5.2 hectares each. Territories were mapped by following families; generally points of boundary disputes counted as boundaries, while on segments where no disputes were seen the mapped lines (fig. 5) lie near the midpoints between the wanderings of each two pairs, whether these wanderings overlapped or not. Fortunately each pair ordinarily wandered over its whole territory looking for food, and it rarely trespassed more than a few meters into areas where I followed the neighboring families at some time during the nesting season. Dawn-singing areas of

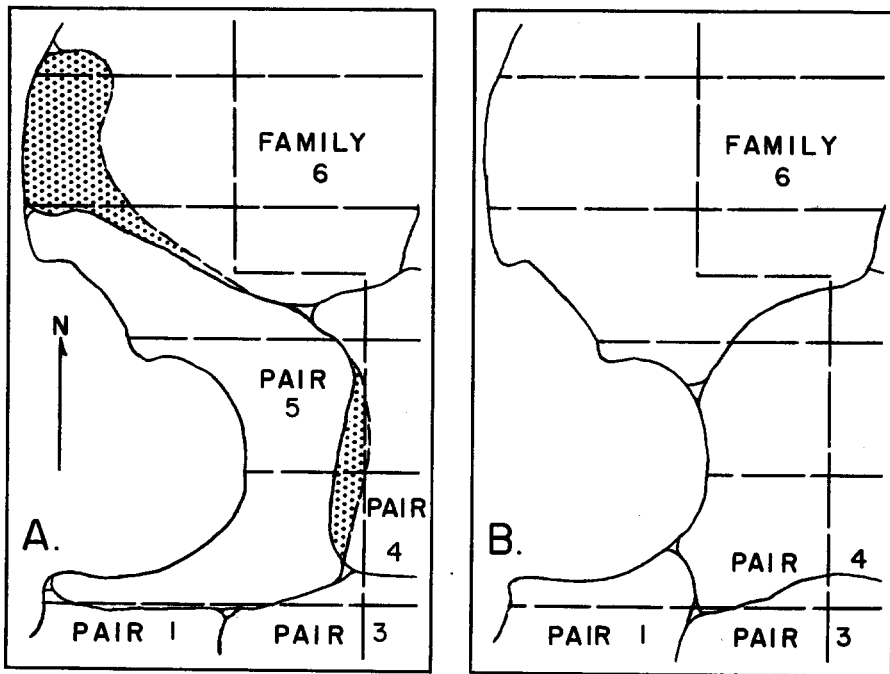


Fig. 6. Changes in the ownership of territory 5. A, February to April. The territory added by male 5B is stippled. B, May to August.

males are not included in their territories when the males sang from areas they never used at any other time.

The censuses of Davis and his co-workers in México (1952, 1953*a*, 1953*b*, 1953*c*, 1955, 1956) have generally reported denser populations of both species on sample plots of 15 acres (about 6 hectares). Most of their estimates show from two to four territorial males per sample block, which if literally interpreted would mean two to five times the density of breeding males I noted at Gallon Jug. However, the probability that most of

the males Davis and his companions recorded had only parts of their territories in these small sample blocks must be taken into account. Other than these censuses, I know of no other estimates of ant-tanager density.

The changes following the disappearance of Red-crown male 5 on April 8 after 7:08 a.m. were quite interesting (fig. 6). He was not at his dawn-singing post the next morning, and that afternoon as I followed pair 4 they drifted across into the territory of pair 5. Male 4 sang occasionally, but no challenges came from any resident male or female.

On April 10 at 3:18 p.m. a new male, distinguished from other males on my study area by two green feathers separated by a red one in his tail, was busy in a boundary dispute with male 6 near the top of the hill near the north end of pair 5's old territory. Whether the female with this new male was the original female 5 is unknown. In the following days disputes between male 5B and neighboring males 4 and 6 were frequent and vigorous, as 5B established his territory over and beyond the area that 5 had defended. By the end of April, 5B had taken up the same dead tree that 5 had used for a dawn-singing perch and was alternating a *peter peter peter peter* such as 5 had used with a variant of his own. But May 2 was the last time I heard his dawn song, and for a time there was no replacement.

Within two weeks, 4 and 6 had halved his area and were using the halves as parts of their territories. August 1, the day before I left Gallon Jug, I met a new, noisy pair in the south half of old territory 5. The male was just changing to the red adult plumage. Possibly this was an early stage of territory establishment.

SUMMARY

At Gallon Jug, British Honduras, the Red-crowned Ant-Tanager (*Habia rubica*) could easily be distinguished from the Red-throated Ant-Tanager (*H. gutturalis*) by its rapid chatter, quite different from the latter's rough and slow "scolds." Chatters were given at a rate of some six notes per second, scolds at a speed of about three notes per second. Other call notes of these sibling species also differed considerably.

The distinctive songs of male ant-tanagers included dawn songs and day songs. The dawn songs of Red-crowns and Red-throats were given at sunrise, but Red-throats also gave dawn songs in the afternoon; the "dawn" songs of the latter species were restricted in the main to times when their mates were not present. Male Red-crowns raised their scarlet crests prominently while engaged in dawn singing, but the seemingly nonfunctional crests of male Red-throats were rarely lifted.

Female ant-tanagers had species-specific "courtship" notes. The short, rough notes of female Red-crowns were used when males chased them; noisy outbursts came from female Red-throats when their males sang day songs. Chases were infrequent in the courtship of the latter species. The precopulatory displays of females of the two species differed mainly in the peeping notes that accompanied wing-fluttering and tail-lifting. The peeps of female Red-throats came at the rate of about six per second and varied in pitch; those of female Red-crowns came more rapidly and held a constant pitch.

Male ant-tanagers defended large territories during the breeding season. The males seemed able to tell a mounted male of the other species from one of their own species, attacking the latter and ignoring the former in most tests. The females and immatures of ant-tanager families rarely participated in territorial disputes between adult males, which usually came at the boundaries between territories. The displays of Red-throats at such boundary disputes were brief and uncomplicated bluff displays. Disputes of Red-crowns were prolonged exchanges of a great variety of songs and calls and a few displays, with intervals of foraging, preening, and other activities that may have functioned as displays.

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