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BEHAVIOR AND ECOLOGY OF TWO FORMS OF WHITE-CHINNED WOODCREEPERS (*DENDROCINCLA MERULA*, DENDROCOLAPTIDAE) IN AMAZONIA

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Abstract

White-chinned Woodcreepers (Dendrocincla merula) *of two areas near Manaus, in Amazonian, Brazil, differ in voice from individuals studied in nineteen other localities south of the Amazon River and west of the Negro, and may be a separate species. The large size (50-57 g) of Manaus birds, especially males, is attributable to absence of similarly large ant-following antbirds north of the eastern Amazon; White-chins move low over swarms of army ants much like large ant-following antbirds. In other regions, especially in a study area alongside swamp forests at Belém (Brasil), there were so many large ant-following antbirds that White-chins often had to forage 2-4 m up. The medium size (40 g) of White-chins at Belém is perhaps due to absence there of medium-sized ant-following forest antbirds of the genus* Rhegmatorhina.

White-chins are dependent on following army ants for flushed prey, more so than is the related D. fuliginosa *that forages above them. Unlike* D. fuliginosa, *they dispute with each other little. Like it, they wait on perches and sally out for food rather than climb tree trunks in normal woodcreeper style.*

Like D. fuliginosa, *male and female associate mainly for mating, and females care for nests and fledglings alone. White-chin females feed young for nearly three months and let them stay around until males drive them off at the start of the next breeding season. Nesting females overlap on home ranges without much interaction.*

Introduction

Woodcreepers of the genus *Dendrocincla* commonly follow army ants (*Eciton burchelli* and a few other species) for flushed prey in

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most lowland forests from Mexico to Argentina (Willis, 1960, 1966, 1972; Willis & Oniki, 1978). White-chinned Woodcreepers (*Dendrocincla merula*) of Amazonian and neighboring forests have proved to be the most dependent ant followers of their genus. In studies at 21 localities since 1965 (fig. 1), I have never seen one foraging away from ants.

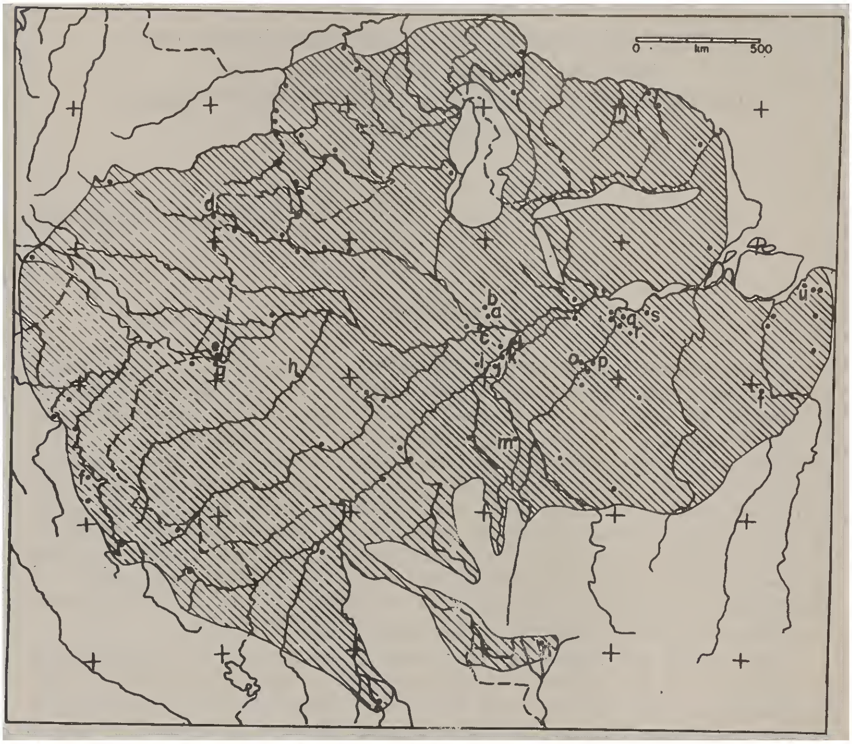

Fig. 1. Distribution of White-chinned Woodcreepers, with study locations: a. Reserva Ducke; b. Km 60; c. Km 23, Manacapuru Road; d. Mitu; e. Leticia; f. Cashibococha; g. Benjamin Constant; h. Carauari; i. Igapó-Açu; j. Borba; k. Coatá; 1. Nova Olinda do Norte; m. Sucunduri; n. Tangará da Serra; o. Maloquinha; p. Miritituba; q. Diamantino; r. Palhão; s. Curuá-Una; t. Marabá; u. Aurá Reserve, Belém.

At 19 of these localities, in the three quarters of the species range from the Rio Negro west around the head of the Amazon and thence east to Belém, the behavior and ecology of these woodcreepers ("castanoptera group" of subspecies: *bartletti*, *olivascens*, *castanoptera*, *badia*) varied little. At two localities just east of the Rio Negro near Manaus (subspecies *obidensis*), the voice and size and ecology of White-chinned Woodcreepers were different from those at the other 19 localities.

Here I ask if the Manaus and other White-chins should be considered separate species, or are just "ecotypes" of one species. The differences are greater than one normally encounters between species in this genus; but the differences can be partly explained by a single ecological change east of the Rio Negro and north of the Amazon: there is no large ant-following antbird (Formicariidae) in this entire Guianan region (Oniki & Willis, 1972) and White-chins move into the vacant niche.

STUDY AREAS AND METHODS

The main studies north of the eastern Amazon were in and near Reserva Ducke, a forest reserve of the Instituto Nacional de Pesquisas da Amazonia (INPA) just north of Manaus, from 5 July 1973 to 25 August 1974. I visited briefly in May 1966, in September 1972, and in July 1976 as well. Moderately tall upland forests at 80-120 m elevation grade into lower woodlands in sandy soils of valleys at 60-100 m elevation. Second growth and forest plantations for various types of forestry experiments cut into the original forest in many areas (Willis, 1977).

The main studies of subspecies *badia* were in and near the Aurá Reserve of the Área de Pesquisas Ecológicas do Guamá (APEG), just east of the city of Belém, from 2 April 1972 to 25 May 1973. Habitats are described in Crump (1971), Oniki (1972) and Lovejoy (1974). Much of the area is swamp forest or "várzea," partially flooded twice daily by tides that bring in white sediment-laden waters from the nearby Guamá River. Slightly higher areas flood only with standing and dark water from rains, and form "igapó" swamps that grade into "terra firme" upland forests at a few meters above sea level. The tall upland forests (Cain *et al.*, 1956) are diverse, but now form only a fringe between igapó or várzea and narrow belts of second growth of various ages.

In both study areas, I kept track of several colonies of army ants (*Eciton burchelli*) by checking for possible bivouac changes in evenings. Patient watching from behind daily swarm raids caused many individuals of ant-following species of birds to become accustomed to me. I noted behaviors, recorded voices with a Uher 4000-S tape recorder, and filmed with Beaulieu R-16 movie camera or Asahi Pentax Spotmatic. Birds were mist-netted ahead of the ants, individually color banded, weighed with Pesola spring scales, and checked for cloacal temperatures (Schultheis thermometer), molt, wing and bill length, and brood patches. White-chinned Woodcreepers occur at low density both at Belém, where 10 were banded, and at Manaus, where 25 were banded.

290 specimens were checked for wing molt, wing and bill length, and information on labels in the major museums of the United States, Venezuela, Brazil, and Europe.

GENERAL APPEARANCE AND BEHAVIOR

Both kinds of White-chinned Woodcreepers are richly reddish-brown birds with grayish-brown faces. Their white chin patches are indistinctly outlined by dark malar lines, which may extend past the base of the bill to the lores. Some forms of the castanoptera group, especially the rather olive-brown *olivascens* of the region from the Madeira to the Tapajós Rivers and south to the upper Paraguay River (Willis, 1976), have small bare pale areas around the eyes. Females, males and young birds are alike in plumage, except that the throat is dirty white in very young birds. Color differences between subspecies are minor.

In the field, one usually encounters White-chins as antbirdlike rattles or shrill notes low around swarms of army ants in upland forest. When the nervously flying birds reappear, they are perched upright like woodpeckers, flicking their wings out as they rattle briefly at the observer. At once, one notes that the bill is short (see below) compared to that of *Dendrocincla fuliginosa*, which is widely sympatric with White-chins; and that White-chins normally perch below *fuliginosa* and flee horizontally rather than vertically.

With further observation of tame birds, it becomes evident that White-chins are acting like antbirds rather than like woodcreepers: they use slender perches near the ground, to which they dart for prey that are escaping the ant hordes; but they rarely perch on thick trunks or fly to foliage or trunks above the ground for prey as do most of the other woodcreepers at the same ant swarms. Large antbirds, if present, attack them vigorously despite their generally vertical postures, so different from the crosswise postures of antbirds on slender vertical stems near the ground. Large woodcreepers, if present, move down at them but rarely take such slender perches.

SIZE

Size of bird is important in discussion of the ecology and taxonomic status of White-chinned Woodcreepers. On the study area at Manaus, they were much larger than on the study area at Belém (Table 1). However, not all White-chins north of the eastern Amazon are large, for the few specimens from Cayenne and several from Guyana are small while a few from Guyana and all from the north bank of the lower Amazon are about the size of birds at Manaus. Todd (1948) described the large birds as *D. m. obidensis,* from Óbidos in Brazil, a name probably applicable to the Manaus birds. The eastern subspecies *badia* (Rio Tocantins east) is also unusually small, for western subspecies approach the size of *D. m. obidensis* at Manaus.

Culmen length (C) increases linearly with wing length (W) in these birds, the approximate relation being $C = 0.275\ W - 1.175$. Manaus birds measured alive tended to have longer bills for their wing lengths than do specimens, but the same slope of curve. (Only two live *badia* were measured.) Weight data are few, and it is not certain that *obidensis* follows the same curve of increase with wing length as in other subspecies (fig. 2).

Dendrocincla fuliginosa males and females differ in wing length more than in weight or culmen, and the difference can help one sex

TABLE 1. Culmen, wing and weights of White-chinned Woodcreepers

Subspecies	Culmen (mm)		Folded Wing (mm)		Weights (g)	
	Males	Females	Males	Females	Males	Females
obidensis[1]	29.4(9)[2]	28.0(6)	109.0(9)	102.7(6)	57.0(10)	49.5(8)[3]
merula	25.3(6)	23.6(5)	101.2(6)	100.8(7)		
badia[1-4]	25.8(2)		97.0(7)		40.6(9)	
badia	25.0(19)	24.4(17)	97.2(23)	94.5(17)		
castanoptera	26.8(14)	26.2(14)	101.7(13)	97.7(13)		
olivascens	27.9(9)	26.0(19)	102.3(9)	99.1(20)	44.5(2)[5]	
bartletti S[6]	27.5(21)	26.5(20)	103.2(20)	99.9(19)	49.0(7)	46.2(4)[7]
C	26.8(12)	26.5(7)	102.3(12)	99.3(7)		
N	27.1(30)	26.0(26)	101.5(32)	97.3(26)		

[1] Live birds, in this study; others are specimens. [2] Numbers in parentheses are sizes of samples; other figures are averages. [3] Ten birds of unknown sex, mostly birds of the year, averaged 55.0 g. [4] The sex of these birds is not certain (see text). [5] Two birds of unknown sex from Sucunduri. [6] "S" birds are from the Madeira River to Peru; "N" birds are from Venezuela, Colombia and northern Brazil; "C" birds are from the north bank of the Solimões. [7] Weights from Balta, Peru, courtesy of L.S.U. Museum; one male and three females from Hacienda Flor, Peru, courtesy of Museum A. König, Bonn, Germany.

birds in the field (Willis, 1972a). Male White-chins also are slightly larger than females, but in most areas the sexual differences are less than in *fuliginosa* (Table 1). Probably young males of the year are intermediate in size and blur the distinctions, as is suspected for *fuliginosa.*

Resident male and female White-chins at Manaus are unusually different in size, when one judges sex by the presence of unfeathered edges of the brood patches in females and such behavioral patterns as the fact that they care for young alone. No resident birds were found at Belém; all but one had the wing length of males in collections, and even that one bird had a feathered brood patch. Since only two had been banded in previous intensive banding programs in the area (Lovejoy, 1974; Oniki, 1972), they were probably mostly birds of the year that later settled elsewhere to breed.

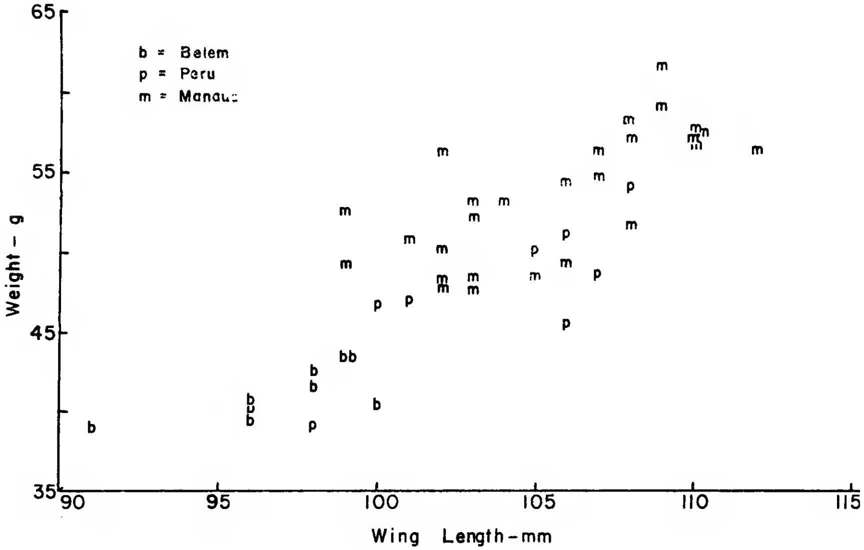

Fig. 2. Weight versus wing length for Manaus (m) and other birds (b,p).

Wandering and young birds of unknown sex also occurred at Manaus. Wing lengths of these birds were about evenly divided between lengths characteristic of adult males and females ($\bar{x}=104.2$; $n = 8$), but all had feathered brood patches. Weights were often high, near the male average or above, for wandering birds even when of female wing length; but 5 of 10 had weights in the upper end of the female range (50-53 g).

TEMPERATURES

Cloacal temperatures were about equally high at Belém ($\bar{x} = 43.6$°C, $n = 8$; range 42.4°-44.7°) and Manaus ($\bar{x} = 43.2$°C, $n = 19$; range 41.7°-44.1°).

VOICE

Appearances of White-chinned Woodcreepers vary little, and size differences are perhaps linked by intermediate forms, but vocal differences between Manaus birds and others are striking:

Chatters: The characteristic alarm call to humans and other predators is an antbirdlike rapid "dit-it-it-it" (fig. 3, A) in all but Manaus birds, where the sound becomes a piercing "deet-eet-ee" or similar series (fig. 3, B, C). The Manaus call is slower (12.5 versus 20 notes per second) but somewhat higher in resonant frequency than is the call in other areas. Chatters are lacking in *Dendrocincla anabatina, D. homochroa, D. fuliginosa* and *D. turdina.* The yellow gape flashes briefly for each note of the call.

Stieking: Only Manaus birds have variable, faint to loud "spee" or "stee" alarm notes, which slightly resemble the alarm calls of the four other *Dendrocincla* species above (fig. 3, D). The yellow gape flashes conspicuously for each note.

Screaming: Both Manaus birds and others scream "eeeeh" or "cheeh" repeatedly in the hand (fig. 3, C). The screaming in the figure seems intermediate between a chatter and stieking, but most calls in this species are simple inverted "U" notes and hence vary mainly in speed and frequency.

Singing: Manaus birds give a simple and loud whistled "KEW KEW KEW KEW KEW KEWP!" or similar song (fig. 3, E), at times slightly upscale or repeated. The head is turned to the trunk to sing. Other subspecies whistle a musical upscale WE WI DI DIT, repeated several times in succession after a few introductory notes at the lowest pitch, like a person practicing scales rapidly on a flute. Two phrases from a distant bird at Miritituba (fig. 3, F) are too faint to show details, but indicate that this song is lower in pitch than that at Manaus and that the phrases are repeated. "Faintsinging" birds of the two forms give faint versions of the respective loudsongs. Repeated upscale songs were noted at Belém, Diamantina, Miritituba, Maloquinha, Nova Olinda, Coatá, Borba, Carauari, and Mitu. Wandering birds rarely sing, but young and settled adults do sing.

Longrattles: Manaus birds scared away from a swarm by humans or competitors go into a long series of rattles, syncopated by intercalation of slight "rrrh" sneezes: "chat-at-at-rrrh, chat-at-at-at rrrh, chat-at-rrrh," etc. At more than a few meters, one hears only the rattles, at a rate of 5 to 6/second, as punctuated series of notes (fig. 3, H). The throat barely pulses and is held close to the trunk. Other subspecies give long uninterrupted monotonous "tik-tik-tik-" or "uk-uk-uk-" rattles at 4 to 5 notes/second, without syncopation (fig. 3, G). Overtones at about 5.5 KHz are normal. All White-chinned Woodcreepers longrattle more slowly than do *D. fuliginosa.*

Rattleting: In close disputes, both forms give a short and faint "wi-i-i-ih" rattlet, reminiscent of rattleting in *D. fuliginosa.*

Growling: As in *D. fuliginosa,* faint growling "chauhhh" notes mark close encounters of young birds playing (fig. 3, I) or of adults attempting copulation, in both forms of White-chinned Woodcreepers. Growl-rattlet combinations were also heard.

Squeaking: Young at Manaus squeak or hiss "chiehhhh" when fed. I have not encountered young of other subspecies except at Coatá (subspecies *olivascens*), which were faintsinging in the absence of a parent. Probably this call occurs in all subspecies, as it occurs in *D. fuliginosa* and most young birds.

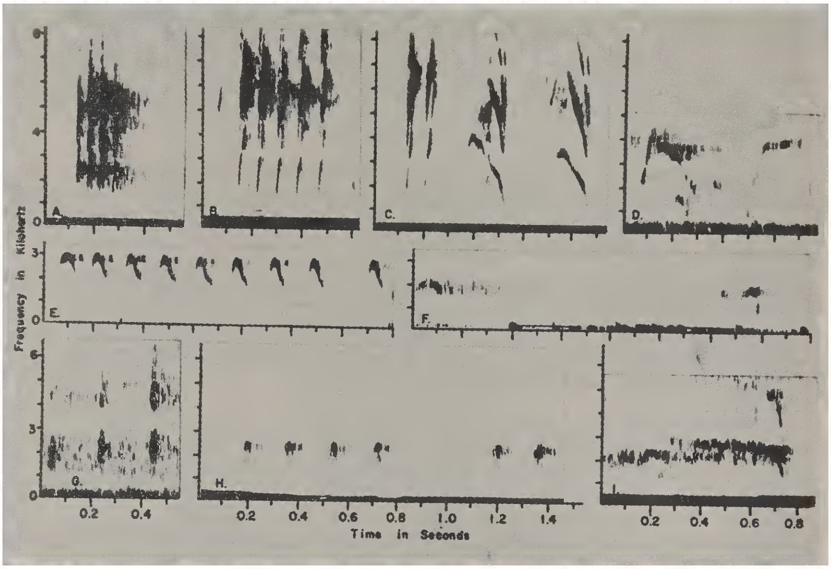

Fig. 3. Sonographs of voices of White-chinned Woodcreepers: A. Chatter at Belém; B. Chatter at Manaus; C. Two chatter notes and two brief screams, from a bird in the hand, at Manaus; D. Stieking at Manaus; E. Loudsong, Manaus; F. Two song fragments, Miritituba; G. Long rattling, Belém; H. Long rattling, Manaus; I. Growling of young birds at play, Manaus.

ALARM BEHAVIOR

All behavior is commonly divided in six parts (Willis, 1973): alarm behavior to predators, agonistic behavior to competitors, maintenance behavior to polluting agents, foraging behavior to foods, reproductive behavior to kin, and spatial behavior to larger desirable units. Ecological terms in use for these behaviors are, respectively, predation, competition, pollution, growth, reproduction, and dispersal. One normally sees alarm or antipredator behavior first when encountering White-chins, so it will be considered first. Three types of alarm behavior are evident: panicking, freezing, and mobbing. The last was noted only in Manaus birds.

Panicking: White-chinned Woodcreepers flee and chatter when one appears at their ant swarm or is in their way as they dart rapidly low through the undergrowth from one ant colony to another. Chattering but longer segmented calls of this type (chirring, rattling, etc.) are commonly mobbing calls to ground predators in antbirds at the same ant swarms, and to some extent mammals must find the chatters of White-chins irritating enough to send them away. (I find antbird chirring irritating or intimidating, for some seem to mimic carnivore growls. The shorter White-chin calls are more startling than intimidating.) White-chins of both types use this call more like the even shorter "chipping" sharp calls of antbirds or the "stieking" of *D. fuliginosa,* as alarm notes in panicked fleeing before hawks or other immediate danger. A *Xiphorhynchus pardalotus* and a *Gymnopithys rufigula* at Manaus froze at the chatters of White-chins, and both *D. rufigula* and *Pithys albifrons* fled with chipping at the note on several other occasions. I recorded chattering specifically for raptors (*Micrastur ruficollis,* 20 times at Manaus, once each at Coatá and Palhão; *Micrastur semitorquatus,* 1 at Manaus; *Leucopternis melanops,* 1 Manaus; *L. kuhli,* 1 Palhão), mammals (to me, many times; once each to a passing man and a bulldozer; once to a tayra, *Eira barbara,* at Cashibococha; and to a rapid chase of two brockets, *Mazama americana,* at Manaus), treetop large birds (toucans and oropendolas at Coatá; yelling parrots at Diamantina), to a falling large leaf, and to a windstorm.

Gradually the chattering White-chins return after a falcon-caused or other "dread" has scattered them from an ant swarm. They dart about rapidly, hide or swing behind tree trunks repeatedly, and are hard to see. I have seen them swing behind saplings at passing caciques (*Cacicus haemorrhous*) or at a passing smaller woodcreeper (*Dendrocincla fuliginosa*), and flee at chipping or rattling noises of small antbirds. In the brief instants when one sees the panicking White-chin, he notes occasional sudden flicking of the wing tips, a long or extended neck, a sleeked head but spread tail, and sudden jerks of the head from one side to the other. The yellow gape does not flash much, for the bill opens only briefly for each note of the chatter.

Mobbing: Manaus birds, but not birds of the castanoptera group, add piercing "spee" notes among their chatters if they stay within sight of the observer. Although this call resembles alarm "stiek" notes in *D. fuliginosa,* it is used more like the rattles or chirrs of antbirds at the same swarm of ants: the Manaus White-chin is mobbing the observer, flashing the yellow gape at him with each irritatingly shrill note as it hesitates to leave the swarm. I think it is a "stay" call while chattering is a "flee" call. Once the shoulders were out. The neck is short and the head is not sleeked. Specific records were much as for chattering, for the two calls often alternate in excited situations: 9 times to *Micrastur ruficollis,* twice to humans (many other times to me), once at *Leucopternis melanops,* once at brockets racing past. However, mobbing records to *M. ruficollis* were mostly of birds watching while the falcon chased insects over the ants.

Freezing: White-chins of both types often freeze behind a vertical perch at danger or the alarm calls of others, even trying to do so behind slender saplings of 2 cm diameter. The body and head sleek while the eyes bulge. The bird crouches close to the perch with legs splayed (unless on a slender sapling), concealing the white throat by bringing the head especially close, and becomes a dark bird on a dark trunk near the forest floor. No sound is used, though birds scared away from a swarm by an observer, hawk, or dominant White-chin may freeze and give longrattles (I consider this a different type of freezing, described below as agonistic behavior). Specific records of alarm freezing were noted to alarm notes of other woodcreepers (*Dendrocincla fuliginosa* at Belém and Manaus, *Dendrocolaptes picumnus* and White-chins at Manaus).

Struggling: White-chins screamed repeatedly in the hand or mist net, flashing the yellow gape at the observer, but did not peck or struggle except for occasional sudden attempts to fly. I once heard a woodcreeper of another species screaming as it was carried away by a raptor (probably *Micrastur semitorquatus*) at Manaus. Banding

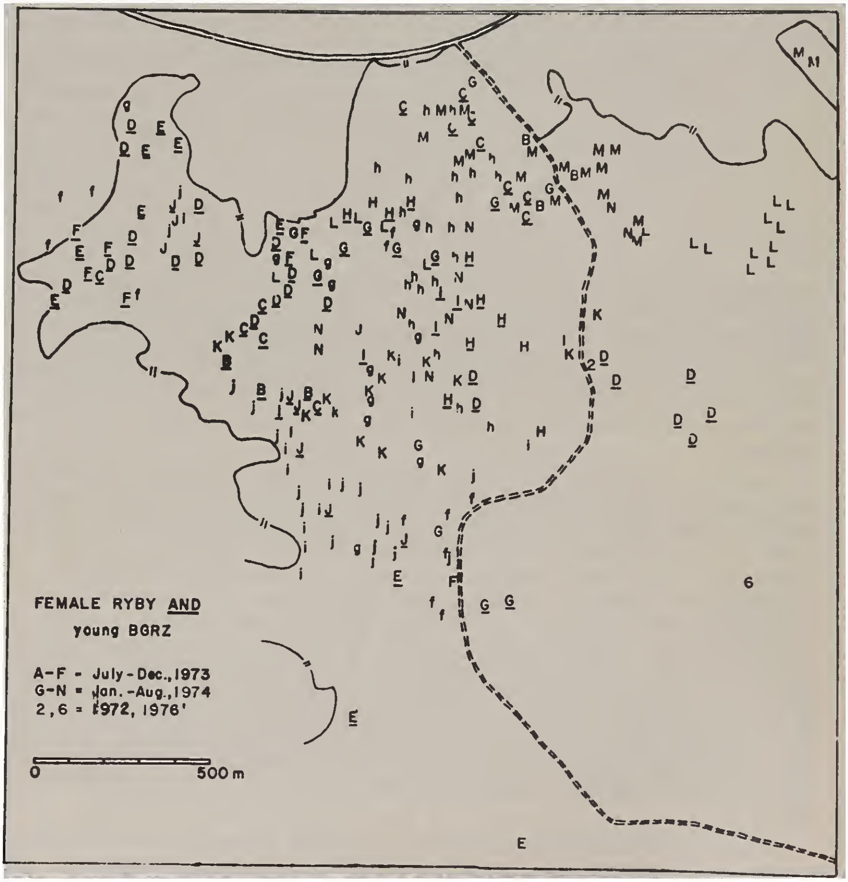

Fig. 4. Localities at and near Reserva Ducke for female RYBY (capital letters indicate months of record) and her young bird BGRZ (underline of female record if with her; lower case letter if not).

birds often caused them to desert a given ant colony or to become wild again after they started to get tame.

Taming: White-chins varied greatly in tameness. Old resident adult birds at Manaus were least tame, and required several weeks to get over their panic and mobbing each time I appeared. They never quite trusted me, although after a year with certain individuals they foraged without alarm behavior as long as I was more than 5 m off. Young birds at the same locality were never very wild, and eventually became very tame. One young bird, by the time it was six months old, flew up near me each time the swarm stopped raiding and eventually started to clamber all over me, pecking busily as in "play" reproductive behavior. I allowed it to clamber over my clothes or notebook as I wrote, but shooed it away whenever it tried to peck my glasses. Repeated accidental netting of this and another young bird never seemed to disturb them after the screaming of handling was over. Once one young bird peered at two Saturniid moths near the ground, but investigation of possible predators (or me) was not noted otherwise. At Belém, all the birds became accustomed to me readily, as did most wandering birds at Manaus. In other areas, some birds became tame and others stayed wild in the few days to two weeks I usually had for studies; probably tame birds were young ones. At times, nervous birds calmed within a few minutes if a tame

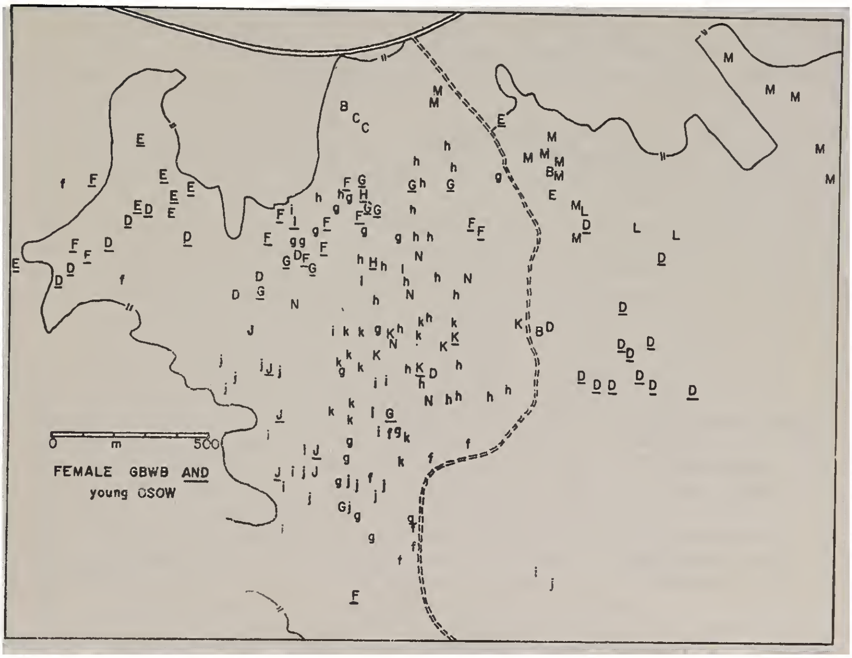

Fig. 5. Localities at and near Reserva Ducke for female GBWB (capital letters) and her young bird OSOW (underline of female record if with her; lower case letter if not).

one was working near me. The birds were unusually nervous in semiopen habitats, such as the rows of tree plantations at Manaus (see spatial behavior).

Manaus birds tamed rather little to the forest-falcon *Micrastur ruficollis*, which persistently followed army ants there. They fled, chattering, each time it flew up; and they stieked at it from behind tree trunks later. Some White-chins foraged tentatively at the far ends of swarms with attending falcons. D. Wechsler was watching at one swarm when the large forest-falcon *Micrastur semitorquatus* attacked; the White-chins quickly deserted, and showed up at a swarm 1.5 km away, where I was watching, within 1 hr.

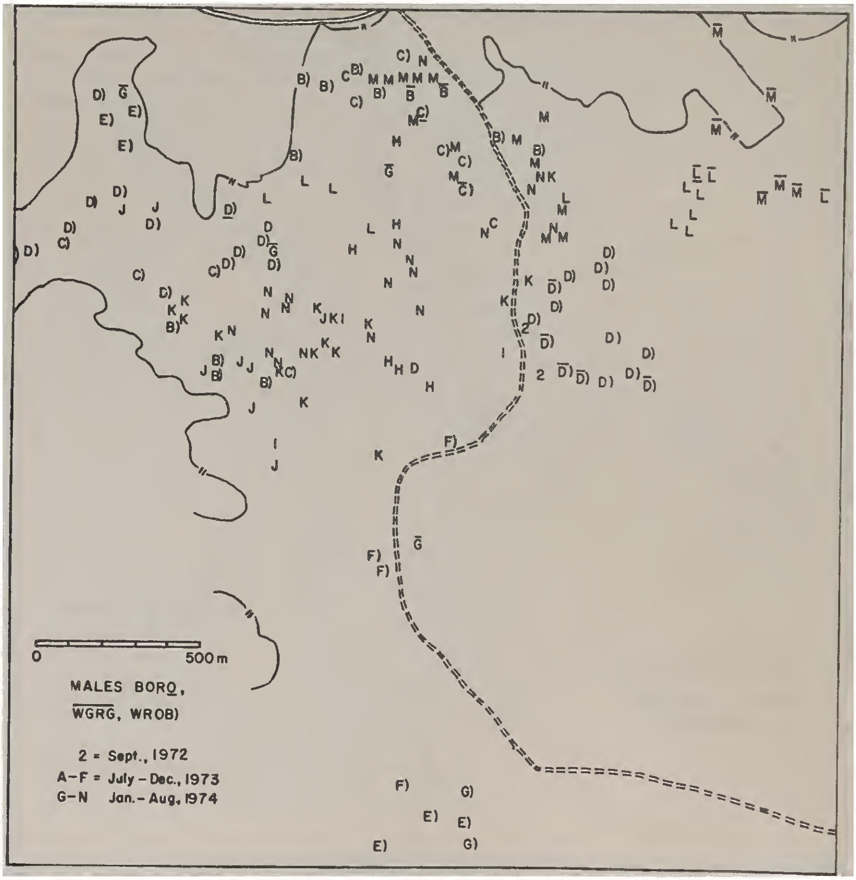

Fig. 6. Localities at and near Reserva Ducke for males BORO (letter indicates month; underline if with another male), WGRG (overlined letters only), and WROB (letters with end parentheses).

FORAGING BEHAVIOR

Once White-chins become tame enough to show little alarm behavior, one can watch them foraging and begin to understand why Manaus birds mob or flee from the observer while others flee from him. The considerable alarm of both forms is probably related to considerable danger from ground mammals, for *D. merula* everywhere forages closer to the ground and ants than do any others of its genus except Trinidadian *D. fuliginosa* (Willis, 1966) and Central American *D. anabatina* (Willis, 1960).

Manaus birds forage near the ground more than do others (Table 2). 87.9 percent of their foraging records were 1.0 m or less, as against 58.1 percent for Belém birds. Other species (mostly large woodcreepers; see under agonistic behavior) attacked Manaus birds under 1.0 m only 0.5 percent of the records in that zone, for there is no large ant-following antbird near the ground in the Guianan region. Other species (mostly *Phlegopsis nigromaculata,* a 50-gram antbird) attacked Belém birds under 1.0 m for 6.6 percent of the records in that zone. Between 1.0 and 8.0 m up, Manaus birds were attacked only in 0.5 percent of the records. Above 8.0 m, Belém birds were attacked for 3 of 3 records but Manaus birds were undisturbed in 4 records.

Belém White-chins often wandered over the ants as if searching for suitable places among the large antbirds. Manaus White-chins more often waited stolidly without much movement. Both forms normally moved about 1-2 m up when moving from place to place over ants, and dropped down to forage. Manaus birds often moved to places where smaller antbirds were actively foraging or fighting, and took their places.

Belém birds stayed on vertical perches more than did Manaus birds, avoiding the horizontal perches that are often taken by aggressive *Phlegopsis nigromaculata* there (Table 2). Moreover, Belém birds less often perched across a perch in antbirdlike fashion than did Manaus birds (Table 3). They are clumsy in this posture, and are easily attacked. However, they stand high on their legs better than do *D. fuliginosa.* (A bird with a perch angle between 340° and 0° is on a stem that angles less than 20° downward toward the head end; 0° represents a horizontal perch and 90° a vertical one.)

This woodcreeper is unusually good at using slender perches near the forest floor, otherwise used more by antbirds than by woodcreepers (Table 2). However, Belém birds tended to avoid the slender perches used by *Phlegopsis nigromaculata* there, and hence concentrated on perches of pole size (6-15 cm diameter), like the related *D. fuliginosa* (Willis, 1972a). On vertical perches under 1 cm in diameter, the tail ordinarily curves past the perch on each side, or several tail feathers slip past and the bird is supported only by the central tail feathers. The small feet are offset, one above the other, on perches under about 2 cm in diameter. Perching vertically on perches under 1 cm in diameter is much more difficult than is the horizontal perching of antbirds, and White-chins occasionally flutter or try to perch across such perches. Even this woodcreeper tends to leave 1-cm perches for antbirds, despite an abundance of such slender seedlings near the forest floor. At times, the bird perched on two such seedlings, one for each foot. On perches larger

TABLE 2. Heights, angles, and diameters of perches of foraging birds

Height (m)	Percent		Angle(°)	Percent		Diameter (cm)	Percent	
	Manaus n=1516	Belém n=809		Manaus n=1418	Belém n=630		Manaus n=1252	Belém n=585
0.0	0.7	0.1	340- 0	2.3		0-1	6.7	4.1
0.1	6.1	0.2	20	4.9	1.6	2	17.0	13.2
0.2	31.6	3.5	40	6.8	3.2	3	14.9	12.8
0.3	27.0	14.7	60	2.9	2.4	4	10.7	10.8
0.4	11.5	12.4	80	8.7	11.1	5	10.4	12.0
0.5	5.2	10.4	100	72.5	77.0	15	26.4	37.4
0.6	2.0	5.9	120	1.9	4.4	25	8.9	8.0
0.7	1.3	4.7	140	0.1	0.3	50	3.4	1.5
0.8	1.1	2.0				100	1.1	0.2
0.9	0.5	1.6				100+	0.4	
1.0	0.9	2.6						
2	5.7	24.4						
3	2.4	9.4						
4	1.5	4.9						
5	1.0	1.5						
6	0.5	0.9						
7	0.5	0.5						
8	0.3	—						
9	0.1	0.2						
10	0.1	0.1						

than 10 cm, the small feet of this woodcreeper spread wide, and the bird seems to drag its belly on the trunk to climb, unlike its larger-footed relative *D. fuliginosa.* White-chins do not climb much; they ordinarily fly from one perch to another, even when moving nearly vertically. One bird almost alighted on a spiny pupunha (*Guilielma gasipaes*) trunk, but fluttered off at the last instant.

TABLE 3. Perching crosswise

Perch Angle	Number of Records		Percent	
	Manaus	Belém	Manaus	Belém
340- 0	9	0	28	0
-20	18	2	28	20
-40	12	2	14	10
-60	0	1	0	7
-80	3	1	3	1

Manaus birds occasionally hopped or fluttered through dense treefalls, but Belém birds merely watched smaller *Pyriglena leuconota* doing so. Both at Belém and Manaus, White-chins preferred the open understory of upland forest and avoided the dense understory of second growth and creeks. However, Belém White-chins avoided the often open understory of floodplain swamps, even if Maloquinha birds sometimes used open seasonally flooded creekside undergrowth.

Occasionally a White-chin flashes one wing around a trunk, then looks for prey; but this foraging pattern was much rarer than in *Dendrocincla fuliginosa,* a woodcreeper that takes more food from the trunks. As in ant-following antbirds, the most common foraging behavior of White-chinned Woodcreepers is a drop to the ground for prey, ending in a quick return to a perch above the ants (Table 4). Occasionally a White-chin remains on the ground briefly, but is likely to be attacked by ants and to have to jump about while pecking them out of its plumage. One White-chin did remain among the ants several seconds, jumping and lifting its tail each time it landed splay-legged on the ground. Actual gleaning or pecking prey from the ground is not common, and usually is done from a low perch above the ants. White-chins at Belém sally to foliage and debris above the ground more than do White-chins at Manaus; the former also glean more from foliage and from trunks than do the latter. This diversification of foraging behavior is like the diversification in subordinate antbirds of various species (Willis, 1972b for instance), while concentration on the ground is characteristic mainly of dominant and subdominant antbirds.

Even at Belém most of the food of White-chins comes from near the ground (Table 5), and most of the perches from which the birds tried for prey were low ones (Table 6). This indicates that the Belém White-chins were rather unsuccessful when they did take high perches, and that attacks by *Phlegopsis nigromaculata* were the main factor keeping them from foraging as low as at Manaus. However, Belém White-chins did find proportionately more food at 1-4 m above the ground than did Manaus White-chins. Other species of woodcreepers took most of the food at these levels at Manaus.

TABLE 4. Foraging motions and places for White-chins

Place	Foraging Motion (%)		
	Sallying	Gleaning	Leaftossing
Ground	68.6 (89.3)[1]	1.5 (1.7)	— (0.1)
Trunk, stem	1.8 (0.8)	3.6 (1.7)	
Debris	3.3 (0.2)	0.4 (—)	
Foliage	10.2 (2.9)	2.6 (0.4)	
Air	1.5 (1.3)		
Unspecified	6.2 (1.2)	0.4 (0.3)	

[1] Belém percentages based on 274 foraging attempts; Manaus percentages, in parentheses, on 1562 attempts.

At Manaus, White-chins captured ground prey closer to the perch than at Belém. The ratio of captures 0-0.2 m distant to those 0.3-0.4 m distant was 76:41 at Manaus and 13:19 at Belém. Probably the Belém birds were taking perches somewhat more distant from the best sites over the ants. In both areas, few ground captures were over 1 m off: 6 of 145 at Manaus, 2 of 42 at Belém. None were over 2 m off, although a few sallies in both areas were to trunks or leaves just over 3 m off.

Angles of perches before food attempts (Table 6) were not very different from angles of all foraging perches (Table 2). However, Belém White-chins did better at food attempts from 1 and 2-cm perches than from other perches (Table 6 versus Table 2); they were probably avoiding slender perches mainly because *Phlegopsis nigromaculata* dominates these perches. Very large trunks produced little prey both at Belém and at Manaus, in part because on thick trunks there are other woodcreepers that have better foot and tail adaptations (*D. fuliginosa*) or are dominant (see below).

TABLE 5. Heights of food capture for White-chinned Woodcreepers

Height (m)	Percent[1]	
	Belém	Manaus
Ground	72.9	92.6
0.1 — 0.5	3.0	2.7
0.6 — 1.0	1.5	0.9
— 2.0	8.3	2.3
— 3.0	6.0	0.8
— 4.0	6.8	0.3
— 5.0	0.4	—
— 6.0	0.4	0.1
— 7.0	—	—
— 8.0	0.4	—
— 9.0	0.4	0.2

[1] Of 266 records at Belém and 1537 records at Manaus.

TABLE 6. Heights, angles, and diameters of perches before food attempts

Height (m)	Percent		Angle (°)	Percent		Diameter (cm)	Percent	
	Manaus n= 256	Belém n= 76		Manaus n= 242	Belém n= 72		Manaus n= 226	Belém n= 68
0.1	7.4		20	8.7	1	1	6.2	12
0.2	40.6	9	40	6.6	4	2	16.8	15
0.3	21.9	26	60	3.3	4	3	15.5	18
0.4	10.9	17	80	10.3	8	4	12.4	6
0.5	0.8	5	100	67.8	78	5	11.5	6
0.6	1.6	5	120	2.9	4	15	26.5	41
0.7	0.4	4	140	0.4		25	6.2	3
0.8	0.8	—				50	3.5	
0.9	0.4	—				100	1.3	
1.0	0.8	1						
2	9.4	17						
3	2.7	7						
4	0.8	5						
5	0.4	1						
6	—	1						
9	1.2							

Types and sizes of prey were much as in ant-following antbirds of the same body (but not bill) sizes as White-chins (Table 7). Belém birds concentrated on small prey. Long centipedes and short spiders or whip-scorpions had to be flailed against trunks and chewed back and forth, dropping the projecting legs in the case of the last two. Roaches, crickets, grasshoppers and other small prey required hitting and chewing at times, but were generally swallowed whole. Scorpions were chewed on the cephalothorax and eaten whole. Lizards were eaten whole after pounding, but in one case the lizard escaped and the bird ate its wriggling tail. Both at Belém and Manaus, exoduses of ants with larvae attracted them to peck off larvae as if from a shooting gallery, but smaller antbirds more often could perch on the slender stems where these ants climbed and hence were more regular at eating them (even in front of one baffled White-chin). Winged ants were taken on the wing, but worker ants never taken.

Emergences of winged ants above the ground attracted veritable "woodcreeper circuses" at Manaus, as many as seven species in frenzied activity. White-chins joined such activities only peripherally unless the emergences were near the ground. They did not attempt to join in one case when the circus was 24 m up. The hollow tree acariquara roxa, which ants loved to raid because of the many inquilines, also attracted other species of woodcreepers, and was thus too competitive a place for most White-chins. They looked up at the other woodcreepers, champed their beaks, and stayed low on most such occasions.

In general, both kinds of White-chins took the same kinds of prey. Both seemed to avoid large prey, which even small antbirds capture and carry to the ground to dissect, for these woodcreepers rarely dissected prey briefly on the ground. However, their bills are longer than those of similarly sized antbirds (other woodcreepers, similarly unable to dissect prey on the ground, have even longer bills than do White-chins) and thus sufficed for prey of medium to large size without ground dissection.

Ground dissection, in antbirds, allows the bird to chew a small part of the prey and drop the rest of the prey on the ground while eating it; trunk dissection, in woodcreepers, requires that the bird have a long enough bill to engulf the largest part of the prey while small projections like legs or wings either conform to the prey body or are dropped and hence not used. Woodcreepers thus have to have longer bills than do antbirds for prey items of a given size. Therefore, woodcreepers have longer bills for a given body size than do antbirds even when they forage like antbirds. (Woodcreepers that capture much prey on foliage or in trunks have even longer bills for their size. In part, this may be because katydids and other laterally flattened foliage-dwelling prey are harder and more sclerotized than are the flat roaches, spiders, and other ground-living prey taken by low foraging birds; and also, long bills are useful at going through foliage after prey whereas the ground is rigid.) Occasionally White-chins, which often chew prey near the ground, fly to it to pick up dropped pieces.

Anting behavior, rubbing captured prey in the feathers of the under sides of wings and tail, was occasional.

TABLE 7. Types and sizes of prey

Prey	Prey size (mm)							
	0-10	-20	-30	-40	-50	-70	-90	?
Scorpion					(3)			
Whip-scorpion			(1)					
Spider		4(3)	1(12)					(2)
egg sac	1(0)							
Centipede				1(0)	(7)	1(2)	1(1)	(2)
Roach		1(4)	3(13)	1(4)				(2)
Cricket		1(0)	(4)					(2)
Grasshopper		1(0)	(4)					
Beetle				(1)				
Moth		1(1)						(2)
Skipper								1(0)
Ant larvae	5(10)							
winged ad.			(1)					(4)
Lizard				(1)	(1)			(1)
Unknown	3(13)	(13)	(11)	(4)	(1)			2(0)
Total	9(23)	8(21)	4(46)	2(10)	0(12)	1(2)	1(1)	3(15)

MAINTENANCE BEHAVIOR AND MOLT

Maintenence behavior is mainly the province of the physiological ecologist, and to the behavioral ecologist does not show great differences in the two kinds of White-chins. Wiping the beak on trunks after chewing prey is maintenence, as is the usual woodcreeper custom of lifting the tail briefly off the trunk when ejecting feces. Ejecting a solid pellet of insect chitin fragments from the mouth was noted once for a tame young bird before my feet. One was seen to nibble the drip-tip of a wet leaf for water (actually foraging behavior), but most water must come from the prey.

Spreading out on the ground to "sun" in sunflecks was recorded for both forms, as was yawning. Flexing both wings over the back, and stretching tail and wing and leg to one side, were noted at Manaus.

Preening often followed bouts of foraging, or occupied time when the ants started to retreat at the end of the day or at a forest border. Both forms scratched the head over the wing, once for a tick on the face. Preening was often on foraging perches, but perches under 2 cm in diameter were avoided for preening both at Manaus and Belém (comparing Table 8 with Table 2), as were non-vertical perches and ones under 0.2 m up. Preening Belém birds were especially likely to avoid low and slender perches, probably because of danger of supplantings by *Phlegopsis nigromaculata*. They were less likely to take vertical perches than birds at Manaus, unlike foraging birds at the two localities; probably vertical perches were more common at Manaus because the vegetation there is older and taller on the average than at Belém.

Molt of the wings overlaps with molt of the tail. Primary molt on each side is from number 1 (innermost) distally, tail molt from number 1 (innermost) distally, as in *Dendrocincla fuliginosa* (Willis, 1972a). A few birds recaptured twice during molt at Belém or Manaus molted 2 or 3 primaries per month, so that primary molt lasts 3-5 months. Tail molt requires an additional month at least. One bird that lost tail feathers out of season was with tail feathers barely over half the normal length two months later. A young bird that lost tail feathers in the net had serious problems using vertical perches for two months; the few remaining feathers were curved and battered by the time the new ones grew long enough for support. It soon learned to use horizontal or slightly inclined perches, and even perched crosswise on nearly vertical perches a few times.

Seasons of molt differ over the range. Manaus birds started in late September for the most part, with two females that had young out of the nest at that time delaying their molt. By February and March, wing molt was near completion even for females. Three specimens of *obidensis* in museums were in molt in December, one in molt in August.

Belém birds, however, were in wing molt in March and April and in tail molt in June. One was starting molt in October, perhaps a young bird molting out of season. Specimens of *badia* are mostly birds not in wing molt, collected June to August. One April bird was in the middle of wing molt and one October and two June birds at the end of wing molt.

TABLE 8. Heights, angles, and diameters of preening perches

Height (m)	Percent		Angle(°)	Percent		Diameter (cm)	Percent	
	Manaus n= 102	Belém n= 31		Manaus n= 101	Belém n= 28		Manaus n= 93	Belém n= 27
0.1	4		-20	1	4	1		
0.2	14		40	4	—	2	10	
0.3	30		60	2	—	3	13	7
0.4	17	23	80	11	25	4	12	26
0.5	8	10	100	80	71	5	17	15
0.6	9	6	120	2		15	33	41
0.7	3	10				25	9	11
0.8	1	3				50	5	
0.9	3	—				100	1	
1.0	1	3						
2	9	29						
3	—	10						
4	—	6						
5	1							
6	1							

Belém birds resemble birds from Venezuela and northern Brazil (*bartletti*) in molting in the northern spring, as do some (but not all) *castanoptera* from the east side of the Tapajós. West of the Tapajós, *olivascens* resembles Manaus birds in molting in the southern spring, as do *bartletti* west of the Madeira into Peru. June to October specimens (22) of *bartletti* west of the lower Rio Negro were not in molt, except for two July birds at the end of molt and one August bird; probably molt is in the northern spring. One would expect small *merula* from the Guianas to molt in the northern spring, but there is little information other than that December specimens from Cayenne are in rather worn plumage and one is in wing molt.

Of 268 seemingly adult specimens, only 60 or 22 percent were in wing molt. This indicates a molt season of 0.22 year or 2.6 months, which is too short for the field data (except perhaps for adult females). Almost certainly nonmolting young birds are among the 268 specimens. Black bills, rather than bills that are pale below, probably indicate young birds. Certainly all short-tailed young in collections are black billed, even if live young at Manaus had pale bases to the lower mandibles. If one excludes 16 birds of the above 268 that had black bills, 60 of 252 or 24 percent were in molt, indicating a molt season of 2.9 months. Probably other unrecognized young birds in the collections have bills that are somewhat pale below and hence were not recorded as black; or collections were not random with respect to molt seasons.

AGONISTIC BEHAVIOR

Interspecific aggression is more prominent than intraspecific in the supplantings and displacings recorded for White-chins both at Belém (Table 9) and Manaus (Table 10). In this respect, White-chins differ greatly from *D. fuliginosa* (Willis, 1972a). In the tables, "returns" represent cases when a subordinate species moved in quickly to the site of a dominant one after it left for some such reason as food dissection or my movements. Belém birds are persistently attacked by the large (50 g) *Phlegopsis nigromaculata*, while Manaus birds constantly supplant the medium-sized antbird (30 g) *Gymnopithys rufigula* and the small but infiltrating (20 g) antbird *Pithys albifrons*. Large woodcreepers moving down from above attack White-chins in both areas. The related *Dendrocincla fuliginosa* normally forages above *D. merula* and is subordinate to it, even at Belém where *D. fuliginosa* is about the same weight as it. Medium-sized *Pyriglena leuconota* (36 g) at Belém attracted attacks of White-chins less than sneaky displacings, partly because the hopping antbirds readily leave a perch at a mere pointing movement of the woodcreeper and partly because supplanting an antbird conspicuously tended to attract large *P. nigromaculata*.

In other areas, antbirds supplanting or displacing White-chins were *P. nigromaculata* (Cashibococha, Peru; Coatá, Palhão, and Maloquinha, Brazil), *Skutchia borbae* (Coatá and Sucunduri, Brazil), *Myrmeciza fortis* (Carauari, Brazil), *Rhegmatorhina hoffmannsi* (Borba and Coatá, Brazil), and *R. cristata* (Mitu, Colombia). Normally White-chins dominated *Gymnopithys lunulata* (7 of 8 supplantings at Cashibococha), *G. leucaspis* (Mitu) and a few *Hypocnemioides maculicauda* (Maloquinha). Woodcreepers dominant to White-chins included

Dendrocolaptes picumnus (Cashibococha; Diamantina and Palhão, Brazil), *D. hoffmannsi* (Maloquinha and Borba), *Xiphorhynchus guttatus* (Cashibococha), and *X. ocellatus* (Maloquinha). Ordinarily *Dendrocincla fuliginosa* was subordinate (except for one displacing of a White-chin at Letícia, Colombia), as was *Glyphorynchus spirurus.* As at Belém and Manaus, and as is general among ant-following birds, those birds that were supplanted generally weighed less than did their supplanters.

Phlegopsis nigromaculata at Belém seemed very antagonistic to White-chins, especially when they took low perches at easily visible sites in open undergrowth. The large antbird often attacked with a rapid and audible whirr of wings, snapping of the bill, and a loud huffing "chah" as if to blow the woodcreeper off its perch. At times the antbird flew 2 m to do so, or flew up to 1-2 m up especially to supplant the woodcreeper before returning to normal foraging 0.2-0.4 m up. At times the White-chin circled and returned persistently despite attacks. Occasionally a surprised White-chin chattered as it fled, but most were fast enough to escape silently in plenty of time.

TABLE 9. Agonistic encounters of White-chins at Belém

	Activity			
Species	Sup- planting	Displacing	Returning	Fighting
Phlegopsis nigromaculata	115/[1]	25/	8/	
Pyriglena leuconota	2/13	2/21		1
Dendrocincla fuliginosa	4/24	/5		2
merula	27	6		
Dendrocolaptes certhia	6/	1/		
Xiphorhynchus guttatus	6/	1/		
spixii	/1			
Hylophylax poecilonota		/1		

[1] Records above a diagonal line give the number of times the given species dominated White-chins; records below a diagonal give the number of times a White-chin dominated that species.

TABLE 10. Agonistic encounters of White-chins at Manaus

	Activity			
Species	Sup- planting	Displacing	Returning	Fighting
Gymnopithys rufigula	1/356	/15	/3	
Dendrocincla merula	187	17		6
Pithys albifrons	/123	/6	/8	
Dendrocolaptes picumnus	48/	4/	2/	
Dendrocincla fuliginosa	/21	/3		
Hylexetastes perrotti	18/	2/		
Percnostola rufifrons	/5	/1		
Xiphorhynchus pardalotus	/4	/1		
Dendrocolaptes certhia	4/			
Automolus ochrolaemus	/1			
Hylophylax poecilonota			/1	

Small antbirds at Manaus were not always so lucky in escaping an attack by White-chins, although they did flee successfully most of the time. Sudden chipping by a *Pithys albifrons* or *Gymnopithys rufigula* showed narrow escapes, and some had to struggle and scream to escape the clawing and pecking of the vicious attack. White-chins ordinarily attacked quickly and silently, giving the small antbirds little time to react. Preliminary movements of pointing the bill at the antbird evidently gave little warning, for cases of displacings (when the antbird had time to get away before attack) were rather uncommon.

Large woodcreepers occasionally take the places of White-chins low over ants, but were ineffective in doing so because they are too large to perch on stems or to maneuver in slightly cluttered places. They nearly always leave many vacant places over swarms both for White-chins and for antbirds. Most attacks of large woodcreepers were silent, but were slow enough that White-chins had time to flee without calling or fighting.

Occasional inversions of the normal peck order often involved surprise attacks from the rear or vigorous display by the smaller bird involved, including loud "bugling" calls by a small (25 g) *Gymnopithys lunulata* at Cashibococha. One aggressive wing-flicking *Xiphorhynchus spixii* hitched down at a wing-flicking White-chin, which gaped and pecked and hitched around the perch at it before supplanting it. Several supplantings of White-chins by *D. fuliginosa* involved birds 6-7 m up, where White-chins rarely go and hence are likely to be little disposed to defend themselves. Also, White-chins were clumsier than *D. fuliginosa* at sallies for prey above the ground, losing prey to their more aerial relatives in cases when both tried for the same prey. Spread-winged pecking duels were recorded between the two species, and similar fights between White-chins or of White-chins with a few antbirds.

Attacks were at times related to tries for food: in 17 of 140 cases for *P. nigromaculata* supplantings or displacings, in 45 of 371 cases of attacks on *G. rufigula*, and in 22 of 129 attacks on *P. albifrons*. For 52 *D. picumnus* attacks, 6 were during or after a try for food by White-chins. Intraspecific attacks (and attacks by less important species) were generally less directly linked with food: 1 out of 33 intraspecific supplantings and displacings at Belém, 8 of 204 at Manaus.

The results of these competitive patterns are that the productive low and central zone of ant swarms at Manaus is generally sequestered by White-chins (unless large woodcreepers are present), while *G. rufigula* and *P. albifrons* occupy a ring about the center. At Belém, White-chins occupy jointly with *Pyriglena leuconota* the ring about the center, while large *P. nigromaculata* occupy the center. Other differences attributable to the different competitive regimes have been noted under foraging behavior. Table 11 indicates the foraging-zone differences at Manaus and Belém by giving records from field notes of White-chins foraging over the "center" of swarms, at their "left" or "right" ends, "behind" or "ahead", "high" over ants, in unusually "open" sites (where large antbirds were nervous and often fled, being rather poor fliers and dependent on cover). Manaus records for "center" are indicated with a "+" because foraging at the center was normal there and hence unlikely to be recorded; all records for "high" have "+" signs, because I normally recorded exact heights rather than use a word. Records "near me" were normally behind and left of the raid center, and tended to be occupied by birds of intermediate or low dominance (especially young birds). The excess of "right" records over "left" and of "ahead" over "behind" ones at Belém is attributable to this effect, for the fairly timid White-chins tended to stay ahead or right; similar records made for tamer *Pyriglena leuconota* at the same swarms showed an excess of "left" and "behind" records.

Belém birds were infrequently at the center of swarms, and were very likely to be attacked there. At such times, they moved upward or peripherally. High birds and ones at either end of the swarm were fairly likely to be attacked, for young or other subordinate *P. nigromaculata* often occupied those zones, as was the case near me. Behind and ahead of the swarm were fairly safe, but produced little food (21 percent of 71 feeding records for which location was noted, in contrast to 52 percent for left and right birds and 14 percent for central birds). The few birds that were tame enough to stay behind captured as much food as the larger number that moved ahead.

Manaus White-chins were attacked little, even at the center of swarms. Few moved ahead, behind, or high over swarms, but some used the ends of swarms rather than the centers (since center records are considerably underrepresented at Manaus, all other percentages from there are exaggerated in Table 11.)

Heights of supplantings and displacings reflect the greater availability of food near the ground and monopolization of the ground by dominant species: 29 of 39 supplantings of White-chins at Belém were below 1.0 m, and 16 of 31 at Manaus; but only 9 of 23 supplantings of other species by White-chins were below 1.0 m at Belém while 64 of 74 were below 1.0 m (48 of 74 below 0.2 m) at Manaus.

TABLE 11. Locations of White-chinned Woodcreepers at ant swarms

Position	Percentages of Records			
	Belém (n= 388)		Manaus (n= 696)	
Center	12	(52)[1]	29+	(1.0)
Left	20	(12)	30	(0.5)
Right	30	(13)	29	(0.0)
High	10+	(13)	0+	(0.0)
Open	4	(7)		
Ahead	18	(7)	4	(0.0)
Behind	4	(0)	3	(0.0)
Near Me	3	(18)	4	(0.0)

[1] Percentages of the preceding records in which the White-chin was attacked by another species.

INTRASPECIFIC COMPETITION

When more than one White-chin is at ant swarm, there are often chases or other behavioral patterns, such as spacing, that indicate competitive or agonistic behavior. Spacing out without any overt evidence of display is the most common pattern, so that information on other patterns is limited: aggressive and submissive displays, attacks, fleeing and fighting.

Aggressive "challenging" displays were best seen when dominant males arrived at antswarms at Manaus, but similar displays were seen in other areas. The most obvious form of the display was a slow and at times jerky spreading or "double wing flashing" of both wings above the back, much like a Mockingbird (*Mimus polyglottus*) flashing as it forages on a lawn (Hailman, 1960). Several double wing flashes marked the course of the dominant male or other bird at several perches, some of the wing flashes being only partial ones. Single wing flashes occur in foraging in this and other *Dendrocincla* species (Willis, 1960; 1972a), but single flashes were used only in a few cases when an opponent was a few cm to that side in this species. In other species, I have not seen wing flashing used in aggression except in spread-winged fighting at close range (this type of double wing flashing also occurs in White-chins).

Double wing flashing displays the somewhat yellow wing linings in both forms of White-chins. The white throat is also fairly conspicuous, as the heads of the birds are farther from the trunk than in normal postures. Once at Manaus an aggressive bird puffed the throat out, and once at Belém a submissive one did so, but I have not seen it used otherwise. The related *D. fuliginosa* commonly fluffs out its much less prominently pale throat when attacked by a larger species, but I do not know how White-chins use their most conspicuous field mark. Submissive individuals do keep their throats concealed by keeping their heads close to the trunk.

Two other movements of the wings were frequent in both kinds of White-chins: sharp and separated flitting of the wing tips as in alarmed birds; and rapid fluttering of slightly lowered wings. Flitting seems a sign of general excitement or nervousness, and was more used by supplanted birds than by dominant ones. Fluttering was used about equally by birds before or after attacks. Since young birds often use fluttering, it may be a type of juvenal behavior that tends to ward off attack while the bird is gathering courage to attack, if it can do so.

The wings are often slightly lowered as the bird watches competitors nearby, whether or not the wrists emerge from the body feathers, even when the competing White-chin is not fluttering or flitting or double-flashing them.

Ruffling the crown feathers was noted for one bird that attacked, but as in *D. fuliginosa* (Willis, 1972a) may be a form of pre-attack ambivalence rather than aggressive display. One ruffled the forecrown when a *P. nigromaculata* moved nearby. Spreading the body and tail and sleeking the head are common in aggression in Formicariidae and Dendrocolaptidae ("rule of angles": Willis, 1967), but were not noted for White-chins.

Attacks were fairly frequent, though chases back and forth were less frequent and less complicated than in high-foraging and more aggressive *D. fuliginosa* (Willis, 1972a). Simple supplantings are the rule, except for sexual attacks and "play" attacks of young birds (see below). "Tailgatings," or slow and close fluttering chases of another bird back and forth, occur mainly in "play" or sexual situations, unlike aggressive tailgating in the more aerial *D. fuliginosa.*

Attacks often were silent, but sometimes involved a loud flutter of wings as in interspecific behavior. Chattering sometimes came from the attacking bird, rarely from the attacked bird, in both intraspecific and interspecific supplantings. It may be an aggressive or flight noise, as it is also used in alarm against the observer. Manaus birds occasionally stiek when attacked suddenly, suggesting that this is an alarmed noise or one that marks the tendency of the bird to try to stay rather than fly. Other subspecies, which lack this note, are generally silent as they flee; presumably any noise would only attract large antbirds.

When the attacked White-chin does not flee, it may hitch rapidly upward or around the trunk a short distance, or may even remain. Young birds were especially likely to remain and to try gaping, fluttering, screaming, growling, or rattleting as the attackers pecked at their backs or almost mounted them in what seemed sexual behavior. A few times, the attacker desisted and took another perch. More often, the young bird fled after repeated pecks. Fights were uncommon (Table 10), representing 6 of 210 records or about 3 percent at Manaus, none of 33 records at Belém, and none of 44 records at other places where "castanoptera" birds were studied. Several of the "fights" at Manaus were probably play-squabbles of young, so that fights are uncommon in White-chins generally as compared to *D. fuliginosa* (4 percent; Willis, 1972a).

Submissive display involved holding the head and throat close to the trunk, fluttering the wings, and gaping. At times the bird growled or gave a growl-rattlet. The display was infrequently observed, except for young birds. There, the head was retracted and puffed to gape and squeak. One attacked bird turned the nape to the attacker, which began to preen. Attacked birds occasionally wiped the bill afterward. In contrast to *D. fuliginosa,* male White-chins supplanted females of the same areas in the few cases where attacks were recorded. Females occasionally supplanted females without any correlation with home areas, and males occasionally supplanted males, but ordinarily there were no disputes. Young birds at times supplanted their mothers or other females, as well as wandering birds; occasionally wandering birds and settled males supplanted young birds; rarely a female did so. Probably the small size of females allows young dominance. In April of 1974, when two young birds of the two local females were independent and over six months old, and nesting was about to start again, the male whose area centered in my study area suddenly became very aggressive toward them for several weeks. He chased the older and dominant young bird about swarms persistently, even when it tried alighting near me for protection. The other and rather female-behaviored young was mounted and pecked repeatedly when it tried to stay. The male's ire extended even to settled females, but they escaped most attacks (see below). At this season, two settled males never stayed together for long at the same ant colony. By June, both young birds had disappeared from my study area. Wandering unbanded birds, probably other immatures forced out of crowded areas by rising male aggressivity, were also attacked persistently by other males at the corners of my study area in June and July. Presumably these immature birds settle wherever there are few adults. The study area at Belém seemed such an area, one in which there was essentially no breeding.

Long-rattling is a final behavior pattern that seems connected with competition. A bird chased from an ant swarm, or one excluded by the observer, may long-rattle persistently a few tens of meters from the swarm. The head and hence throat are close to the trunk.

REPRODUCTIVE BEHAVIOR

Information on reproductive behavior is available mainly for Manaus. As in other members of the genus (Willis, 1972a), females alone care for young. Probably the local settled male, after driving young of the previous year away, half attacks the female; she, by staying, permits him to climb and start nibbling her back as the first stage of copulation. Only the attack stages were seen, but the other stages are recorded for *D. fuliginosa* and in seemingly sexual play among young White-chins. Male and female associate irregularly for a month or so and may investigate suitable nest sites together, as in *D. fuliginosa;* however, the nest is unknown and nest searching has not been seen except for young birds at play. Probably the nest is a cavity low in a small-diameter forest tree, much as in similar woodcreepers. Presumably, too, the female cares for egg(s) and nestling(s) alone as in other members of the genus.

At Manaus, one local female disappeared and reappeared every hour or so at a swarm, as if incubating, in late June, 1974. She and three other females had had young recently out of the nest from late August to early October, 1973. The nesting season is therefore brief, confined to the three months of the northern summer, and precedes the molting season (she herself molted late, ending in February or March, after her young bird was independent).

Belém records of presumed immatures, and three black-billed museum specimens from near Belém, suggest a brief nesting season in the southern summer. At Coatá, short-tailed young were out of the nest on 2 April 1966, suggesting breeding in the southern summer and after rather than before the normal molting season for the race *olivascens*. Young birds in museums are all from February through July, including 22 June 1917 from Tamanoir, Cayenne, for typical *merula*. Other records from north to south are these: 3 May 1947, Cerro Yapacana, Venezuela; 1 July 1929, Iauareté, Rio Uaupés, Brazil; 12 May 1936 at Lago Tapayema, Rio Amazonas, Brazil; 9 February 1830 at Borba, Rio Madeira, Brazil; 27 June 1930 at Rosarinho, Lago Sampaio, Brazil; and 25 March 1928 from Lagarto, upper Ucayali, Peru.

Sixteen black-billed birds, which are presumably older young, range from February and March to September, with most early birds having lightly worn wings and tail and late ones having moderately worn plumage. One very worn bird is in actual molt (March, Miritituba), while one from Caño Matacaura in Venezuela has light wear in October. The Miritituba bird is likely to be a bird one year old that had not yet gained the adult bill color. The Caño Matacaura bird indicates nesting in the northern summer, but all others (including one May bird from Puerto Yapacana, southern Venezuela) suggest nesting in the southern summer or (in the case of lightly worn February birds from Vila Braga and Hyutanahan) spring.

The breeding and molting seasons need further confirmation, but there is enough evidence to suggest that birds of the castanoptera group nest mainly in the southern summer whether they molt in the southern spring or fall, while birds at Manaus nest in the northern summer and molt in the northern fall. Perhaps small *merula* from the Guianas nest late in the southern summer while northernmost birds of the castanoptera group nest in the northern summer, but only one record is available for each group.

Four young birds out of the nest were observed at Manaus, two for long periods; and I briefly observed two young at Coatá. As in *Dendrocincla fuliginosa,* the young bird flies well and is nearly adult size when the female first brings it near ant swarms. The tail is about one third adult length, and the bill small and black but for the pale base of the lower mandible. The gape angles are pale; but the throat feathers are dull whitish rather than bright. The young bird remains persistently in an area up to 100 m from the swarm, flying in a circle and returning to the original area if chased. The female chatters and stieks loudly if she sees one near it, and it chatters in response to her chatters or sings in response to her songs as she leads it off rapidly through the forest understory. Within two weeks it is more often over or next to the swarm than far from it, has tail feathers two thirds the adult length, and is peering and fluttering or sallying to the ground as if trying to forage. Within a month after leaving the nest, the tail is nearly full length and the young bird is definitely sallying to the ground for some of its food. The female still feeds the young regularly two months after it leaves the nest, and occasional feedings were recorded about 80 days after departure. The first young at Manaus, which left the nest about 20 August, was still begging from the female and following her about now and then on 23-24 January; the second young, which left the nest about 10 October, was squeaking and nibbling the back of its mother on 3 February. Much of the time the mother and young wander separately after the young bird is three months out of the nest, however.

To feed the young bird, the mother flies to where it was or sings, at which it flies to her or sings before flying to her. It gapes and squeaks with head retracted, then grabs the food from her bill, as both perch side by side on a trunk. Both chatter if it chases her first. Once a female waited until the young ate a prey it had caught, then hitched down and poked a large prey into its bill. Chatters of the female merely attracted the young to her when I was nearby, but her stieking caused it to freeze and stop squeaking. Songs of the young got chatters or songs from her in response. Young persistently following the female fluttered and gave squeaks or growls followed by segmented notes, "chauhh-i-i-i-if," reminiscent of "rattlets" in *D. fuliginosa.* They sometimes pecked at her back or half mounted her. When beginning foraging, the young often came up with a dead leaf instead of an insect on sallies to the ground. Distant songs or chatters of the female were answered by the young, which followed her to another branch of the swarm or to a distant ant colony.

One female was first seen to supplant her young 7 months after it left the nest. Even a month later, however, she ignored her young when it alighted beside her. Neither female reacted much to the young until they disappeared one to two months later, perhaps because of frequent chases by the local male. The two young acted differently to him. The earlier young fled, and was chased repeatedly around the swarm; it disappeared after a month of such treatment. The later young stayed and gaped, or fluttered; it was treated like a female, with nibbling in the back preceding attempts to mount. Once the adult male nibbled its back, then hitched rapidly up past it and waited above it as if inviting it to nibble; but the young bird begged and squeaked, head retracted and body fluffed; the adult male left. It endured chasing for a month and a half after the male became aggressive in early April, then disappeared.

The two young had been playing together for months before their expulsion, with the earlier young generally chasing and nibbling and trying to mount while the later young gaped and turned the head and hissed or squeaked like a female. At times, lifting the tail and growling backward repulsed the mounting bird. The later young was out of the nest only about two weeks on 21 October, when the earlier young alighted by it, watched it squeak and gape, then pecked in its rump feathers and snapped at its head. The later young begged from a wandering male when it caught a 20-mm prey, but was pecked on the head despite its flutters; a settled male then ignored its flutters. A few days later, the settled male pecked it in the back as it stieked, chattered, squeaked, and fluttered. The next day, it gaped at him instead of flying. By 1 December, the earlier and later young were regularly alternating in such behavior, one chasing and the other gaping-fluttering-squeaking or fleeing slowly for a time and then vice versa. Both flew to a crevice in a low stub and peered inside; sometimes both entered at once as in "cavity-sitting" nest site selection in adult *Dendrocincla fuliginosa* (Willis, 1972a). The older young then tried nipping off rootlets nearby as if to build a nest. The later young even fed the earlier one a prey once.

In January to April the two young often chased with slow flights, alternated nibbling in each other's backs, and squeaked. In April, the two were seen to exchange food or bits of debris back and forth during their frequent bouts of playing. The later young took to alighting on my boot and pecking busily, as if inviting me to become a woodcreper, after one day when it coughed up a pellet in front of my feet when the ants stopped raiding. A stare at it caused it to dart and attack my pen near my face. For several weeks it alighted on me at any interval between foraging activities, pecking busily at such bright objects as my watch. At times it picked up bits of debris and "anted" under its wing with them, or "anted" under its wings when its pecks failed to remove my buttons. The pecking and mounting attentions of the local settled male then took over for a few days before the young bird disappeared. Many of these play activities seem like sexual behavior in the related *D. fuliginosa* (Willis, 1972a).

DISPERSAL AND SPATIAL BEHAVIOR

Most swarms of army ants, both at Belém and Manaus (Tables 12, 13) had two or fewer White-chins. Small colonies or colonies that swarmed irregularly, such as "statary" colonies, often lacked White-chins. Colonies that moved into second-growth areas often lost their

TABLE 12. Numbers of White-chins at swarms of *Eciton burchelli* (Belém)

Month	Number of swarms with given number (n) of birds				
	n=0	1	2	3	4
April, 1972	25	2			
May	14	11	1		
June	12	5	3	1	
July	5	6	1		
August	14	10	1		
September	0	2	3	2	1
October	7	6	5	3	1
November	7	1	3	3	
December	1	9	1		
January, 1973	7	3	3		
February	8	5	2		
March	6	5	6	1	
April	12	9	1		
May	7	1	7	9	1
Total[1]	86	62	36	19	3

[1] June, 1972-May, 1973 only. Omitted from the column n=0 are all swarms in a várzea study area never reached by White-chins (swarms from March, 1972 to May, 1973, respectively, were 1-3-0-0-2-0-0-17-33-31-10-6-10-18-26) and all swarms in a second-growth area not reached by the species (swarms from April to July, 1972, were respectively, 6-16-21-5).

TABLE 13. Numbers of White-chins at swarms of *Eciton burchelli* (Manaus)

Month	Number of swarms with given number (n) of birds						
	n=0	1	2	3	4	5	6
July, 1973	3	3	8	2			
August	14	22	17	3	1		1
September	50	17	8	5	2	1	2
October	26	8	15	7	9	6	3
November	54	20	28	5	3	2	
December	63	18	14	8	6	1	
January, 1974	66	24	21	10	3		1
February	43	23	7	16	5		
March	27	13	12	8			
April	28	21	8	5	1	3	
May	29	13	13	6			
June	24	20	10	4			
July	11	23	14	5	1		
August	8	11	9	2	3		
Total[1]	429	211	159	81	33	13	6

[1] September, 1973-August, 1974 only. Some swarms in the n=0 column were in second-growth habitats usually avoided by White-chins.

White-chins from one day to the next, while colonies that moved into open scrub or yards of the research station or other houses always did so. In one case, the White-chins sang loudly as they wandered on abandoning a colony that entered an open area. One young bird waited patiently for a colony to cross a small manioc plantation in the woods. White-chins deserted colonies that climbed into trees to raid nests of carpenter ants (*Camponotus* sp.) or ones that broke up swarms in flooded or dry, hot terrain. At one colony that started tree raids, the White-chins waited with sunken heads although now and then one flew up to 3-4 m to look about briefly. Individual birds often visited two different colonies each day, and a few visited three colonies in one day, moving as much as 1.5 km through the forest to do so.

White-chins searching for ants move low and rapidly through the forest, silent except for the whish of wings or for chatters when they see the observer. At stops they flit the wings, but do not often climb; flight is their *modus operandi.* One loudsang near the location where ants had been three days before, then moved in to where small antbirds were at the swarm. They visit inactive or active statary bivouacs, circle the base of the tree, and follow any line of ants to the distant swarm. I have seen them arrive at an ant bivouac very early, before the ants started raiding, but they more often arrived later (06:30-07:00) than did antbirds. Apparently the White-chins then joined the antbirds, which are better able to hop and search for an inactive bivouac near the ground.

Three or more birds per swarm were recorded mainly in May to November at Belém and September to February at Manaus. The latter peak is composed mainly of young birds, settled adults, and a few wandering birds; it closely follows the breeding season and probably reflects well the annual peak throughout the population. The peak at Belém, however, lacks young birds and is composed mainly of wandering young more than six months old. The true peak in population numbers would lie earlier in the year, had I been able to extend my studies into breeding areas somewhere off to the north near the Belém water supply (Utinga Reservoir), for breeding in this region is mainly in the southern summer.

Movements of several individuals at Manaus are mapped in figs. 4-6. Individuals move over areas at least 2 or 3 km across. The two settled females that raised young on my area overlapped widely in their distributions, and even foraged at the same ant colony at times. Female RYBY tended to center more to the west, female GBWB more to the east. This behavior is quite unlike *Dendrocincla fuliginosa* in Panama, where settled females stayed on almost exclusive territories (Willis, 1972a). Settled male White-chins also overlapped in their movements, although male BORO tended to center on the west of my study area and male WGRG to the east.

They were rarely seen together from April to July. In one case, male WGRG took over the ant colony as it moved eastward. There were several other males around, who stayed in the area a few months and then moved off south or disappeared. One, male WROB, was so regular as to seem a replacement for BORO in the nonbreeding months of October to December. (BORO was not seen November to January). However, WROB moved off south in January, as did male GYBR, long before BORO began to be aggressive to local young birds in early April. The two young birds of the study area often associated, as has been noted, and disappeared in May and June before the breeding season.

As in other dendrocinclas, there was little evidence of pairing between males and females or of other nonparental associations, except for the loose one between the two young birds. Male BORO and female RYBY associated rather often in the months before breeding, April to June, but did not stay together. Once male BORO longrattled when female GBWB came up, as if intimidated by her, before female RYBY supplanted her. Both male BORO and female RYBY preferred to follow the largest ant colonies around, and this rather than mating may have kept them together. Two wandering males associated rather often in August to October, perhaps for the same reason. Parental associations, between mother and young, were close for three months and then irregular; females tolerated their young but did not feed them, until the young disappeared after 9 months out of the nest. The young occasionally supplanted their mothers, but mostly ignored them, after stopping desultory begging when about 5 months out of the nest. They do stay much longer with the females than do young *Dendrocincla fuliginosa* (Willis, 1972a).

White-chins rarely used low second growth at Manaus, where second growth is a forest fringe. At Belém, they used dense and tall second growth but were most regular in old forest of the main 77-ha study tract. A 24-ha adjacent study area that was entirely overgrown rubber plantations and other second growth was not used at all. In the main study tract, the birds followed ants into the edges of the flooded várzea swamps, but never visited another 78-ha study area deep in várzea, where there were many army ants but also many *Phlegopsis nigromaculata*. It seems likely that the patchwork of terra firme forest and capoeira where they did occur at Belém was not used for breeding, and served only as a stopping station for immatures after they left their parental areas in the main terra firme forests off to the north (Utinga Reservoir area).

At Manaus, White-chins sometimes used saplings and dense rows of vegetation in forest plantations and experimental areas. A few followed ants into the sandy valley woodlands and through grassy seeps along forest creeks, but waited long periods for little prey in such areas. The best area for them was the normally open forest undergrowth of upland woods, where concentrations of individuals followed the largest ant swarms. They seemed less common off deep in the upland forest than within a kilometer of its edge; perhaps the moderate human disturbance at forest edges somehow favored them. However, it may be that the forest edge acts as a trap or guiding line for ant colonies and thus causes their concentration there, for White-chins were fairly common at the few ant colonies I encountered deep in Reserva Ducke.

With the above caveat that White-chins may have concentrated somewhat in my study area at Manaus, I estimate that over the 2.8 km^2 of forest in the study area there were 0.6 settled male, 0.8 settled female, 0.7 wandering birds, and 0.4 young per km^2 in May of 1974, at or close to the annual low. This gives 136 g per km^2, a very low biomass; it is barely over one third the density of Ocellated Antbirds (*Phaenostictus mcleannani*) on Barro Colorado

Island in Panama before their decrease to local extinction there (Willis, 1973). In October of 1973 at Manaus, there probably were twice as many wandering White-chins and young as in May, for a peak annual density of 195 g/km^2. or 3.6 birds/km^2. High September densities in the 77 ha of the upland study area at Belém were comparable, about 4 birds or 162 g/km^2, despite their failure to breed in the area; they were absent, as has been noted, in 78 ha of várzea and 24 ha of second growth. At Belém, their biomass even in the upland study tract was very low compared to that of the ant-following antbirds *Phlegopsis nigromaculata* and *Pyriglena leuconota.*

Survival of adult White-chins seemed fairly good at Manaus. One female banded in 1972 was still alive in 1976, and two birds banded in 1973-74 were still present. However, the wandering of birds made it difficult to determine mortalities.

DISCUSSION

Both at Belém and Manaus, White-chinned Woodcreepers try to act like ant-following antbirds: they take low and slender perches whenever possible, and sally to the ground for prey flushed by army ants. At Belém, they are relatively unsuccessful because a larger ant-following antbird, *Phlegopsis nigromaculata,* takes this niche. Presumably the White-chins must have been nesting back in extensive upland forests where this antbird was less common than it was in and near the swamp forests of the study area. White-chins at Manaus have no large ant-following antbird for competitor, and have managed to dominate the medium and small antbirds of the region. Probably this has allowed them to become as large as *P. nigromaculata.*

The small size of White-chins at Belém, and indeed east of the Xingu River, is probably caused by the absence of medium-sized antbirds of the genus *Rhegmatorhina* east of the Xingu (Willis, 1969). With a large competitor above and no medium-sized one below (except for *Pyriglena leuconota* of second growth and other dense woodlands), White-chins shift toward the niche of the medium-sized antbird just as Manaus White-chins, with a medium-sized competitor below (*Gymnopithys rufigula*) but no large antbird above, have become unusually large for their species.

Species Status. Are the Manaus White-chins a different species? Size alone is not decisive, for I would no more call them a separate species based on large size than I would call Belém White-chins a separate species based on small size. Differences in foraging behavior I would attribute to the different competitive regimes for the two forms: it is no novelty to find a *Dendrocincla* foraging differently in different parts of its range because of a competitive difference. Trinidad versus Panama for *D. fuliginosa* (Willis, 1966) almost mimics the Manaus versus Belém situation for White-chins.

The differences in voice between Manaus and other White-chins, however, suggest that two species are involved. Even if some of the differences are likely to be connected with size (the different rate of the chatter, for instance), others are not. The stieking alarm of Manaus White-chins is likely to be adaptive for a large dominant bird that can hold its position against competitors while sticking to drive away mammals, and valuable to it because it is constantly foraging low where mammals could catch it. However, the other White-chins should have this call if they are really the same species. They should also have a song on one pitch instead of their usual upward scales. The difference in longrattling is nearly as notable as the difference in the call between either White-chin and *D. fuliginosa.*

Based primarily on the vocal differences, I suggest that Manaus and castanoptera-group White-chins are separate species. However, more study is needed to determine if Manaus and Óbidos birds (large birds with the name *D. m. obidensis*) belong to small nominate *merula* of the Guianas or if nominate *merula* is part of the widespread castanoptera group. Voice studies and recording of *merula* could settle the question; it could be a small bird but have a "big voice," like Manaus birds, or have a "small voice" like *bartletti* just west of it in Venezuela. It may be possible to find overlap or hybrid zones between the large-voiced and small-voiced forms in the Guianas, in southern Venezuela, or in northern Brazil.

Molt and Breeding. Although equatorial birds, White-chins have short breeding and molt seasons. The latter overlap breeding minimally if at all. *Dendrocincla fuliginosa* at Manaus and perhaps Belém also have short breeding seasons, even shorter than they do in Trinidad (Snow & Snow, 1964) or Panama (Willis, 1972a). Perhaps short breeding seasons are due either to low food supplies in the Amazon, so that breeding is successful only in a brief period each year when supplies rise slightly, or to the many interspecific competitors in the Amazon that leave only low food supplies for these woodcreepers. Intraspecific competition could add to the problem of raising young, by encouraging evolution for adult survival ("K-selection") mechanisms or predator-avoidance mechanisms ("α-selection") at the expense of evolution for higher reproductive rates ("r-selection").

White-chins across the Amazon from Manaus, in the region between the Madeira and Tapajós Rivers (subspecies *olivascens*) and from the Madeira west (southern *bartletti*) breed at the opposite season from Manaus birds, or in the southern summer. However, they molt at the same season as Manaus birds, hence in the southern *spring.* This means that molt *precedes* breeding from the Tapajós west. This peculiar arrangement has also been noted for the chief competitors of *olivascens,* namely the medium-large ant-following antbirds *Rhegmatorhina berlepschi* and *R. hoffmannsi* (Willis, 1969). While it is easy enough to suggest that earlier breeding with increasing southern latitude across the Amazon is caused by the general tendency for food supplies to increase earlier in the year as one goes southward (Snow, 1976), it is not easy to suggest a reason for delaying molt with increasing west *longitude* as one crosses the Tapajós River. (East of the Tapajós, White-chin subspecies molt in the southern late summer or fall).

Possibly the southern fall is unfavorable for White-chin molt or breeding west of the Tapajós because it corresponds with the annual peak in numbers and is unfavorable (relative to those numbers) or unpredictable in weather. It is not obvious why the weather west of the Tapajós is more difficult at this time of year than that east of the river, except that cold waves from the Andes and Argentina (*friagens*) occasionally strike southern and western Amazonia late in fall (Willis, 1976).

More information is needed on the seasons of molt and breeding west of the Tapajós, for complete molt prior to breeding is rare in birds. Snow (1976) could be right that molt (being a part of adult survival and hence of K-selection) becomes very important in these tropical birds and shifts to take the most dependably favorable time of year. This would avoid losses of adults in unfavorable periods, while breeding could take the less dependable part of the good season because occasional loss of a few young would matter little. Also, however, genetically related young out of the nest could benefit from having adult demands on local food supplies delayed until near the breeding season of the next year in the case of molt before breeding. This would perhaps be of little help to related offspring in temperate regions, where the annual peak in food supplies is likely to be sufficient both for molt and for immature survival; but tropical peaks in food are likely to be less extreme. The disadvantage of molt before breeding would be that molt would cut into the breeding period more certainly at the start of breeding than at the end, when it may be impossible to produce young anyway because of lack of time for them to grow.

Sociality. It is a general rule among ant-following antbirds that only the dominant species are very social (Willis, 1967; 1972b; 1973). The lack of sociality among subordinate species is attributable to the necessity for them to separate so as to infiltrate at scattered places around ant swarms; if they concentrate like dominant species at good sites, they quickly attract dominant species that supplant them. The lack of sociality in *Dendrocincla fuliginosa* was attributed to a similar phenomenon, for it is a solitary species very low on interspecific peck orders (Willis, 1972a). White-chins are slightly more dominant than is *D. fuliginosa,* and at Manaus rise high in the peck order over ant swarms. Is there any evidence that they become more social because of their high status?

In two respects, White-chins at Manaus were more social than were *D. fuliginosa* there or elsewhere: females cared for young longer, three months as against one or two; and young stayed wandering in the general area of the mother for several months, until driven out at the start of the next nesting season by the local male. The tolerance of the female for young, and her extended care of it, may be attributed to the high interspecific dominance of the species; she controls such large areas at a swarm that she can easily let her young forage nearby. Feeding it for a long period and tolerating it for even longer allow it to gain more experience and can be explained on the basis of kin selection.

Another possible reason for feeding the young for a long period, that of its niche being difficult to learn or relatively unproductive, does not seem likely to apply. In general, young ant-following antbirds of dominant species are fed by their parents for shorter periods than are young of subordinate species. The only exception is *Pithys albifrons,* a subordinate antbird that forages like a dominant species, near the productive centers of ant swarms. However, White-chins forage near the centers of ant swarms yet have a longer period of care of the young than do *D. fuliginosa,* which forage diversely and peripherally. Perhaps the long period of care in White-chins is based on its low dominance in regions other than Manaus, regions in which it must be more difficult for the young to find food. If so, White-chins at Manaus would have to be derived from the castanoptera group rather than the reverse.

Other than long association between mother and young, White-chins seem little more social than is *D. fuliginosa.* Female and male White-chins do let others wander over their home ranges, but this seems more sociality by laissez faire than by preference. Since the female *fuliginosa* can forage away from ant swarms if none are on the local territory, she need not forage on the territories of other females. Female White-chins, however, must move about because they never forage away from ants. Probably the trespassing female White-chin thus becomes difficult to evict, and the resident female no longer wastes energy and time trying to do so. Under these circumstances, it should be more efficient for the resident females to harass wandering young females low in the peck order, who do not fight back, and thus reduce the density of females locally without much effort (Rohwer, 1975). I saw little evidence of this for female White-chins, but something like this must limit the local female populations in cases when numbers rise.

Male White-chins overlap extensively in home ranges when not breeding, but drive out young of the previous year and seem not to forage with other males during breeding months (a limited or weak territoriality may occur during these months). This, plus some association with local females, seems more a protection of their genetic rights than of their foraging rights. Young of the previous year could reduce chances of young of the new brood surviving, while trespassing males could steal copulations. While the male attacks the resident females at times, I am not certain that he tries to keep out wandering females. Perhaps he exerts some population control by forcing wandering females to move on or breed, merely to insure the greater success of young raised by females in his area.

White-chins are definitely less social than are similarly foraging antbirds of their dominance level. The low sociality of White-chins probably is a relict character retained from a generalized ancestral dendrocincla like *D. fuliginosa,* a bird low on the peck order that had to forage alone. The lack of help by male dendrocinclas at nests must have originated with females that drove males away because such males hindered more than they helped. (Males commonly help females in other woodcreepers and in the related Furnariidae.) This would be true only if the pair were subordinate and unable to maintain an area over army ants. If the pair were dominant, they should forage together and raise more young than can a female foraging alone. As argued elsewhere (Willis, Wechsler & Oniki, 1978), other possible reasons for a female to reject help by her mate seem unlikely in similar species: nest size cannot limit brood size, nor are predation pressures likely to do so, since hole-nesting birds are little subject to nest predation and since they can easily fit more eggs than one or two into their nests.

Phylogeny. One concludes from the social structure of White-chins, as well as their highly specialized foraging, that they are derived and modified, probably new forms in their genus. It is easy to imagine them as local derivatives of *D. fuliginosa,* perhaps ones like *D. f. meruloides* of Trinidad, that started foraging low because they lacked competitors (Willis, 1966). Or, one can propose that the ancestral White-chin started foraging low when spreading back into an area already occupied by high foraging species like *D. fuliginosa.* It retained its original nonsocial behavior even as it became more dominant, even though nonsocial behavior was not as efficient as would be the joint nest care found in ancestors of the genus. The female White-chin lost her territoriality because she had to forage widely to stay with army ants, leaving the male free to regain his dominance and territorial aspirations in the breeding season because he gained genetically. Reversing or changing this scenario is difficult, despite its requirement for evolution away from parental care followed by evolution back.

I am not certain about locality of origin of these forms yet, although it is currently popular to analyse from a distance Amazonian animals and plants in terms of Haffer's (1969) theory of local forest refugia. If the large Manaus White-chins are behaviorally similar to Guianan ones, I would accept that they have originated in Haffer's Guianan Refuge, which even today is isolated by two large rivers (Negro and Amazon) and by a savanna region across Venezuela. If not, they must have originated or be separated from nominate *merula* by the savanna regions east of Óbidos. White-chins of the castanoptera group divide into subspecies based on present-day river barriers, whenever the rivers have savanna regions blocking movement around their headwaters: the Tocantins separates eastern *badia* from *castanoptera;* the Tapajós separates *castanoptera* from *olivascens,* which extends west to the Madeira; but *bartletti* extends right around the upper Amazon because the headwaters of the Amazon's upper branches are mostly forested. For this group, it is not necesary to look into potential past history to explain present distribution; present-day barriers are sufficiently difficult for this forest-inhabiting bird to cross.

In general, I favor the idea that most new forest ways of life tend to develop in the most complex forest ecosystem available. Species may gain reproductive isolation in isolated refugia (Haffer, 1969), but ecological isolation follows mainly when the refugia (or isolated populations) come back together. While the carrot of life in the refugia (which presumably lost species and hence would have increased opportunities for those that remained) may have led to some adaptive or accidental changes in foraging behavior, I attribute really directed change to the stick of competition once the forms came into competition with each other. Thus, the upper Amazonian centers of species diversity in ant-following antbirds seem the most likely regions for castanoptera-group White-chins to have evolved their tendencies to low foraging. I do not think that noncompetitive *D. fuliginosa meruloides* of Trinidad is necessarily like the ancestral *D. merula,* which may have speciated right in one of the upper Amazonian refugia, along with a diverse fauna of ant-following birds.

I also doubt that Manaus White-chins evolved low foraging and later spread to other regions as the forms of the castanoptera group. The changes at Manaus seems mostly derivatives of behavior in other White-chins, not the ancestral features found in *D. fuliginosa.* Even stieking in Manaus White-chins seems to me a new development, not like the alarm note of stieking in others of the genus. It is a mobbing call or a "stay" call, not the alarmed or "flight" call that it is in *D. fuliginosa.*

Since there seems no evidence in the genus *Dendrocincla* for a "return to Eden", or the movement of a species from a less competitive ant-following avifauna into a more competitive one, I propose that the species of the genus represent successive Amazonian forms that are moving or being pushed outward. White-chins are the newest form, being restricted to Amazonia. *D. fuliginosa* has spread beyond Amazonia, giving rise to the slightly different *D. turdina* in southern Brazil. It and antbirds that occur with it have pushed northward two other forms, *D. anabatina* and *D. homochroa*, that represent older and less adapted stocks of the genus. These older forms are poorly adapted to competition with the antbirds, which are speciating actively in Amazonian regions and have allowed *D. merula* to wedge into their niche only recently. Haffer (1975:72) has suggested that several other forest groups show successive waves of spread out of Amazonia into Central America, and no one has yet shown a case of movement in the reverse direction.

Studies of *D. anabatina* and *D. homochroa* would be interesting, as would studies of the Andean large *D. tyrannina*. It may be the oldest stock of all, or it may be a remnant of some old radiation in isolation like the larger White-chins at Manaus. It is important to hurry with studies, for the forests in which these woodcreepers live are being cut everywhere. In a second-growth area like much of the forest reserve at Belém, one could never study White-chins if they were not immigrating from forests of the Belém water supply.

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