

A STUDY OF THE FORAGING BEHAVIOR OF TWO SPECIES OF ANT-TANAGERS

EDWIN WILLIS

THE great similarity in appearance of the Red-crowned Ant-Tanager (*Habia rubica*) and the Red-throated Ant-Tanager (*Habia gutturalis*), widely sympatric denizens of the undergrowth of Central American lowland forests (Figure 1), raises a number of questions. Some of the most interesting relate to the ecological niches of the ant-tanagers, and in particular to their reputedly similar foraging activities. In an attempt to discover differences and similarities between these sibling species, I conducted field studies in British Honduras from February to early August 1957.

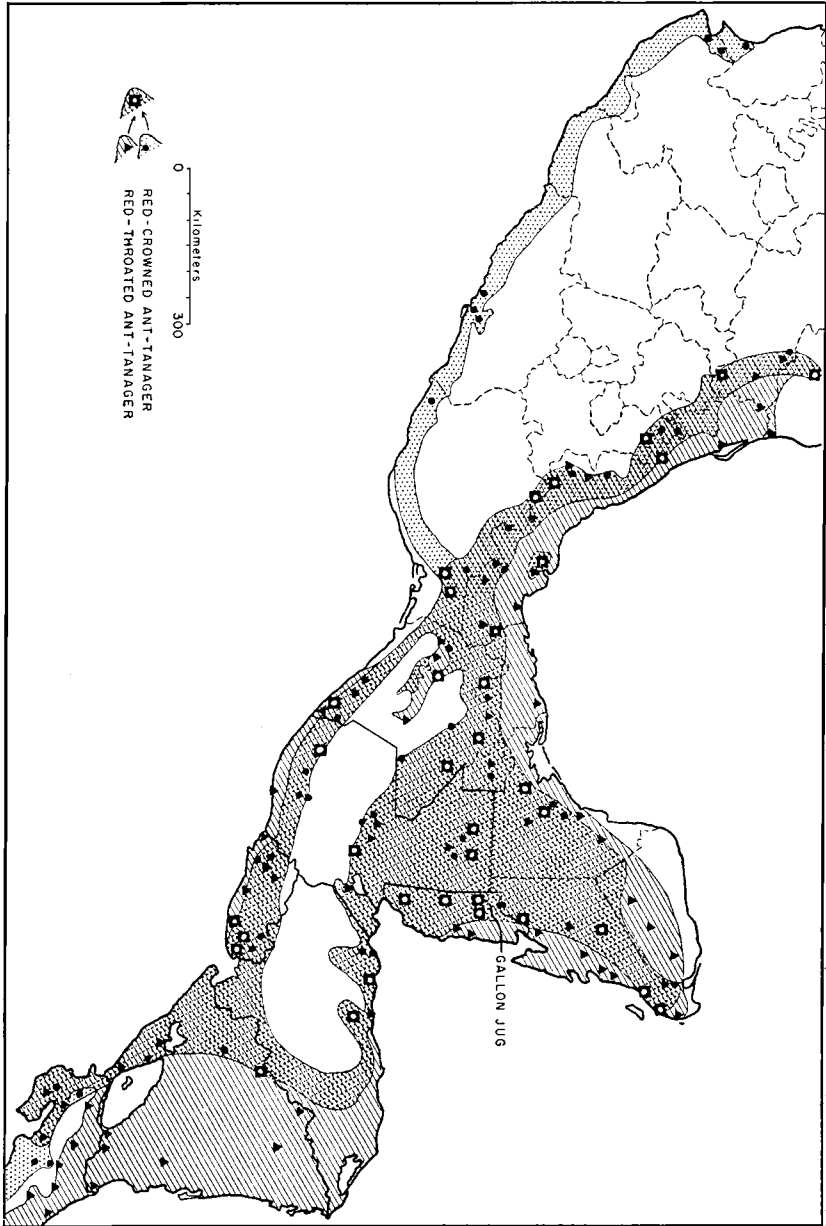
Hellmayr (1936: 300-316) recognizes three species of *Habia*. In *H. rubica*, with subspecies ranging from Mexico to southern Brazil, males are dull red, with a short crest bordered by narrow, blackish stripes; females are mainly olive, with a yellowish crown patch. The complex of forms included in *H. gutturalis*, ranging from Mexico to the valleys of central Colombia, is more varied. The forms (*salvini* group) north of Costa Rica resemble *H. rubica*, but males have dusker cheeks and lack the dark borders of the crests. Females lack the yellowish crown, are browner on the breast, and have a more distinctly yellow throat. The third species, *H. cristata*, is restricted to the mountains of western Colombia; both sexes are red and have long crests. The British Honduran populations are designated by Hellmayr as *H. rubica rubicoides* and *H. gutturalis rooensis*. In general appearance, these ant-tanagers are rather similar to the Hepatic Tanager (*Piranga flava*), but they differ in habitat and behavior.

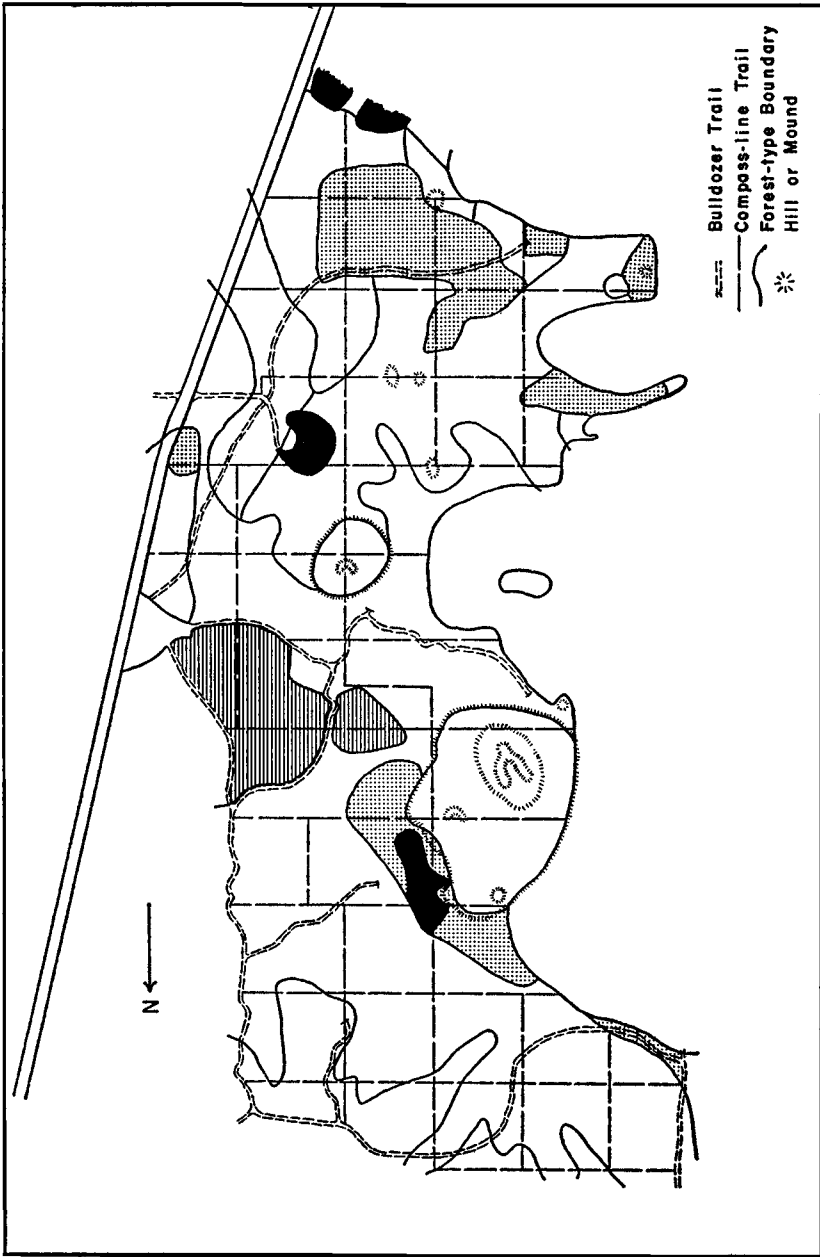
Other bird names used in this paper come from Blake (1953).

THE STUDY AREA

In early March, I set up a study area of 42.6 hectares (approximately 105 acres) of "evergreen seasonal forest" (Beard, 1955) on the rolling hills about a kilometer north of Gallon Jug, British Honduras (17°33' N, 89°02' W), at about 125 meters above sea level. A grid of compass-line paced trails (the broken lines in Figure 2), established with the help of a local boy and his machete, proved valuable in many phases of

Figure 1 (p. 151). Probable distribution of Red-crowned Ant-Tanagers, *Habia rubica* (stippled), and Red-throated Ant-Tanagers, *Habia gutturalis* (diagonal), from Costa Rica north. This shows all areas where the two species are known to be sympatric except a small area in Panama.





the study. The vegetation types marked on Figure 2 are discussed elsewhere (Willis, 1958); for present purposes, it is sufficient to note that "high huamil" refers to Moho (*Belotia campbellii*) and other second growth six to 15 meters high and "low huamil" to dense second growth of under six meters.

GENERAL BEHAVIOR

Both species of ant-tanagers are highly vocal, scolding loudly when a human intruder enters their haunts, but quickly disappearing behind the vegetation when a close approach is attempted. Red-throats seemed particularly inquisitive; their rasping calls were common noises of the dark, lower layers of forest and second growth. Red-crowns were less inquisitive, but easier to follow and observe; their voluble chatter was often given when they were in plain sight.

DIFFERENCES IN DISTRIBUTION AND HABITAT

A number of ornithologists have reported Red-crowns commoner at higher elevations, even into subtropical cloud forests (in El Salvador, according to Dickey and van Rossem, 1938; and in San Luis Potosí, México, according to R. J. Newman, personal communication), and Red-throats commoner at low elevations, especially on the coastal plains.

Several ornithologists (Paynter, 1955; Peters, 1929; Dickey and van Rossem, 1938; Sutton, 1951a; and others) have noted differences in the forest-type preferences of the two species in Central America. At Gallon Jug, there were also slight differences in this respect between the ant-tanager species. There the Red-crowns rarely foraged outside the borders of the high forest, and generally avoided the edge of the forest. High huamil was used, especially when the sun was low (Figure 3), but low huamil was rarely visited. Red-throats showed less aversion to huamil, foraging not only through high huamil but also along the edges of woods or low huamil bordering roads or plantations.

One Red-throat pair drifted through the first-year huamil out to the forest "island" to the west of the center study area (Figure 2) at times, but the local Red-crown pair never left the shade of the main forest, although the island was suitable Red-crown habitat. Just southwest of the study area was a small, isolated patch of forest in which lived a group of Red-throats but no Red-crowns. The group used the surrounding low

Figure 2 (p. 152). The study area and its vegetation. Second-growth successions are shaded (fields, solid; low huamil, lined; high huamil, stippled). Forest is unshaded. Length of N arrow represents 100 meters.

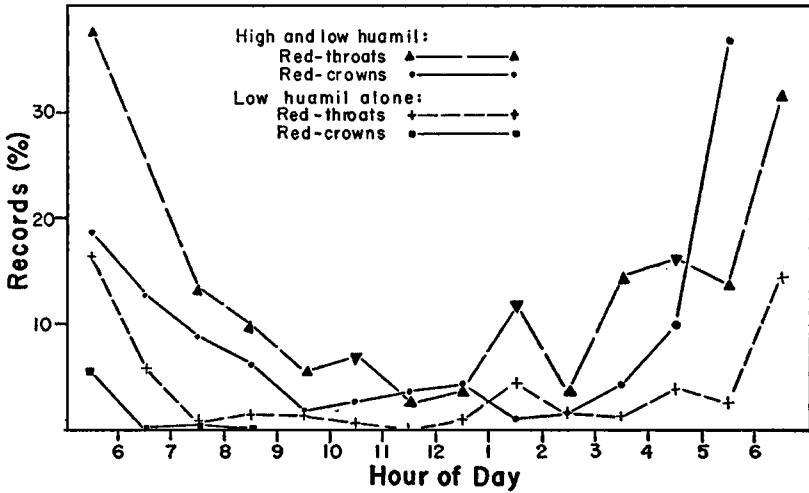


Figure 3. Occurrence of ant-tanagers in second-growth or "huamil" at different hours of the day. Computed as percentages of 3,485 recorded observations for the Red-throated Ant-Tanager and 2,726 for the Red-crowned Ant-Tanager.

huamil for part of its territory, as did many of the forest-edge Red-throat pairs on my study area. I have seen Red-throats, while foraging along the edge of a cornfield, dash out into it after insects. Once I saw a male alight on a gravel road and hop along, jay-fashion, with head high and tail slightly raised.

Wherever the high forest around Gallon Jug had been reduced to a mosaic of plantations, huamil, and forest, Red-throats were generally more common than Red-crowns. But in unbroken areas of hill forest Red-crowns outnumbered Red-throats. The forest of the study area was intermediate between these extremes, and the two species were approximately equal in abundance.

DIFFERENCES IN FORAGING LEVEL

To gain an idea of the vertical distribution of the two ant-tanager species in the forest of the study area, I made estimates of the height at which the birds perched while foraging and recorded each such estimate in one of 12 divisions: 10 strata, each a meter deep, plus a separate category for the ground and another for above 10 meters.

Although the resulting 4,000 estimates for Red-throats and 5,000 for Red-crowns (presented in percentages in Figure 4) should be interpreted with caution, a few generalizations are probably safe. Most

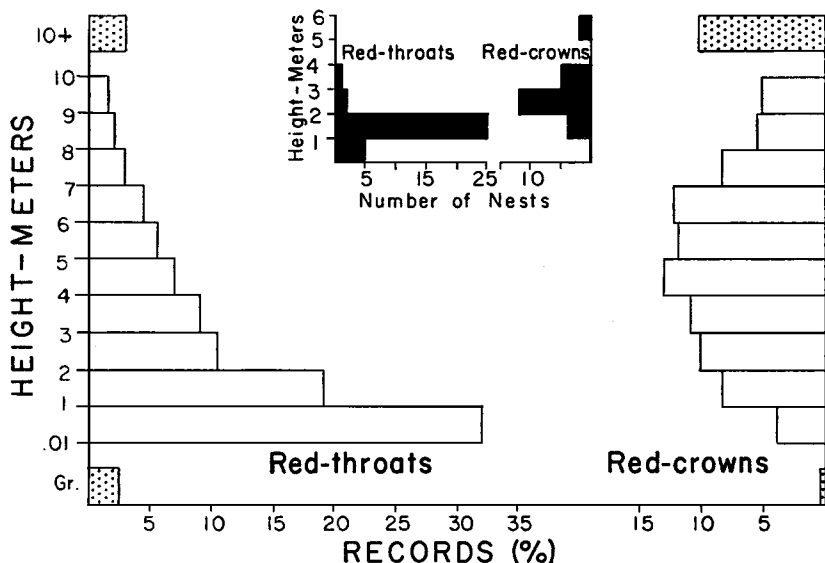


Figure 4. Height (in meters) of ant-tanager foraging and of nests (inset). Percentages are based on 4,000 records of foraging height for Red-throated Ant-Tanagers and 5,000 records for Red-crowned Ant-Tanagers.

important, Red-crowns generally foraged higher than Red-throats. Moreover, it seems that the Red-throats are restricted to a narrower as well as a lower foraging stratum. In foraging near the ground, the Red-throats have departed farther than the Red-crowns from "typical" tanager foraging style: according to Skutch (1954), most tanagers are tree-top or upper-level birds. There may be some correlation between ordinary foraging height and nest height (Figure 4).

Red-crowns sometimes, particularly in the early morning and late afternoon, foraged high in the under-canopy of the forest, 20 and more meters above the ground. Red-throats never approached such a height while foraging. On the other hand, Red-crowns rarely visited the ground except when looking for an insect that had dropped before capture. But the ground was an important source of food for the Red-throats, which regularly followed the army ants.

ANT-TANAGERS AND ARMY ANTS

In the American tropics, swarming army ants (*Eciton burchelli* and *Labidus praedator*) in search of prey stir up many fleeing insects and other arthropods from the forest floor (see Schneirla, 1947). Where such ants occur, certain birds habitually attend the ant swarms and

snap up the arthropods they flush (Johnson, 1954, and others). The name "ant-tanager" was doubtless adopted because naturalists had reported *Habia* species following these ants.

Dickey and van Rossem (1938) thought that both Red-crowns and Red-throats followed army ants in El Salvador. Two other reports of Red-crowned Ant-Tanagers following swarms of army ants may have been misidentifications: Nutting (1883) took specimens, originally listed as *Phoenicothera rubicoides*, which Ridgway (1902) referred to *Phoenicothera salvini discolor* (= Red-throated Ant-Tanager) upon re-examination; Gaumer (in Boucard, 1883) reported Red-crowns (*sub nom. P. rubicoides*) following ants in northern Yucatán, but Sclater (1886) referred Gaumer's specimen and his published record to *P. salvini*. Other reports I have read of ant-tanagers at ant swarms all refer to the Red-throated Ant-Tanager subspecies found north from Nicaragua. At Gallon Jug, I saw Red-throats at ant swarms 63 times, the Red-crowns only twice.

Casual foraging by Red-crowned Ant-Tanagers at ant swarms. Time after time, a Red-crown group, chattering and foraging busily, drifted over a swarm that was putting up insects in large quantities. Yet the Red-crowns seemed to take no interest in this abundant supply of food, which was to be had with much less effort than they were expending in their careful search through the limbs. Several times, while Red-throats and other species were busy at a swarm, the Red-crowns and other species of a wandering flock stayed in the vicinity for an hour or more; but members of the wandering flock seldom joined the ant-swarm birds.

At 9 A.M. on 26 April, as I was watching an incubating female Red-crown, an ant swarm passed under her. As the swarm and the ant-following birds moved past, the ants flushed a host of earwigs, which flew all over me in the blind and over all trunks and bushes nearby. As the earwigs alighted near the female Red-crown, she abandoned her quiet pose for a few moments and half rose to pick off all within range of her bill. Her mate drifted by several times as the swarm moved slowly past, and may have captured some of the high-flying earwigs.

My only observation of true swarm-following was on 26 July, when a male and immature male Red-crown came down to a swarm from which a Red-throat group had just departed. For two or three minutes, the Red-crowns and their companions, the Tawny-crowned Greenlets (*Hylophilus ochraceiceps*), chased insects and fluttered from limb to limb less than a meter above the swarm. All drifted off before the Red-throat family returned and did not join the latter at the swarm, though they remained in its vicinity for three hours longer. These

Red-crowns never visited the ground to pick up insects from the middle of the swarm as Red-throats regularly did.

Regular foraging by Red-throated Ant-Tanagers. Despite abundance of food, concentration of birds at the "feeding tables" of the swarms meant increased competition for feeding room. Red-throated Ant-Tanagers were usually present in groups, but individuals generally kept at least one-third meter apart. Many of the infrequent loud sounds from Red-throats at the swarms were rough scolds of displacement or argument. Most of the time the usually noisy Red-throats gave only faint *wik* notes. Some of the scolds followed sudden sounds or movements resulting from falling twigs, passing birds, or my activities.

There was considerable subdivision of the swarm-following niche among Gallon Jug ant-followers. Among them, Red-throated Ant-Tanagers occupied positions at the center of swarm activity, commonly less than a meter above the pillaging hordes. Since swarm ants spread out on a broad front, the major flushing of arthropods was in a zone about a meter deep and five meters wide near the front of each swarm; the ant-tanagers were thus in a good position to intercept arthropods escaping from the ants. The ground was not used for perching; the Red-throats paid only brief visits to it while snapping up insects. The rest of the time they watched from a convenient low twig, fallen log, or other more or less horizontal (rarely a vertical) perch.

The ant-tanagers sometimes stood in the middle of a swarm for several moments while pecking at some insect. But occasional flicks of their wings or sudden leaps of a few centimeters into the air suggested that the tanagers had been victims of sudden ant bites. Red-throats did not react to columns of ants probing along branches hardly a centimeter away, unless such a column flushed some arthropod.

Red-throats were rather active birds when foraging at an ant swarm. They turned from side to side frequently, employing a kind of "rapid peering" (as defined by Grinnell, 1921) in scanning the ground for prey. Such a turn put first one eye and then the other to use in looking at some object. As the tanager turned, its legs seemed to be springs, and the whole body (especially the tail) went down slightly at the center of the motion. From the side, the most noticeable part of the turn was the slight dip of the tail and the change in head position. Such a turning motion was perhaps the most characteristic movement of the ant-tanagers (particularly Red-throats), at swarms or away from swarms. Another common movement was the frequent "about-face," as attention was turned to other sectors of a swarm.

Red-throats darted along low branches, hopping so fast they seemed to be flying, snapping up a blundering moth or beetle at the end of each dash. Now and again, one hopped or fluttered from perch to perch, peering intently down and around so that no suitable prey would escape. The tanager might flutter up and snap an insect off the underside of a leaf, hovering briefly before dropping off and away to another perch, much like a trogon on a fruit-picking flight. Then the tanager would batter the insect energetically and swallow it whole or piecemeal. A few wipes of its bill and the bird would quickly look back to the swarm for a good vantage point. Having detected a roach that was avoiding the army ants below it by running up the stem of a little bush, a Red-throat would hop up a branch, make a lunge, and snap up the insect. Even flying insects, if large and slow, were occasionally snapped out of the air. Several other authors have described similar behavior from ant-tanagers at ant swarms; Sutton's (1951b) descriptions from Gomez Farias, Tamaulipas, at the northern limit of ant-tanager and swarm-ant ranges, agree particularly well with my own observations.

At swarms each Red-throat generally sat with legs spread somewhat apart and tail partly spread. The tail proved a sensitive index to ant-tanager "excitement," being spread wide when one was scolding, but folded, even notched, in quieter moments. The tail and body were usually in line, and the body angled from near or below the horizontal to some 30 degrees above it. Tilt of the body was somewhat indicative of ant-tanager interest in a swarm and food; the birds sat upright during intervals of loafing and preening.

Whenever a swarm reached the edge of an open area, such as a bulldozer trail, the ant-tanagers drifted above the ants out onto projecting limbs along the edge, and often stationed themselves there as the broad front of the swarm moved onward. Their sallies after fleeing insects became longer and longer, and they hesitated only briefly before taking their booty back to the edge of the trail. Finally, perhaps after a brief period of scolding and preening, the tanagers ascended limb to limb on their side and one by one darted down across the trail, often with sudden chatters, to resume feeding above the front of the swarm, now at the other edge of the path. Occasionally, one perched briefly on twigs in the middle of the trail while the front of the swarm crossed. Since the ant swarm moved about 100 meters a day, the crossing of a bulldozer trail two or three meters wide required some 10 to 15 minutes.

Foraging behavior of other ant-followers. The Tawny-winged Woodcreepers, *Dendrocicla anabatina*, usually clung to tree trunks at points slightly higher than the ant-tanagers and from there looked around for flying insects. The woodcreepers were rather successful at intimidation of the other ant-followers, for

even the slightly heavier ant-tanagers usually gave way to them. The woodcreepers picked some insects off the ground and low twigs, and, occasionally, I heard the loud *cherp* of a woodcreeper ring out, followed by a rasping note from an ant-tanager as in a flurry of wings one beat the other to a morsel. However, the insects in the air and on tree trunks, not the ground and twig insects favored by ant-tanagers, were the main food of the woodcreepers.

The third common swarm-follower at Gallon Jug was the Ruddy Woodcreeper (*Dendrocincla homochroa*). It is interesting that both dendrocinclids followed the swarms while only one ant-tanager did so. Certainly, the Ruddy Woodcreeper's situation otherwise paralleled that of the Red-crowns, for this dendrocinclid, like the Red-crowns, foraged above its sibling, and is as small compared with the Tawny-winged Woodcreeper as are Red-crowns compared with Red-throats.

The third woodcreeper in vertical range at the swarms was the Barred Woodcreeper, *Dendrocolaptes certhia*. This large woodcreeper profited mainly by the occasional columns of ants that ascended trees in the paths of swarms. It took insects mainly off the bark of those trees, even clinging in the midst of ant columns in doing so. It infrequently came low enough to dispute with ant-tanagers, and did not snap up flying insects as often as did the dendrocinclids.

Formicarius analis, the Black-faced Antthrush, occupied yet another swarm-following niche. One or more antthrushes were at every swarm, but instead of waiting in the thick of activity they roamed about on the outskirts of the swarm, particularly behind it, where they flipped leaves over in their usual manner. The advantage of this behavior was obvious; the insects that had escaped from the ants and ant-followers had often taken temporary refuge in places where the antthrushes found them much more easily than on undisturbed areas where the insects had had time to entrench themselves.

Henicorhina leucosticta, the White-breasted Wood-Wren, was the only small resident that was a regular ant-follower. By moving through dense fallen vines in the paths of swarms, this agile hopper took many minute insects the larger birds could not reach.

From February into April, the Hooded Warbler (*Wilsonia citrina*) and the Kentucky Warbler (*Oporornis formosus*) made regular appearances at the swarms, the former capturing small insects from positions near the ant-tanagers and the latter taking small insects from the ground.

A few other species (a tinamou, *Crypturellus boucardi*; a cuckoo, *Piaya cayana*; a woodcreeper, *Xiphorhynchus flavigaster*; two wrens, *Thryothorus maculipectus* and *Uropsila leucogastra*; and a tanager, *Eucometis penicillata*) followed the swarms at times.

Importance of army ant swarms to foraging ant-tanagers. Schneirla (*in litt.*) estimated the abundance of swarm-ant colonies on Barro Colorado Island, Panama Canal Zone, to be about six colonies per 100 hectares (45 colonies each of *Eciton burchelli* and *Labidus praedator* on 14.5 square kilometers as perhaps a safe minimum estimate), whereas six Red-throat groups on my study area occupied about 34 hectares (84 acres). If only half the colonies swarmed on the average on any given day (the fraction is actually more than three-quarters for *E. burchelli*, but may be less than three-quarters for *L. praedator*), and if

ant colonies are as abundant at Gallon Jug as on Barro Colorado, there would be an average of at least one swarm per day for each six tanager groups. The actual ratio may be even higher, as is suggested by the fact that in late July I usually found one swarm for each two or three ant-tanager pairs carefully checked. If there is, on the average, one swarm or more per day for every six ant-tanager groups, in the non-breeding season (when two or three groups sometimes join at a swarm) the tanagers may have swarms to follow as much as half the daylight hours. However, in view of the many variables ignored in the above calculation, quantitative field studies are necessary to determine the fraction of the time during which the territorial ant-tanagers actually are able to follow the wandering army ants.

Swarm ants and ant-tanager distribution. While Red-crowned Ant-Tanagers occur on the Pacific coast of Mexico northwest to Nayarit (Figure 1), Red-throated Ant-Tanagers do not extend farther northwest than the middle of the Isthmus of Tehuantepec. Schneirla (*in litt.*) lists no specimens or observations of the two swarm-ant species on the Pacific coast northwest of the latter area. Apparently, lowland ant-following species other than ant-tanagers are also lacking northwest of this area.

SPECIAL METHODS OF ANT-TANAGERS IN FORAGING FOR ARTHROPODS

In searching for arthropods, both species of ant-tanagers investigated dried, rolled-up leaves pendent above the ground in the manner of the Worm-eating Warbler (*Helmintheros vermivorus*) in British Honduras, but not so persistently as that species. If poking and inspection revealed prey, the ant-tanager grabbed the whole leaf, perhaps on the wing, trogon-style. With a soft run of conversational notes, the bird then took the leaf to the steady top of a huge palm leaf, the top of a log or large, horizontal limb, or to the ground, and worked the leaf over with its bill, extracting and crushing the insect. Then down went the food whole or bit by bit, and up went the tanager and wiped its bill on a twig.

With swipes of their bills, the ant-tanagers threw dead leaves one way and then the other from the tops of the huge leaves of Bayleaf Palms (*Sabal* sp.), looking carefully after each toss and frequently pecking as if an insect had been uncovered. Araceous and bromeliad epiphytes, whose leaves collected debris, were visited at times, especially if there was enough room for such large and wary birds as the tanagers to work and to make hasty exits if disturbed.

Ant-tanagers generally looked carefully each time an object dropped off a limb or twig when they alighted. On occasion, the tanager darted

downward quickly enough to capture an insect or small twig before it hit the ground. More often, the bird alighted on a bush stem or little branch a meter or less above the spot where the object had hit the ground and scrutinized the area. Leaf-tossing was necessary at times before capture of the arthropod.

The ant-tanagers rarely clung to the underside of a twig or limb in the manner of the furnariid *Xenops minutus*, the greenlet *Hylophilus ochraceiceps*, or the temperate-zone titmice. If some large insect was detected under twigs or leaves from a considerable distance, the ant-tanager would fly up and hover briefly under it, plucking it from the under surface and dropping to a perch to finish it off. Another method of obtaining insects under twigs or leaves, and perhaps the method most often employed by ant-tanagers, was that of perching beside the prey and leaning over underneath the leaf or twig.

Although both ant-tanager species were agile enough to snare some flying insects, they were much less expert than such flycatching birds as the jacamar *Galbula ruficauda*, the shrike-tanager *Lanio aurantius*, the woodcreepers *Dendrocincla anabatina* and *D. homochroa*, and the numerous becards and tyrannids. The ant-tanagers usually depended on seeing where an insect alighted.

Another group that had a different niche from both ant-tanager species were the "trunk-climbers." Although an ant-tanager in its foraging occasionally detected an insect on a large limb or tree trunk and snapped it off clumsily, hovering briefly or partly clinging against the trunk on a vine or epiphyte, in general ant-tanagers paid much more attention to twigs and leaves.

Certainly the ant-tanagers made no attempts to crawl up into the pendent, dead leaves under a huge bromeliad as the Ivory-billed Woodcreepers (*Xiphorhynchus flavigaster*) often did. The ant-tanagers did not examine cracks and crevices in trees as did all eight species of woodcreepers at Gallon Jug, especially for such small insects as those that interested the Olivaceous Woodcreeper (*Sittasomus griseicapillus*). The ant-tanagers were definitely not equipped, as were the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and Plain Xenops (*Xenops minutus*) with their wedge-shaped bills, for poking under lichens or bark strips. The Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*) and the Barred Woodcreeper (*Dendrocolaptes certhia*) probably took more insects of interest to ant-tanagers than any of the other trunk-climbers, but the former was rare in this lowland forest, and both species foraged more on tree trunks and epiphytes than on the twigs where the ant-tanagers did most of their hunting.

Occasionally, an ant-tanager clung to the slender stem of a sapling and peered around, for the moment as deliberate in its motions as a Thrush-like Manakin (*Schiffornis turdinus*), before the resemblance ended when the ant-tanager suddenly darted away. Since limbs were

sparser near the ground, Red-throats might be expected to cling to sapling stems more often than do Red-crowns, but actually both tanagers spent most of their time on horizontal or near-horizontal limbs.

It is possible that the deliberate behavior of *Schiffornis* may have allowed it to detect insects that ant-tanagers overlooked in their rapid travel. It would be interesting to investigate whether such differences in foraging speed, as between vireos and warblers, may result in birds taking different foods. The difference between preferred perching sites (horizontal vs. perpendicular perches) may have allowed *Schiffornis* to detect foods different from those detected by the ant-tanagers.

There seemed to be a slight difference in the way the two ant-tanager species sought insects, a difference that may cause the tanagers to take different foods, even when they forage at the same levels. It was my impression that not only did the Red-throated Ant-Tanagers travel horizontally through the woods, but that they also tended to look horizontally. While Red-crowns did much peering up and down as well as around, the Red-throats seemed to examine more intently the foliage at about their own level. While the Red-crowns often went in any direction for food, commonly the dash of a Red-throat was near the horizontal and often up to a meter or more before the insect was snapped from its hiding place.

Red-crowns often climbed saplings by short hops from limb to limb or by hitching up crosswise, perhaps alternating directions cross-foot style while doing so. More often Red-throats gained height by long flights to distant twigs. At the ends of their climbs, Red-crowns often dropped and flew shrike-fashion to the next tree, whereas Red-throats more often flew directly, more like a jay than like a shrike.

ANT-TANAGERS AND FRUIT

The main zone of the varied and abundant fruit supply of the study-area forest lay above the foraging zones of ant-tanagers, and the high-foraging Red-crowns apparently gained more benefit from the supply than did the low-foraging Red-throats.

Of the favorite fruits of the ant-tanagers during the months I was at Gallon Jug, Bullhoof (*Drypetes Brownii*) and Give-and-Take (*Cryosophila argentea*) lasted the longest. The hard Bullhoof berries had to be very ripe before the ant-tanagers could bite into them, but Red-crown pairs often ascended into Bullhoof trees and fed with saltators, grosbeaks, parrots, trogons, howler monkeys, and other animals much better fitted for eating hard fruits than were ant-tanagers. The first ant-tanager peck at a ripe fruit often sent it hurtling toward the ground, where it was followed hastily by the bird, which there ate the gritty pulp, leaving only one or two white seeds. At other times, the bird pecked at several berries

in succession. Red-throats never joined the flocks in the high trees, but occasionally fed on fruits on fallen branches, and once fed in a tree cut down at the edge of a milpa (corn plantation). In 150 or more hours of observing Red-crowns, I recorded 30 instances when a bird fed on Bullhoof fruit; for Red-throats, there were five instances in somewhat over 53 hours. (Although many instances were not recorded, the fraction recorded should be nearly the same for both species.)

The abundant large clusters of Give-and-Take fruit were already somewhat battered by the time I arrived in February, though the final few to withstand the attacks of many birds lasted well into May. Either species of tanager (49 instances for Red-crowns, seven for Red-throats) now and then fluttered up and picked off a berry, perhaps clinging briefly against the bunch with tail spread wide for support. The bird then took the berry to a perch, where it rotated the fruit with the tongue while biting the thin, stringy flesh off in strips until finally the large seed and part of the pulp dropped from their own weight. After some gulping, the pulp that had not dropped out the corners of the bird's mouth went down its throat. Sometimes, two or three Red-crowns visited the same cluster at the same time. Generally, one or two fruits each were all they swallowed before they moved on restlessly, only to go up to another bunch of fruit a hundred meters farther on and repeat the process.

When the conspicuous orange-red fruit clusters of the wickedly spined climbing palm, Basket Tie-tie (*Desmoncus* sp.), brightened openings in the forest in July, Red-crowns at times clung to a bunch and pecked at a fruit or two before flying on.

In June, as the Bullhoof supply was failing, Cojoton (*Stemmadenia Donnell-Smithii*) fruits attracted parrots and toucans from far and near. Occasionally, their bites sent the fruits plummeting through the limbs; the thud of a baseball-sized fruit beside my blind at one Red-crown nest startled me more than once. After a short time on the ground, each milky, kidney-shaped fruit split down the middle, exposing the seeds in their bright-red, waxy coatings. The incubating female several times made a meal of these seeds at one or more spots around my blind, and several times a day the pair of Red-throats nesting down the hill drifted by and fed on the fallen fruits.

There were many small fruits that both ant-tanagers picked off and ate whole. Among their favorites were the purple berries of Sugarloaf (*Miconia impetolaris*), a member of a family (Melastomaceae), much loved by Central American birds (Skutch, 1954) for its juicy berries. Sugarloaf, in fruit during May, was one of the few berry bushes that ever detained a wandering ant-tanager family for more than a few berries: for Red-crowns, 34 instances; for Red-throats, 10 instances. Another favorite (six instances for Red-crowns, 11 for Red-throats), during its week of fruiting in late March, was *Casearia sylvestris*, whose clusters of tiny berries attracted such unexpected species as the fly-catchers *Tolmomyias sulphurens* and *Myiodynastes maculatus* as

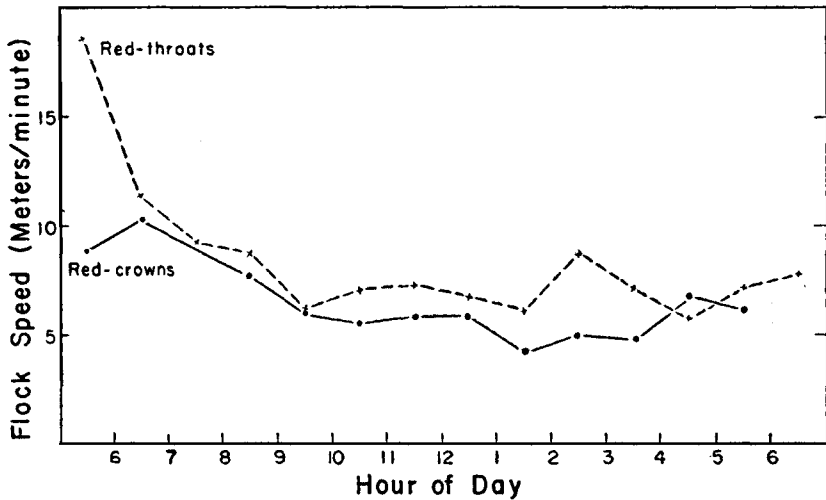


Figure 5. Speed of ant-tanager flock movement when followed (meters per minute). Based on measurements of mapped paths as in Figure 6, for 150 hours' observation of Red-crowned Ant-Tanagers and 53 hours' for Red-throated Ant-Tanagers.

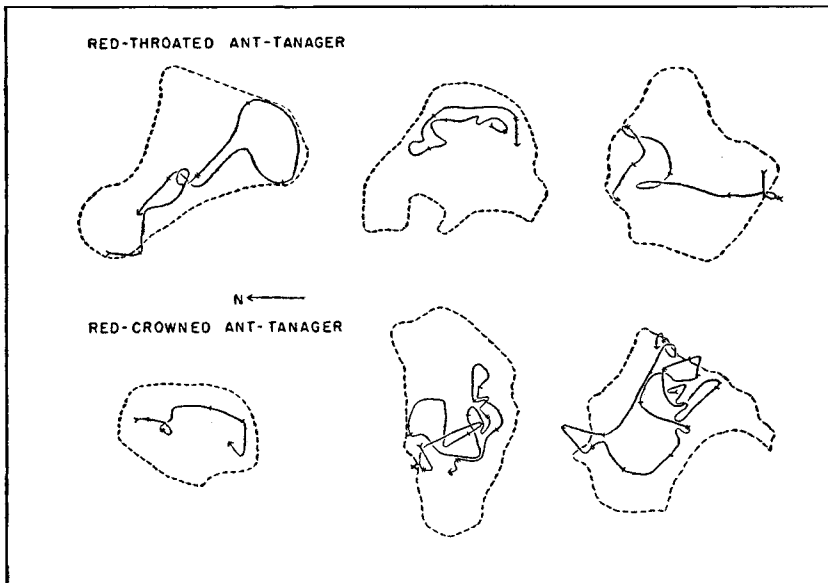


Figure 6. Paths of foraging ant-tanagers, marked at quarter-hour intervals. Broken lines indicate territory boundaries, determined from such maps as these, from records of territorial encounters ("x"), and from nests. Length of N arrow represents 100 meters.

well as the usual fruit-eating birds. In April, the juicy, red berries of the so-called "Cherry" (*Pseudolmedia* sp.) were often taken by the ant-tanagers: there were 45 instances for Red-crowns and 11 for Red-throats. The list could be extended, but the above were the fruits most commonly taken by the ant-tanagers during the time that I was at Gallon Jug.

ANT-TANAGER FLOCK MOVEMENT

When foraging, small groups of ant-tanagers moved rapidly (Figure 5) and erratically (Figure 6) through the forest, a type of foraging movement that has led all who know these birds to speak of "wandering bands" and "restless flocks." The average speed of ant-tanager movement (Figure 5), based on measurements of such mapped paths as those in Figure 6, was somewhat greater in Red-throats than in Red-crowns. The former stayed in a narrower stratum and spent less time climbing, but the time saved tended to be used in individual wandering over an area 20 or so meters to either side of a flock's path and so did not bring about an increase in group speed; the greater speed of Red-throat group movement probably reflects instead the greater wariness of Red-throats when followed. The speed of flock movement was greatest in the early morning for both species.

ANT-TANAGER GROUP COMPOSITION AND FORAGING RANGE

The groups of ant-tanagers were apparently pairs and their grown young of the previous year. With each adult male there was always at least one female, as the ant-tanagers were paired even before the breeding season. A few males were known to be bigamous. The other individuals with each adult male were usually in immature plumage during the breeding season. In late July and August, some of the young males were molting into the red adult plumage. During my stay, the only increases in group size came when the young of the year left the nest; decreases, which were occasional, probably signified the death of birds. Possibly, there may be some permanent shifting of immature birds from one group to another, but this remains to be proved.

At Gallon Jug, even counting young of the year, I never saw a Red-crown group of more than five birds or a Red-throat group of more than eight. Usually, Red-crown groups included two to four birds, while Red-throat groups included up to five. Paynter (1955) noted similar group sizes in Yucatán, and Skutch (1954) got a similar impression of Red-crown groups in Costa Rica.

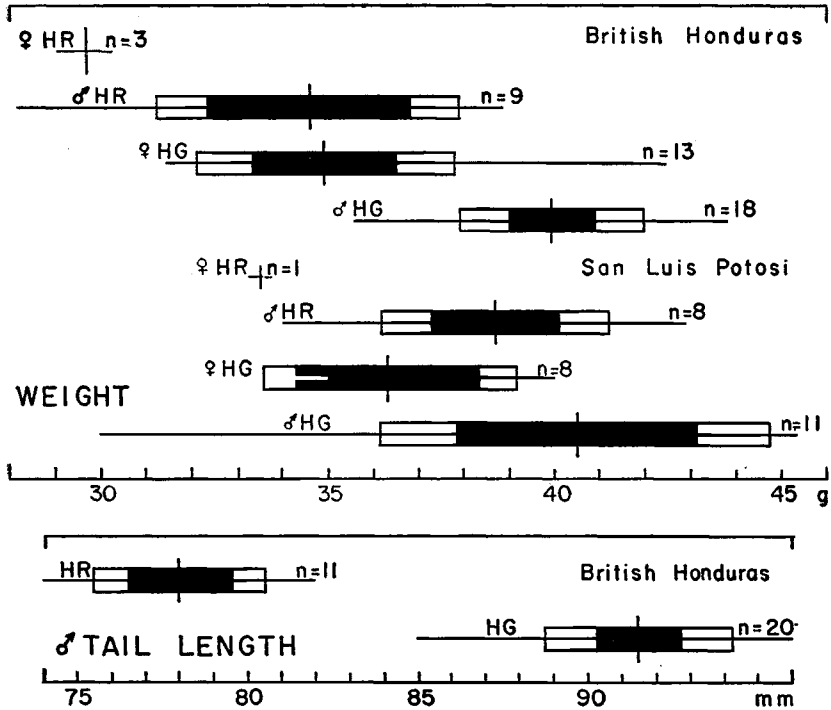


Figure 7. Differences in size of Red-crowned Ant-Tanagers (HR) and Red-throated Ant-Tanagers (HG). Horizontal line—range; vertical line—mean; black bar—two standard errors on either side of mean; open bar—one standard deviation on either side of mean.

In the months I watched them, groups of both ant-tanager species obtained nearly all their food from areas that may be called territories (territorial defense occurred during the nesting period). These were rather large areas of four or five hectares each. At times, a group trespassed briefly into the territory of a neighboring group (Figure 6), but such intrusions were few even before territorial defense began. Before nesting began, two groups of the same species occasionally foraged together, generally along a boundary line, but eventually the groups went back to their respective territories. Red-throat groups were occasionally together at ant swarms near boundary lines before nesting began, but when I scared them, each group darted back to its own area. After nesting began, an ant-tanager group seldom joined another group of the same species while foraging, although females and immatures might forage near each other while adult males disputed

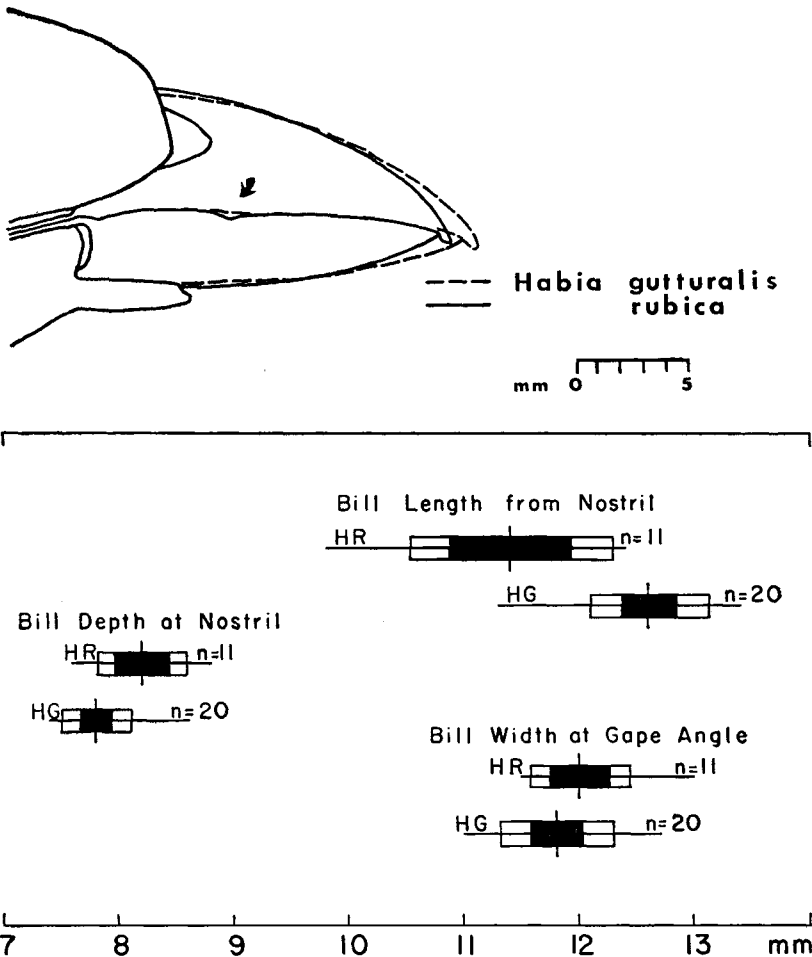


Figure 8. Differences in bill shapes between male ant-tanagers in British Honduras. Note the "tooth" on the bill of Red-crowned Ant-Tanager (arrow). Symbols as in Figure 7. Measurements as in Baldwin *et al.* (1931).

along a territorial boundary. Foraging groups of one species often joined groups of the other species.

SIZE AND BILL SHAPE IN RELATION TO FOOD SIZE

Difference in size, especially of bill, is sometimes correlated with a difference in foraging habits between closely related bird species. Since Red-throated Ant-Tanagers average slightly larger in size (Figure 7)

than Red-crowns, it might be assumed that, on the average, they would capture larger food than Red-crowns. However, several factors cast doubt on this assumption. Ant-tanagers ordinarily tore apart large arthropods or medium-sized fruit by pounding and bill manipulation, so that the small Red-crowns had no more difficulty in consuming large food than did the barely larger Red-throats. Indeed, some of the largest orthopterans and argioid spiders I saw at Gallon Jug were those captured and torn apart by Red-crowns. Secondly, the fact that male Red-crowns average about the same in weight as female Red-throats in British Honduras seems very odd if interspecific food competition has had much to do with the size divergence. Indeed, the geographically distant and thus noncompeting Red-crowns from British Honduras and San Luis Potosí, Mexico, differ more in weight than do "competing" Red-crowns and Red-throats in San Luis Potosí.

The smaller Red-crowned Ant-Tanager may even take larger foods than does the larger Red-throated Ant-Tanager. The bill of Red-crowns is slightly shorter than that of Red-throats, as might be expected from the smaller size of the former species; yet it is very slightly deeper. This slightly heavier bill (Figure 8) may be better suited for tearing apart large insects and fruits than the bill of Red-throats. The tooth on the upper mandible is more prominent in Red-crowns than in Red-throats; it may help in tearing apart fruits or arthropods. Certainly, Red-crowns brought large particles of food to their young more often than did Red-throats (Willis, ms.), thus more frequently causing an impasse when the nestling could not swallow the food. Red-crowns did dissect large insects and medium-sized fruits more often than Red-throats did while I was watching (but it is possible that the shyer Red-throats merely carried their food away from me before dissection).

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SUMMARY

A study of Red-crowned and Red-throated Ant-Tanagers (*Habia rubica* and *H. gutturalis*) at Gallon Jug, British Honduras, showed some differences in habitat and foraging behavior between these sibling species.

The fact that Red-crowns stay in high forest while the Red-throats are less restricted, foraging in low second-growth as well as high, was confirmed by this study.

The major foraging differences between the two species were that (though both were birds of the forest undergrowth) Red-crowns generally foraged higher than Red-throats and that only Red-throats regularly followed army ants (*Eciton burchelli* and *Labidus praedator*), picking up many of the insects flushed by the ant swarms.

Ant-tanagers used various techniques in capturing arthropods and consuming fruit. Most ant-tanager foraging was done on twigs and branches of trees rather than on tree trunks or in the air.

Ant-tanager groups did most of their foraging while wandering irregularly over "territories," the boundaries of which were defended during the breeding season.

A slight difference in body size is apparently not directly related to differences in foraging; the smaller bird, the Red-crowned Ant-Tanager, may tear apart larger arthropods and fruits with its slightly thicker bill.

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