ECOLOGY AND BEHAVIOR OF THE CRESTED ANT-TANAGER

EDWIN O. WILLIS

The Crested Ant-Tanager (*Habia cristata*) lives in a narrow subtropical band in the Western Andes of Colombia (fig. 1), not in the tropical lowlands as do the four other species of the genus. The lowland species resemble each other in ecology and behavior (Willis, 1960a, 1960b, 1960c, 1961, MS). Where adverse factors such as poor soil, low rainfall, periodic floods, and previous clearing of the forest for agricultural uses hold development of the tropical forest at an immature stage, these Ant-Tanagers inhabit the leafy undergrowth that is shaded out in more mature forests. Red-crowned Ant-Tanagers (*Habia rubica*) and Black-cheeked Ant-Tanagers (*Habia atrimaxillaris*) forage higher in the undergrowth and consequently often use more mature forests than do Red-throated Ant-Tanagers (*Habia juscicauda*) and Sooty Ant-Tanagers (*Habia gutturalis*). But none of the lowland species is successful in the open undergrowth of fully mature forest. The questions thus arise: does the subtropical member of the genus differ greatly in its ecology and behavior although it differs little morphologically; and what factors restrict the species to the Western Andes?

PLUMAGES

The Crested Ant-Tanager is a cardinal-like bird with a long, silky crest of bright scarlet. In life this crest is usually folded until it forms a bright line down the center of the crown and projects behind the head as a spike or wedge (fig. 2). The dusky scarlet of the face and crown grades into the bright reddish of the throat and upper breast. The bright red shades of the head contrast with the dark-reddish mantle and the paler reddish-dusky underparts. The flanks are grayish and the tail coverts a dull orange-red, rather like the darker purplish-red of the tail. Males and females are similar in plumage. Females may prove to average slightly duller and shorter-crested than males when enough carefully sexed specimens are available.

Some birds in family groups had dull or dusky-orange heads with short reddish crests, dingy cinnamoneous underparts, dusky mantles, and dull-orange tail coverts. The unsuccessful food-begging behavior of two birds in this dull plumage suggested that they were immatures, probably ones that had completed the postjuvenal molt.

In plumage *Habia cristata* resembles *Habia rubica* more closely than it does other members of the genus. Both the large Crested Ant-Tanager and the small Redcrowned Ant-Tanager behave alike in foraging; thus the two may be closely related.

HABITAT

Crested Ant-Tanagers are known from at least 16 localities in the Western Andes (this report and de Schauensee, 1948–1952), as well as from the indefinite localities Bogotá and Antioquia. All but three localities (Peque, San Antonio, and Cerro Munchique) lie on the humid Pacific slope of the cordillera. All three eastern-slope localities lie near the crest of the range, so that specimens may have been brought in from the nearby western slope. Perhaps the species occurs on the eastern slope where heavy rainfall spills over passes or surrounds isolated peaks, but failure to cite slope on specimen labels and in faunal accounts has obscured the evidence.

The mapped distribution (fig. 1) corresponds fairly well with the upper edge of a belt of torrential rainfall, four to 10 meters per year, on the Pacific slope of Colom-

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Figure 1. Map of the probable range of the Crested Ant-Tanager along the Western Andes (Cordillera Occidental) of Colombia. Sites where the species has been seen or collected are underlined.



Figure 2. a. Head of a foraging *Habia cristata*. Only the rear half of the crest is visible from the side. b. A foraging posture. The crest is folded to a narrow line along the center of the crown.

bia (West, 1957). This belt extends into northwestern Ecuador, so that the species may yet be discovered south of Cerro Munchique $(2^{\circ} 30' \text{ N}, 76^{\circ} 58' \text{ W})$.

Except for lists of localities, nothing has been reported about the habitats of Crested Ant-Tanagers. In an area where the distance of a kilometer or two can mean the difference between mossy cloud forests and cactus scrub, locality labels reveal little. Contemplating the variety of habitats on the western slope of the Western Andes makes one realize that the habitat and slope should be specified on every specimen label and in every faunal list.

In searching for the elusive Crested Ant-Tanagers I visited six major habitats. These were the lower montane rain forest, the midmontane rain forest, the uppermontane cloud forests, and the second growth and edges of each. In these habitats I watched for ecologic counterparts of ant-tanagers whenever the latter seemed to be absent. Because of the competitive exclusion principle, the presence of a counterpart species usually means that the species in question will be rare or absent.

In the foothills of the Western Andes below 600-meter elevation at El Tigre and Anchicayá (3° 41' N, 76° 54' W), *Tachyphonus delattrei* and other species seem to replace ant-tanagers in the forest undergrowth. From 600 to 1200 meters in the forest along the road above Anchicayá, *Chlorothraupis stolzmanni* is the counterpart species. In lower montane second growth and forest edge at El Tigre and along the Río Anchicayá, *Mitrospingus cassini* behaves and forages as an ant-tanager. Above Bitaco, in the undergrowth of secondary forests and mossy cloud forests at 1800 to 2000 meters, the ecologic counterparts of the ant-tanagers seemed to be the common furnariids *Anabacerthia striaticollis* and *Syndactyla subalaris*. On the ridge west of Queremal between 1700 and 1900 meters second growth forms a very humid, mosscovered chaparral. The common ecologic counterpart here is the bush-finch *Atlapetes tricolor*.

With some hesitation I next turned to the only remaining habitat that seemed likely to hold ant-tanagers. The heavy rainfall of the Pacific slope creates hundreds of streams and rivers, which cut deep V-shaped gorges into the crumbling western wall of the Andes between about 400- and 2000-meter elevation. At higher elevations the streams are small and do not cut such gorges; at lower elevations the terrain becomes less rugged. In these steep gorges frequent landslides maintain the forest in a perpetually immature state. Slumps and landslides create holes in the canopy and let in light, which in this constantly moist and equable climate means that the undergrowth springs up in bewildering confusion. Melastomes, gingers, philodendrons, geraniums, tree ferns, and other bushes and vines cling to crumbling cliffs and spongy slopes beneath scattered tall trees that have weathered the landslides. Waterfalls and rapids cascade between slippery trunks and mossy saplings. Even the rocks are buried in the lush vegetation. At lower elevations mosses and epiphytes give way to monocotyledonous forbs and dicotyledonous bushes. It is one of the few tropical habitats that deserves the cliché, "green hell."

On 16 March I lowered myself over a slippery cliff into such a landslide forest along a plunging creek at Kilometer 50 on the Cali-Buenaventura Road, just below Queremal $(3^{\circ} 32' \text{ N}, 76^{\circ} 43' \text{ W})$. As I crashed downward through the thick but brittle vegetation along a noisy little creek, a sudden outburst of shrill and jaylike *chiv-eek*! calls burst from the dense bushes. After two weeks of searching, I had found the habitat of the Crested Ant-Tanager.

For the following two weeks I studied the three families of ant-tanagers in this and nearby ravines. On 28 March I watched another family in a similar patch of forest and second growth on two ravines and cliffs beside the rushing Río Blanca above Las Cascadas ($3^{\circ} 39'$ N, $76^{\circ} 47'$ W; Kilometer 72 on the highway). One of the people at the nearby bridge said "gallos de monte" ("cocks of the woods"—the name presumably refers to the red crests) occasionally visit scattered trees around the bridge. The elevation there is about 700 meters, whereas the elevation at Kilometer 50 is about 1400 meters. "Gallos de monte" were reported to live also in ravines below La Elsa ($3^{\circ} 33'$ N, $76^{\circ} 47'$ W; Kilometer 62) at about 1000-meter elevation. Most records in the literature range from about 700 to 2000 meters. However, the latter elevations are too high if the collectors obtained birds from stream valleys below camps.

The present evidence indicates that the native habitats of Crested Ant-Tanagers are the landslide forests on steep-sided gorges of rushing creeks and rivers at 700 to perhaps 2000 meters on the wet western slopes of the Western Andes. The species



Figure 3. a. Scolding ant-tanager. The bird pivots back and forth between this position and one 50 to 160 degrees to the right. The tail is slightly spread in the direction of its previous movement (right). b. Ant-tanager chewing on a caterpillar, showing the hunched posture of a bird dissecting food.

may occur in midmontane second growth created by man, but the record from Peque is the only one that suggests this. Ant-tanagers used second growth near streams at Queremal but were never found in second growth away from stream gorges.

REACTIONS TO HUMANS

As other species of ant-tanagers, Crested Ant-Tanagers scold intruders violently. The scold is a very loud and sharp *chiv-eek* or *guy-eek*. The first part of the call is a rough noise that resembles the scold of Red-throated Ant-Tanagers in British Honduras. The noise glides upward to a piercing squeak, so that the call as a whole sounds double-noted. The call is normally given two to four times in a row at about two calls per second.

When birds scold (fig. 3a), their yellow gapes flash conspicuously in their dark beaks. The tail is often somewhat spread. Notched when closed, it becomes doublerounded when half-opened. The head is extended horizontally as the bird points the body downward. The wings often flit out with each call. The long crest is slightly raised, but it does not widen conspicuously.

As they scold, ant-tanagers dart from one perch to another or remain on a perch and pivot from side to side. With each pivot of about 90° , the bird turns the opposite face toward the observer and spreads the tail asymmetrically in the direction of its previous movement. Birds dash behind cover the moment one turns their way, only to reappear the moment the observer looks away. After a minute or two the birds fly off through the undergrowth, calling *chip* or a sharp series of *chee* notes. Loud *chiveek* calls burst out periodically from the dense tangles ahead as the birds lead the observer up and down ravines through the undergrowth.

FORAGING BEHAVIOR

The foraging behavior of Crested Ant-Tanagers is remarkably similar to that of other members of the genus, especially *H. rubica*. Groups of two to five birds, probably both parents and young, move rapidly through the dense undergrowth capturing small arthropods or briefly visiting fruiting trees.

When not followed, a group may move rather slowly. On one occasion a family moving along the edge of a woodlot by the river covered 100 meters in 85 minutes.

Individual birds usually stay from one to 10 meters apart. They cross paths frequently and wander away from each other, but they keep in contact with sharp chip! notes, easily audible over the roaring of nearby cataracts. When a bird flies to rejoin others or moves ahead, it often calls a sharp *chee chee chee chee chee chee!* or a similar series of notes. At times the call is a faint *ch'ree ch'ree* that resembles a call of Red-crowned Ant-Tanagers.

Crested Ant-Tanagers move up and down bushes or vines rather than horizontally in the fashion of *Habia fuscicauda*. A Crested Ant-Tanager often ascends from twig to twig and then drops in the fashion of *Habia rubica* or a shrike as it flies to the next tree. At times the bird sidesteps up a slender vine or pivots one way and then the other as it ascends a sloping sapling. The bird commonly flicks its wings and tail as it ascends. It normally stays on a perch five to 10 seconds as it turns its head to scan the foliage above or below it. At times one peers for as long as a minute as it looks about. Occasionally one descends a sloping frond of a tree fern by reversing or pivoting back and forth, but normally birds fly when dropping to snap prey off a leaf or vine or to catch falling prey. The ant-tanagers capture prey both above and below them in the fashion of *Habia rubica* rather than concentrating on prey at their own level as does *Habia fuscicauda*. They flutter up to a meter from perches and hover briefly as they peck insects or fruit from leaves or twigs.

Although Crested Ant-Tanagers often peck prey off nearby twigs and leaves, they seldom bend over or clamber and peck prey below them in the fashion of small tanagers (*Tangara* and *Chlorochrysa*) or Black-and-White Warblers (*Mniotilta varia*).

Normally Crested Ant-Tanagers stay on perches that slope less than 30° and are

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less than three centimeters in diameter. Thus the species commonly forages in bushes or toward the periphery of a tree rather than on the trunk or large inner branches.

Mossy trunks and branches are avoided, as are dense tangles of vines, moss, dead leaves, or epiphytes. Probably this is one reason that ant-tanagers never moved far into the mossy forests at the upper ends of their territories at Kilometer 50 and that I was unable to find them in the mossy forests above Queremal.

Foraging *H*. cristata often investigate or pluck off dead and rolled-up leaves. Once a bird unrolled a pupa until the silk holdfast was as long as the bird. Such prey is extracted with the beak, for the feet are never used in conjunction with the bill by this or other species of ant-tanagers. A bird that captured a caterpillar three times as long as its beak hunched over a twig as it chewed the prey back and forth, then dropped three-quarters of the caterpillar on a nearby tuft of moss. The tuft of moss was used as a table each time while the bird ate a quarter of the caterpillar at each mouthful. This hunched posture is usual when birds dismember or chew large prey or fruit (fig. 3b).

Commonly the ant-tanagers stay within the foliage when they forage at the edge of the forest. On dark and cloudy mornings they sometimes foraged atop tree ferns and bushes overhanging the open river. Occasionally one foraged in weak sunlight. The species is more like *fuscicauda* than like *rubica* in being willing to cross the clearings and river openings to move into isolated trees in pastures or to cross clearings that dissect woodlots. Perhaps the families have to forage in the isolated trees because of recent cutting of forests, but the species probably had to cross rivers before man created clearings.

Once a Crested Ant-Tanager visited the ground and hopped around on roots. Normally birds foraged from one to eight meters up. Occasionally one or more moved to 15 or 20 meters above the ground when on steep slopes or visiting fruiting trees.

On two occasions high-foraging H. cristata were supplanted by Red-headed Barbets (*Capito bourcierii*). On the first occasion the female barbet extracted prey from the rolled-up leaf the ant-tanager had been pecking. The barbets are more sluggish than ant-tanagers but otherwise capture the same types of prey and fruits in the same ways and places in the tree tops.

INTERSPECIFIC FLOCKS

Crested Ant-Tanagers are members of wandering flocks even more regularly than are Red-crowned Ant-Tanagers (Willis, 1960c). No other species associates with Crested Ant-Tanagers as persistently as Tawny-crowned Greenlets (*Hylophilus* ochraceiceps) associate with Red-crowned Ant-Tanagers, although Rufous-naped Greenlets (*Hylophilus semi-brunneus*) sometimes associate with Crested Ant-Tanagers. In 15 flocks at Queremal and one at Las Cascadas, Three-striped Warblers (*Basileuterus tristriatus*) and Canada Warblers (*Wilsonia canadensis*) were the most frequent companions of ant-tanagers (table 1). The more frequently recorded species often moved together for long distances, even when traveling ahead of me at great speed. Thus these groups are definitely social, although some species recorded in flocks must have been passing by.

Once a Three-striped Warbler watched an ant-tanager bounce along a slender limb and dropped down to forage there after the ant-tanager left. Occasionally Canada Warblers closely followed ant-tanagers. Otherwise there was no sign that the associating species flushed food for each other, in spite of the persistence of some flocks

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TABLE 1	
Species Flocking with Crested And	r-Tanagers

Species	Occa- sions	Total individ- uals		Flock number and date							
			3 18/3	7 22/3	10 24/3	11 27/3	13 28/3	14 28/3	15 29/3	16 29/3	
Capito bourcierii	4	8			2		2		2		
Piculus rubiginosus	1	1				1					
Veniliornis fumigatus	3	9			3	3			3		
Picumnus granadensis	1	2							2		
Xiphorhynchus sp.	3	3			1	1					
Lepidocolaptes affinis	4	7			2	2			2	1	
Campylorhamphus pusillus	3	3		1		1			1		
Glyphorhynchus spirurus	3	5				2	2				
Cranioleuca erythrops	3	6					2		2	2	
Premnoplex brunnescens	3	5				2	2				
Syndactyla subalaris	7	7			1	1		1	1	1	
Thripadectes virgaticeps	5	5			1	1	1		1		
Xenops rutilans	5	8	2		2			2	1		
Dysithamnus mentalis	2	3				2		1			
Myrmotherula schisticolor	8	18			2	2	2	3	3		
Pachyramphus versicolor	1	2			2						
Pachyramphus polychopterus	1	2							2		
Masius chrysopterus	2	3			2		1				
M yiobius villosus	3	5		2				1	2		
Pogonotriccus sp.	4	6	2					-	-		
Pogonotriccus (?) sp.	4	8		2		3	2	1			
Henicorhina leucophrys	9	17		2	2	2	2	2	2	2	
Cyphorhinus thoracicus	4	5		-	-	-	1	2	1	1	
Vireo gilvus	2	4					•	2	2	•	
Hylophilus semi-brunneus	3	8	3			3		-	~		
Tundus ignobilis	1	2	Ū			2					
Cyclarhis nigrirostris	-	-				~			1		
Mniotilta varia	6	6		1	1		1	1	1		
Vermivora chrysoptera	4	4		•	1		1		1	1	
Parula pitiavumi	4	7	2		-	2	1		1	1	
Dendroica tusca	5	12	2		2	2	2	2			
Wilsonia canadensis	11	20	2	2	2	2	2	3	2	2	
M vioborus miniatus	3	20	2	2		2	2	4	2	2	
Basileuterus tristriatus	10	31	2 A	2		2	2	2	2	2	
Tanagra xanthogaster	3	6	4	3		3 7	2	3 7	3	3	
Chlorochrysa nitidissima	2	4				2	2	2			
Tangara arthus	1	+			2		2	2			
Tangara icterocephala	1	11			2			•			
Tangara labradorides	4	11	•		3			2	3		
Tangara nigrospiridia	2	4	2		•						
Piranaa flava	2	9			3	6			_		
La nungu juuvu Habia cuistata	1	L CD	2	_	_	_	-		1		
Chlorophingus caring	10	09	5	5	5	5	2	5	5	2	
Allabetes triceler	1	1							1		
Augetes tricolor	1	1				1					
Autopetes orunnei-nucha	3	3		1	1						
Lysurus casuaneiceps	2	2						1	1		



Figure 4. Foraging areas of three families of ant-tanagers on the study area (near Kilometer 50 on the road from Buenaventura to Cali and along the Río San Juan below Queremal).

for several hours. Some of the occasional supplantings occurred at food sources, but most members of these flocks foraged in different ways or places.

At times the ant-tanagers or other birds of the wandering flocks briefly joined large groups of other species feeding on the berries of a fruiting melastome species common in the canopy and pastures at Kilometer 50. Usually the ant-tanagers visited these trees only briefly; they swallowed a few berries and rejoined the wandering flock. The species in the fruiting trees usually were different from species in wandering flocks, although some casual members of the wandering flocks were frequent in the flocks at fruiting trees and vice versa. Ant-tanagers commonly ate palm or other fruits of a variety of types, as did some other members of the wandering flocks. Once a woodpecker (*Veniliornis fumigatus*) supplanted an ant-tanager that joined it on a cluster of palm fruit, but in general the members of the wandering flocks did not join each other at obvious concentrations of food. The food value of association in wandering flocks is thus debatable.

In the early morning ant-tanagers occasionally foraged alone. The wandering flocks built up gradually, so that the largest groups were recorded in the afternoon. The less frequently recorded species usually joined when the groups were large. These

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and some other species, such as the slow-foraging wrens *Henicorhina leucophrys* and *Cyphorhinus thoracicus*, often drifted away from the group and rejoined it later. The composition of the flocks was thus variable, and the flocks were never as large at any one time as is indicated by the totals in table 1.

Ant-tanagers occasionally led wandering flocks, but they often trailed the more active Three-striped Warblers and Slaty Antwrens (*Myrmotherula schisticolor*). Leadership in these flocks, as in most wandering flocks I have watched, seems shifting and irregular.

TERRITORIAL BEHAVIOR

Three families of ant-tanagers occupied the patches of forest and second growth along ravines at Kilometer 50 (fig. 4). As determined by altimeter, Family 1 ranged from 1340- to 1500-meter elevation on these steep slopes. In such steep terrain it is difficult to estimate the sizes of territories; but the birds seemed to use about the same amount of vegetation as do families of other species of ant-tanagers in British Honduras (Willis, 1960a); this would consist of some five to eight hectares per family.

The birds wandered irregularly throughout their territories in the fashion of other species of ant-tanagers. When the owners of neighboring territories were not present, a family sometimes trespassed into areas near its territory. There was thus overlap of foraging areas, although the trespassing was never extensive or prolonged.

When families meet near the centers of overlap zones, they display far more strongly than do *Habia rubica* or *Habia fuscicauda* in boundary disputes. At such times most of the Crested Ant-Tanagers chip and forage actively, wandering about and seemingly intermingling, as two bright-plumaged birds posture at the center of the more or less separate groups of foragers. *Chiv-eek* notes and *chee* series are given by both the combatants and the noncombatants, but such notes may have been a reaction to me. The *chiv-eek* notes of the two combatants are high-pitched; there are frequent *chip, cheep*, or *chee* notes interspersed. *Chiv-er-hee* was a note frequently given, both by combatants and by the female of one pair during one encounter.

The combatants spread and raise their crests maximally. The two fluff out the feathers of the belly until they nearly cover the legs. The gray bases of the feathers then frame the bright red feathers of the head and breast. One male fluffed out the feathers of the head briefly, but normally only the crest is fluffed. The tail is spread widely. The beak is horizontal or tilted upward as much as 30° . The head is retracted. The shoulders and even the edges of the wings are covered by the fluffed ventral feathers at times but at other times are slightly exposed in spite of the ventral fluffing.

Males alternately face each other and turn so that they face opposite directions. Combatants often display less than a meter apart, but they seldom move closer than 0.3 meter. Just before a bird flies at and supplants an opponent or a foraging member of the opposing group, it slowly bends forward and brings the spread tail vertically, so that it seems to fall forward off the perch (fig. 5a).

At lower intensities of display only the crest and tail are spread as the bird forages normally. One or more opponents may assume low-intensity postures or forage during a prolonged dispute.

After about an hour of stiff displays and sputtering calls, interspersed with infrequent supplantings or active foraging, the males part, and the two families forage away from each other. However, each male still seems excited; one called falsetto variants of *chiv-eek* and other notes at least 30 minutes after the families parted. His



Figure 5. a. High-intensity aggressive display of male Crested Ant-Tanager, just before falling forward off the perch and flying at a rival. b. Dawn-singing posture of male Crested Ant-Tanager. The crest is completely folded.

crest and tail were still partly spread. At intervals this male gave dawn songs, although he finally foraged normally.

SONGS

On the drizzling, gray morning of 24 March, I listened for the dawn songs of *Habia cristata* from a house near the K-50 stone. At 0550 Male 3 started to chant monotonously from trees above the garden. As solitaires (*Myadestes valloides*) and other species chimed in, Male 3 crossed into the woodlot on the steep slope above the river and continued his regular series of three to four notes at the rate of 1.7 notes per second and 12 songs per minute. At 0603 it was light enough to see him on a bare limb 15 meters above the torrent and 10 meters below the crown of the tree. He then dropped into the woodlot. Soon he returned to a twig two centimeters in diameter and 20° above the horizontal, below the top of a tree over the river. Except for one more flight into cover, he sang from nearby perches below the crown of the tree until 0621, then turned and dropped into the woodlot.

At about 0605 Male 1 started songs of 10 to 12 notes each from the undergrowth overhanging the river cliffs below the suspension bridge. Soon Male 3 varied his songs from one to 10 notes. Both birds paused two to four seconds between songs. The notes of both males were rather unmusical and monotonous *che'ik* sounds, as if an English Sparrow (*Passer domesticus*) were chirping to the beat of a metronome.

Male 3 kept his crest folded as he sang. His body was rather upright (fig. 5b), his tail was closed, and his flank feathers partly overlapped the lower edges of the wings. He looked about between and during songs, but seldom changed position. Opening the bill to sing was the only other visible movement. The dawn-singing posture resembles that of H. *fuscicauda* in British Honduras, although the simple and rather unmusical song resembles that of some races of *Habia rubica*.

Occasionally somewhat different songs were given by all three males after boundary disputes: *Check, eek, chek, eek, chek* (or *chraik, teef*), three to seven notes per song, were uttered at two notes per second. The crest was never spread; the posture resembled that of foraging or of dawn singing. This faint, unmusical song is rather like the dawn song of *Habia fuscicauda*. This alternating song may correspond to the day songs of *Habia rubica* and *Habia fuscicauda* in British Honduras.

COURTSHIP

The female in Family 1 solicited copulation strongly between 22 March and 24 March, and less strongly on 20 March and 27 March. Her precopulatory display (fig. 6a) closely resembled the same ceremony in *Habia rubica* and *Habia fuscicauda*. She called faint *chie* notes, like those of female *rubica*, five to 30 times in a row as she performed each ceremony. The notes were uttered four to six times per second, or at the rate used by female *fuscicauda*.

The female fluttered the tips of her wings rapidly as she fluffed out her ventral feathers and crouched slightly on the perch. She rarely turned her head from side to side; it was held level and slightly extended. The partly spread wings were always down as in *rubica*, never raised as is sometimes the custom of *fuscicauda*. Her closed tail was slightly lifted.

The tail of the female was raised to the vertical on one occasion when the male supplanted a third bird in red plumage and then hopped near her. She fluttered widely and called almost continuously, lifting her bright crest to its maximum (fig.



Figure 6. a. Low-intensity precopulatory display of female Crested Ant-Tanager. The wings flutter up and down rapidly. b. High-intensity precopulatory display of female Crested Ant-Tanager.

6b). However, the male reversed a few times, stared at nearby leaves as if foraging, and flew away after two minutes. He kept his crest folded and his body in a normal foraging pose but spread his tail slightly. When the male flew, the female immediately stopped displaying and followed him; I then heard her calls once more. Later she hopped down on a dead leaf in vines about seven meters up, sat on it as if on a nest, then lifted her tail and fluttered her wings busily.

FAMILY COMPOSITION

The soliciting female was nearly as brightly colored as her mate. She was almost indistinguishable from him when she foraged. One other bird in the flock was similarly bright. Two other birds were in the dull plumage.

Both birds in Pair 2 were in bright plumage; the female was slightly duller than her mate. Of four birds in Family 3, the male and two others were in bright plumage, and the fourth bird was in dull plumage. A fourth family at Las Cascadas included three birds in bright plumage and one in dull plumage.

DISCUSSION

Crested Ant-Tanagers differ from other members of the genus remarkably little in ecology and behavior, despite the fact that they are limited to upper tropical and lower subtropical ravines on the rain-drenched western slopes of the Western Andes. Evidently in this region frequent landslides make possible the dense undergrowth and immature forest utilized by members of this genus.

The undergrowth in which Crested Ant-Tanagers forage is not strongly affected by the torrential rainfail of western Colombia, since valleys tend to be in rain shadows. The ant-tanagers avoid the mossy and epiphyte-laden limbs usual on slopes that receive the full force of the rains. The undergrowth frequented by these tanagers resembles undergrowth in the tropical lowlands in the prevalence of bushes and vines. Thus the Crested Ant-Tanagers seem to be tied to an unusual kind of immature or "disclimax" forest indirectly caused by runoff from the heavy rains but not directly affected by them.

Since Crested Ant-Tanagers stay near valleys and streams, they probably occupy lower elevation than had previously been assumed. The record at Las Cascadas (700-meter elevation) indicates that the birds frequent the upper tropical zone as well as the lower subtropical zone. The humid lower subtropical zone is nearly absent on the Central and Eastern Andes, since both lie in the rain shadow of the Western Andes. Ant-tanagers may be absent from these two eastern ranges because there is little rain at suitable elevations.

The replacement of Crested Ant-Tanagers by other species in similar habitats on the western slope of the Western Andes should be further investigated. The various species obviously are not identical in their foraging and other requirements, or they would not have divided the habitats rather than replacing each other irregularly. However, it may be that interspecific competition is great enough in areas of overlap to force each species to stay in areas where it can do the things it does best.

Crested Ant-Tanagers forage more like Red-crowned Ant-Tanagers than like Red-throated Ant-Tanagers, but they use a foraging zone one to 10 meters above the ground whereas competing Red-crowns and Red-throats in British Honduras (Willis, 1960a) divide this foraging zone.

The seven or more calls used by H. cristata are as follows: the sharp chiv-eek

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scold; a sharp *chip* as a contact note; a *ch'ree ch'ree* when a bird follows or leads another; a sharp series of loud *chee* notes when a bird flees; a soft series of *chie* notes used by the female soliciting copulation; an alternating song, *chek*, *eek*, *chek*, *eek*; and a monotonous chirping *che'ik* repeated as a dawn song. All these are rather like calls given by *Habia rubica*. However, the scold and the alternating song are also like calls of *Habia fuscicauda*. Most calls of Crested Ant-Tanagers are sharp and loud, perhaps because the birds live in an environment made noisy by brawling streams.

The presence of a strong display in boundary encounters is an important difference between this and other species of ant-tanagers. Song duels, as in *Habia rubica*, would perhaps be inappropriate in this noisy environment. Perhaps the difficulty of sustaining vocal displays encouraged the development of vigorous visual displays in *H. cristata*, although another form (*H. fuscicauda*) seems to get along well enough although neither vocal nor visual displays are well developed.

The crest of *cristata* is raised during boundary disputes, not during dawn singing as in *rubica*. A somewhat sexually dimorphic ant-tanager (*H. gutturalis*) in northern Colombia also spreads the crest during displays at boundaries. Thus only the two strongly crested and slightly dimorphic members of the genus use their crests in boundary disputes.

Territoriality, organization into family-size groups, and association with wandering multispecific flocks are similar in all species of the genus. *Habia cristata* is most often associated with wandering flocks, whereas *fuscicauda* is least often.

SUMMARY

Crested Ant-Tanagers (*Habia cristata*), in contrast to widespread lowland anttanagers (*H. rubica* and *H. fuscicauda*) previously studied, occupy the lower subtropical forests on the perpetually wet western slope of the Western Andes in Colombia. There the species inhabits steep ravines next to rushing mountain streams, where frequent landslides due to high runoff from heavy rains on nearby ridges open the forest canopy and allow dense undergrowth to flourish. The species avoids mossy and epiphyte-laden forests characteristic of ridges in humid or cloud-forest localities in this region; several other behaviorally and ecologically similar species use these habitats on nearby slopes of the Western Andes. Thus the restriction of *cristata* to the upper edge of a zone of torrential rainfall may be due to the creation of perpetually immature forests by runoff rather than to direct effects of rainfall on vegetation.

Crested Ant-Tanagers forage in rapidly moving groups of two to five birds, often in association with other species of wandering forest flocks. The ant-tanagers forage one to 10 meters above the ground much of the time. Foraging birds take a variety of fruits and arthropods in a manner very similar to that of *Habia rubica*.

Many calls of Crested Ant-Tanagers are like calls of *rubica*, but a few are like calls of *fuscicauda*. Most calls of *cristata* are sharp and loud; the sounds are easily audible above the roar of nearby streams.

Habia cristata is as strongly territorial as are other members of the genus. Males of cristata use strong displays in territorial disputes rather than song duels as do males of *rubica*. Crested Ant-tanagers raise their crests when displaying to each other, but not when dawn-singing.

The precopulatory display of females of *cristata* resembles the display of *rubica*, even in the crest-raising; but the precopulatory calls are given at a rate similar to that of *fuscicauda*.

THE CRESTED ANT-TANAGER

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