

## THE BEHAVIOR OF BLACK-BANDED WOODCREEPERS (*DENDROCOLAPTES PICUMNUS*)

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**ABSTRACT.**—In forests and nearby second growth at Manaus, Brazil, Black-banded Woodcreepers (*Dendrocolaptes picumnus*) regularly foraged with army ants as well as away from ants. Like ant-following *Dendrocolaptes certhia* and *Hylexetastes perrotii* in the same study area, they tended to wait or hitch slowly on vertical thick trunks, then sally to or peck at prey. They were intermediate in dominance status and in use of perches near the ground, where ants flushed most prey. Birds of all three species also foraged high above the ground when the ants sent probes up trees. Sleek-headed (presumed female) Black-banded Woodcreepers supplanted their ruff-headed mates and helped in their disputes with neighboring pairs; one or both birds of a pair sang near roost sites in morning and evening; and pairs trespassed to a limited extent on their neighbors' areas. Large young were out of the nest with parents as early as July and as late as January, then wandered away from them. Breeding birds molted at about the time young left. At other study sites, the related species *D. hoffmannsi* and *D. platyrostris* behaved like *D. picumnus*.

Woodcreepers of the genus *Dendrocolaptes* are among species of birds that regularly follow army ants for flushed prey in neotropical forests (Willis and Oniki 1978). The behaviorally little-known Black-banded Woodcreeper (*D. picumnus*) proved to be an important species in the ant-following guild that I studied for over a year near Manaus, Brazil. Here I report on studies of Black-banded Woodcreepers, and compare their behavior with that of related woodcreepers.

### STUDY AREAS AND METHODS

I briefly studied Black-banded Woodcreepers at several lowland forest localities: Nappi Creek and Bartica in Guyana (Oniki and Willis 1972); Umbria, Leticia, and Mitú, Colombia; Limoncocha and Putuimi in Ecuador; Yarinacocha and Andoas in Peru; Diamantina, Palhão, Caruarí, Serra do Navio, Almeirim, and the Campina Reserve (near Manaus) in Brazil. At Reserva Ducke, Brazil, I studied them almost daily from 3 July 1973 to 27 August 1974.

Reserva Ducke (entrance at 2°55'S, 59°59'W) is a 10 × 10 km forest tract of the Instituto Nacional de Pesquisas da Amazônia (INPA), just north of Manaus. Tall upland forests at 100–120 m elevation are broken here and there by medium-height forests in sandy valleys of small streams at 50–60 m elevation. Experimental forestry tracts line an entrance road to a laboratory clearing, and neighboring areas are irregularly cleared for manioc and other crops (Willis 1977).

By watching with binoculars from behind swarms of ants (*Eciton burchelli*), I accustomed individual Black-banded Woodcree-

pers to my presence. I captured and color-banded 13 individuals at the Reserva. I took weights with Pesola scales and cloacal temperatures with a Schultheis thermometer. Vocalizations were recorded with a Uher 4000-Report S tape recorder at 19 cm/s.

### MEASUREMENTS AND SEXUAL DIFFERENCES

I examined 638 museum specimens of Black-banded Woodcreepers, measuring culmen and wing chord for most, and did not find strong sexual differences in color or measurements. Average wing length of males exceeded that of females by 0.5–2.9 mm in seven of eight populations considered, but overlap was great within each population. Moreover, the 0.5-mm difference was in nominate *D. p. picumnus*, which is the subspecies at Manaus. Females weighed more than most males in small samples from Surinam (combined  $\bar{x}$  = 88.7 g,  $n$  = 6) and eastern Peru ( $\bar{x}$  = 86.3 g,  $n$  = 5). From Nicaragua northward ( $\bar{x}$  = 61.0,  $n$  = 6) and in the Colombian and Venezuelan Andes ( $\bar{x}$  = 73.8 g,  $n$  = 4), the specimens of *D. picumnus* were small, but sexes overlapped widely in weight.

In *Dendrocolaptes* species at Reserva Ducke, two types of birds formed pairs: a sleek-headed individual dominated one that ruffed up its head and breast every time its mate came near. In Barred Woodcreepers, one sleek-headed bird that I collected proved to be a female, while two collected ruff-headed birds were males (Willis, unpubl.). I assumed, therefore, that "ruffed" birds were males and "sleeked" birds were females in Black-banded

Woodcreepers also, even though both types weighed about the same at Manaus ( $\bar{x} = 82.8$  g,  $n = 14$ ).

Collectors have not recorded the head ruffling of their *D. picumnus* specimens, but the preceding paragraph is consistent with the fact that more males (303) have been taken than females (240). Sleek-headed birds normally were retiring at Manaus, leaving the subordinate ruff-headed birds to forage near the ground and near me. However, it is possible that males sing more than females at dawn and dusk (see below), a factor that could also bias collecting in favor of males.

## OBSERVATIONS OF BLACK-BANDED WOODCREEPERS

### VOICE

*Song.* Black-banded Woodcreepers at Manaus sang descending series of 15 to 20 simple chirps, lasting almost 2 s (Fig. 1A): “kie-ie-ie-ie-ie-ie-ie-ie-ie-ie-ee-eu-eu-er.” Barred Woodcreepers (*Dendrocolaptes certhia*) at Manaus had a similar but slower song, of 8 notes in 1.4 s. A Planalto Woodcreeper (*Dendrocolaptes platyrostris*) from Fazenda Barreiro Rico, São Paulo, gave a slow evening song like that of a Barred Woodcreeper, 12 notes in 2.3 s (Fig. 1C), but one from Fazenda Klabin, Espírito Santo, (courtesy of Michael Gochfeld) sang a fast song like that of a Black-banded Woodcreeper, 18 notes in 2.3 s (Fig. 1C).

*Rattles.* Series of short chirps at 6–8 per s, fluctuating in volume and changing irregularly in quality “ee-ee-ee-ee-ie-ie-e-e-ie-ei-” and so on (Fig. 1F, H), were frequent after disputes or in response to playback of recordings. They sometimes graded into songs.

*Squeals.* Loud series of several “squeeh” notes were given during fights.

*Snarls.* A growling noise followed by a squeal, “chauh-hh-eesk,” (Fig. 1G) seemed to be an alarm call. At times the last note of a snarl was less piercing, perhaps a different call.

*Grunts.* Short faint series, “uk-uk-uk,” were given at nearby competitors. Barred Woodcreepers in Panama grunted similarly.

*Peepsongs.* The brief songs of fledgling Black-banded Woodcreepers (Figs. 1D, E) consisted of 12 or so chirps in 1 s, the song at times rising and then falling rather than falling throughout: “wh-e-e-e-e-e-e-e-e-up.”

### ALARM BEHAVIOR

*Freezing.* I commonly saw birds simply freeze, pressing their bodies against the limb or trunk and remaining immobile for several seconds to minutes. Immature birds stopped peepsinging while they froze. Occasionally a bird snarled as it froze, but I detected no sound while it

remained frozen. (In many passerines, the thin and high “keening” associated with freezing is difficult for humans to hear.) I noted freezing in response to alarm calls of other birds (Plain-brown Woodcreeper, *Dendrocincla fuliginosa*, 8 times; *D. picumnus*, 2; Black Nunbird, *Monasa atra*, 2; keening of Rufous-throated Antbird, *Gymnopithys rufigula*, 1). Once, one clung close to a tree as Little Chachalacas (*Ortalis motmot*) flew past. Woodcreepers generally seem to be protectively colored, and the pale streaks on a Black-banded Woodcreeper may have increased its resemblance to furrowed bark or to spaces between epiphyte leaves. Streaking appears to be correlated with rapid hitching along dark trunks in woodcreepers; unstreaked and barred forms wait more or use well-lighted trunks.

*Fleeing.* These woodcreepers often fled to avoid danger, sometimes by sidling quickly around a tree trunk, then freezing or hitching upward on the far side of the trunk. During pauses, the bird often turned its head, flitted the tips of its wings or wrists, or peered around the trunk (Fig. 2A). An isolated snarl might break the silence. Another method was flight to other trees, without the usual downward swing to a lower perch characteristic of foraging moves. When the presumed danger was a human or low-flying raptor, the bird often climbed to large branches 20–35 m above the ground. Once, at the sound of a distant gunshot, a bird dropped instead to a low trunk; on another occasion, a woodcreeper snarled and backed down a trunk when macaws (*Ara ararauna*) flew over. The bird might sleek the head or ruff it when near the observer; ruffling could refer to the following behavior pattern, however, as it was most characteristic of a returning bird or one reluctant to move as I approached.

Snarling, usually with fleeing, was specifically recorded at the approach of hawks and falcons (*Micrastur ruficollis*, 4; *Leucopternis albicollis*, 2; unidentified hawk, 2; *Buteogallus urubitinga*, 1), at the sound of avian alarm calls (*Dendrocincla fuliginosa*, 4), at a gunshot or passing macaws, to nets (4) and to me (5). The snarls at me were usually a less sharp version, apparently without a sharp rise in pitch at the end. I noted fleeing or nervous wing-flitting in response to me and to another person who came up to me (even though the bird involved had been ignoring me), to passing cars, to alarm calls (*Dendrocincla fuliginosa*, *Pithys albifrons*, 2; *Ortalis motmot*) and to a hawk (*Leucopternis albicollis*).

Other birds often performed alarm movements or calls following the sharp snarls of Black-banded Woodcreepers, even when the

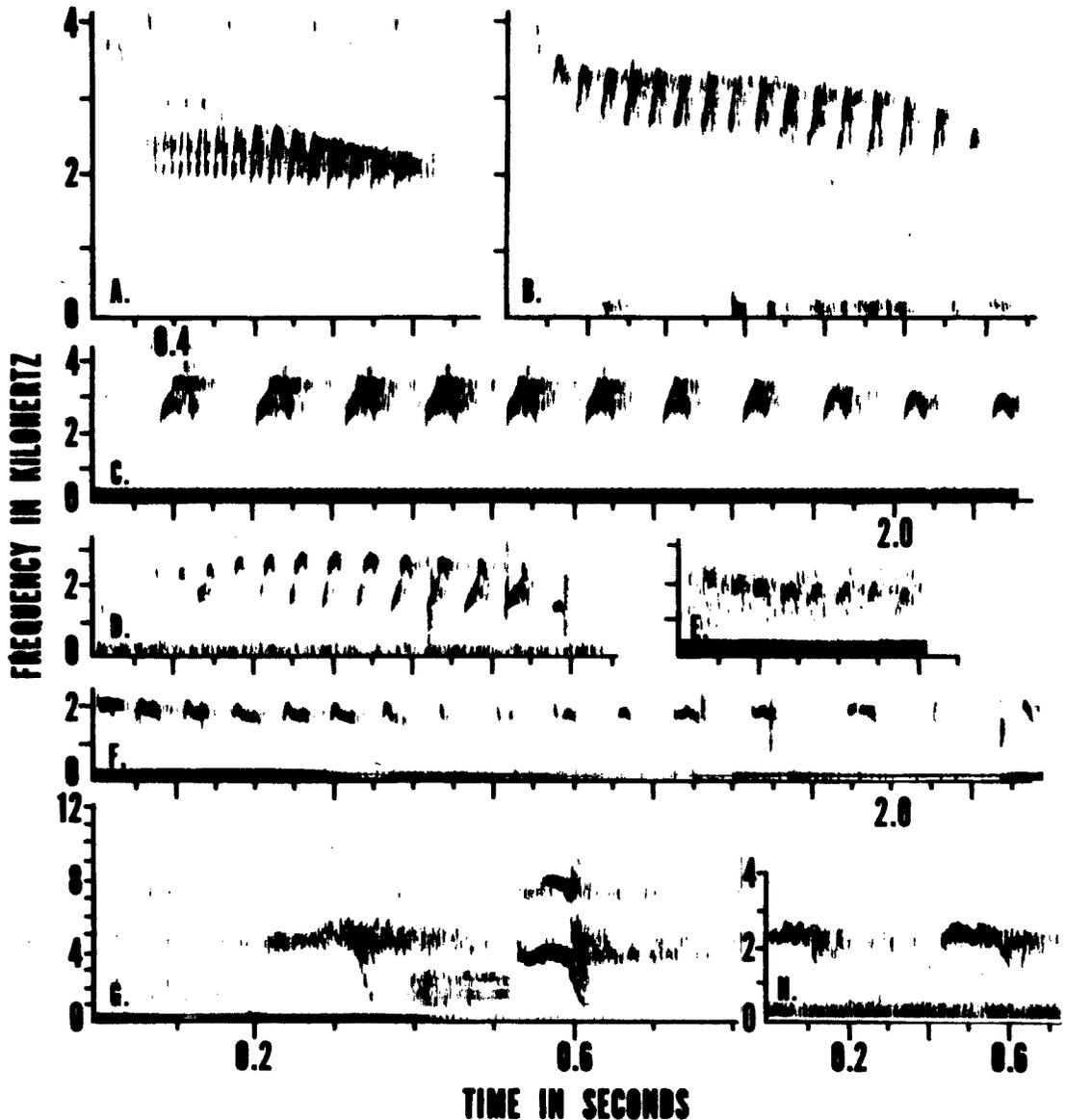


FIGURE 1. Sonograms of Black-banded (B-b) and Planalto (P) woodcreeper vocalizations. A. B-b, song, Manaus. B. P, song, Fazenda Klabin, Espirito Santo (courtesy of Michael Gochfeld). C. P, song at Fazenda Barreiro Rico, São Paulo (note change of scales). D and E. B-b, peepsongs of young, Manaus. F. B-b, rattles, Manaus. G. B-b, two snarls, the first from a distant bird and hence with the growling first note faint, Manaus. H. B-b, two chirping rattles, Manaus.

snarls seemed undirected or were related to intraspecific disputes rather than to predators.

Some Black-banded Woodcreepers preened after freezing or fleeing, before resuming foraging.

*Mobbing.* I saw no evidence of mobbing, except that moderately tame males sometimes ruffed their heads near me, while other birds snarled behind cover.

*Struggling.* In the hand or net, captured woodcreepers occasionally startled the captor with an abrupt snarl or attempt to fly. They struggled little otherwise, and did not peck.

The sharp claws clung tightly except during flight attempts, and soon scarred one's fingers.

*Taming.* Naive woodcreepers often hid high above the observer for an hour or two or showed other alarm behavior, then began to feed if other birds were foraging. After I had studied some individuals for several hours or made scattered observations on them over a few weeks, they became tame enough to descend and forage nearby without much wing-flitting. Young birds were less wary than adults. Like Barred Woodcreepers in Panama but unlike those in Amazonia, Black-banded

Woodcreepers usually continued following ants when the observer stayed nearby. None of the *Dendrocolaptes* observed ever seemed curious or aggressive unless I was near a good foraging site that the bird was approaching.

#### FORAGING BEHAVIOR

Undisturbed Black-banded Woodcreepers sallied from trunks for much of their prey, and seldom investigated crevices to peck out prey in the fashion of true creepers (Certhiidae) or related woodcreepers in the genus *Xiphorhynchus*. Black-banded Woodcreepers commonly followed army ants, but sometimes foraged alone or with bird flocks away from ants.

*Foraging over army ants.* Black-banded Woodcreepers, foraging over army ants at Manaus, foraged below 1 m part of the time, especially when competing Red-billed Woodcreepers (*Hylexetastes perrotii*, 120-g birds) were absent. Black-banded Woodcreepers foraged below one meter 24.7% of the time when Red-billed Woodcreepers were nearby (1,078 records) and 27.9% when they were not (2,480 records). Percentages of records below 1 m (in 0.1-m intervals) for individuals foraging near *H. perrotii* were: 0.4% on the ground, 0.7% up to 0.1 m, 4.7% to 0.2 m, 5.5% to 0.3 m, 4.1% to 0.4 m, 3.4% to 0.5 m, 1.5% to 0.6 m, 1.2% to 0.7 m, 1.3% to 0.8 m, 0.5% to 0.9 m, and 1.3% to 1.0 m. For individuals foraging away from *H. perrotii*, the series of percentage distributions was: 0.3, 0.3, 3.3, 6.3, 5.6, 5.4, 2.4, 1.5, 1.1, 0.7, and 1.4.

Black-banded Woodcreepers foraged high above the ground somewhat more than did Red-billed Woodcreepers, but less than Banded Woodcreepers. Percentages of records of *D. picumnus* 1–10 m up were, respectively (in 1-m intervals), 12.4, 8.6, 12.4, 9.2, 6.2, 4.5, 2.1, 2.9, 3.0 when near *H. perrotii* and 14.2, 8.9, 9.8, 7.9, 5.4, 4.9, 4.2, 2.4, 2.6 when away from it. From 10 to 15, 15 to 20, and 20–30 m up the respective percentages were 8.3, 4.4, 1.2 when near *H. perrotii* and 6.9, 4.1, 0.8 when away from it.

Black-banded Woodcreepers used near-vertical perches most of the time. For 3,158 records of perch angle, percentages in 20-degree intervals from 0° to 180° were (respectively) 0.7, 0.7, 0.7, 6.0, 88.9, 2.5, 0.3, 0.1, 0.03; one record (0.03%) was at 340°. (This notation is best understood by rotating parallel pencils, representing woodcreeper and perch, from 0° or horizontal past 90° or vertical and then past 180° to 360°; the “woodcreeper” starts and ends above the “perch.”)

Diameters of 2,657 perches of Black-banded Woodcreepers over army ants were distributed 0.7% under 1 cm, 2.9% from 1.1 to 2 cm, 4.3%

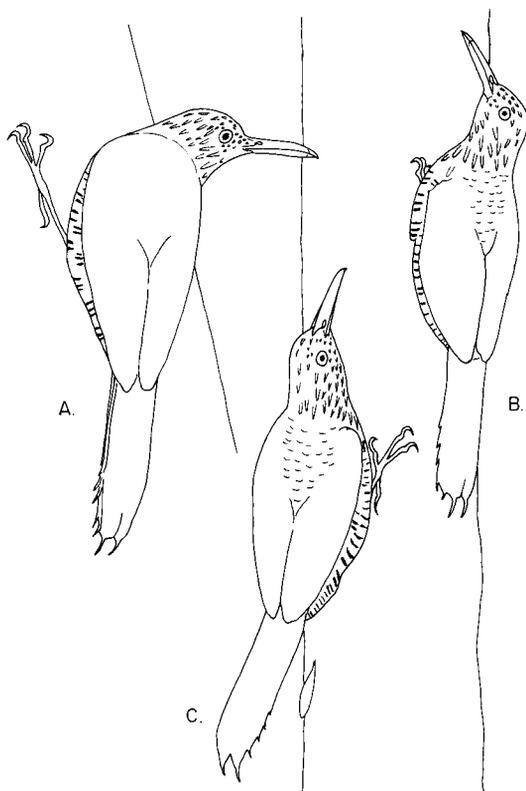


FIGURE 2. Black-banded Woodcreepers, from field sketches. A. Peering after alarm call of a Plain-brown Woodcreeper. B. Resting, with belly on the trunk. C. Defecation, requiring lifting of the tail from the trunk.

from 2.1 to 3 cm, 3.9% to 4 cm, and 5.5% to 5 cm, and 34.1, 24.2, 16.4, 7.3, 0.8% from 5.1 to 15, 15 to 25, 25 to 50, 50 to 100, and 100 to 200 cm diameter, respectively. These birds thus used 5–25 cm perches only 58.3% of the time and captured only 50.5% of 366 prey from them. By contrast, Banded Woodcreepers over army ants at Manaus used perches 5–25 cm in diameter for 73% of 937 records (Willis, unpubl.). Perhaps the former species, being dominant to the latter, was less likely to be chased off a perch under 5 cm in diameter; and Black-banded Woodcreepers often displaced their smaller (65-g) relatives at strong ant probes up very large trunks.

Black-banded Woodcreepers rarely used perches under 1 cm in diameter, which sometimes bent under a bird's weight. Perches up to 2 cm diameter often split the bird's tail, so that it rested on the fragile and quickly damaged inner webs rather than on the stiffened tips of the feathers. Perches less than 3 cm diameter were good vantages for prey, representing 12.8% of 366 perches before captures, largely because the birds often had to use slender saplings in order to forage near the ground

TABLE 1. Places and methods of foraging used by Black-banded Woodcreepers over army ants. The values are percentages of 1,002 prey items.

Place of capture	Method				
	Sallying	Gleaning	Digging	Tossing leaves	Unknown
Ground	29.8%	1.5		0.1	
Trunk, liana, log	4.4	17.4	0.5	0.1	0.1
Leaf, twig	23.4	4.6			0.3
Debris	0.4	0.7			
Termite, ant nest		0.1	0.2		
Air	8.1	1.2			
Not determined	6.0	1.2			
Total	72.1	26.6	0.7	0.2	0.4

(the best zone for ants). Trunks over 15 cm diameter were even better vantages, representing 57.4% of 366 perches taken before prey.

When Black-banded Woodcreepers were hunting near Red-billed Woodcreepers, 28.5% of prey captures ( $n = 274$ ) were on the ground; when away from Red-billed Woodcreepers, 36.3% ( $n = 633$ ) were on the ground. Perches below 1 m were disproportionately represented among prey-capture records compared to records for all foraging perches, both near Red-billed Woodcreepers (28% of 124 records) and away from them (33% of 268 records). Barred Woodcreepers at Manaus captured only about one-eighth of their prey on the ground (Willis, unpubl.). Since Black-banded Woodcreepers captured three times as many prey over ants as did Barred Woodcreepers, the former captured seven times as many prey on the ground and over twice as many prey above the ground as did Barred Woodcreepers.

Black-banded Woodcreepers captured prey in diverse locations, using sallying and other techniques (Table 1). Sallying to the ground (the commonest type of capture in ant-following birds) represented nearly 30% of records, unlike 5–15% for Barred Woodcreepers in various localities (Willis, unpubl.). Sallying to foliage, the next most common type of prey capture, was less than half as frequent as in Barred Woodcreepers at Manaus (where 55.6% of the 295 records were for that species). Sallying to palm fronds accounted for 42% (98/234) of my records of Black-banded Woodcreepers that were foliage-sallying at Manaus, even more than for Barred Woodcreepers foliage-sallying there (24%). Pecking or gleaning prey from trunks or limbs was slightly more frequent by Black-banded than by Barred Woodcreepers at Manaus (10.8%) but not as common as in the latter species in Panama (36.7% of 294 records).

Sallying to the air, as in the aerial sallies performed by Barred Woodcreepers, involved

TABLE 2. Vertical and horizontal distances of sallying Black-banded Woodcreepers over army ants. The values are numbers of records. Upward and downward movements are separated by a slant line.

Vertical distance (m) <sup>a</sup>	Horizontal distance (m)				
	1	2	3	4	5
4	1/0				
3	0/1		0/1		
2	2/1				
1	18/15	3/3	1/0		
0	13	1			1

<sup>a</sup> The bird flies approximately the hypotenuse of the two indicated distances.

mostly diving at or after flying or falling prey, especially during emergences of winged ants. Diving after prey was about as common as sallying upward (Table 2), whereas Barred Woodcreepers mostly sallied upward.

Black-banded Woodcreepers seldom dug or tossed leaves from cavities or termite nests above the ground, a rather frequent technique of large-billed Red-billed Woodcreepers. Gleaning was less common than sallying, unlike such related woodcreepers as the Chestnut-rumped Woodcreeper (*Xiphorhynchus pardalotus*) at Manaus but like Barred Woodcreepers there.

Prey (Table 3) of Black-banded and of Barred woodcreepers were similar at Manaus, except that no fast-flying cicadas nor moths fell prey to the former, a slow-flying species, while more winged ants did so. (Black-banded and other large woodcreepers quickly chased Barred Woodcreepers away from ant emergences.) Grasshoppers, katydids, roaches, and other orthopterans were common prey, as were other large primitive arthropods on decaying trunks. The modal prey length was less than the beak length, and *D. picumnus* captured smaller prey than did *D. certhia*. (Prey size was estimated in the field as a fraction of exposed beak length,  $1B = 35$  mm in this case; prey lengths in Table 3 are head-to-vent and do not include projecting legs, antennae or cerci.) Black-banded Woodcreepers could, perhaps, take small prey because they often hunted near army ants, at ant emergences or on the ground, while Barred Woodcreepers generally sallied to distant foliage and ignored tiny prey. *D. picumnus* captured prey as far as 1.5 m away when sallying to the ground, but 10 of 35 records were less than 0.2 m away, while 28 of 35 were less than 0.5 m off.

Black-banded and Barred woodcreepers both hammered large prey against tree trunks or shook and crushed them vigorously, but did not dissect them piece by piece on the ground. If the former had not had long bills, they could

TABLE 3. Types and sizes of prey taken by Black-banded Woodcreepers foraging over army ants.

Prey	Number of prey of given size (mm)								
	? Up to:	10	20	30	40	50	60	70	105
Scorpion					6	4	7	4	
Whip-scorpion	1		2	2	3				
Spider	1		4	6	5	4			
Centipede				1	3	1	5	4	4
Roach	11		5	17	7	5			
Katydid	9		4	9	17	9	5	2	
Beetle			5	7					
Caterpillar	3		1						
Ant, larva	4		1						
winged	36	3	2						
Lizard					1				
Unidentified		85	29	14	6	2			
Total	65	88	52	57	48	25	17	10	4

not have handled any large prey, whereas antbirds with much shorter beaks easily dissected such prey on the ground. Black-banded Woodcreepers gulped down the prey body and let projecting wings or legs fall off to the ants below. Large katydids sometimes pushed vigorously with their spiny legs, causing the woodcreepers to almost release them or to juggle them upward for recapture. Tiny prey was sometimes crushed in the tip of the beak rather than in the gape, as if noxious; the bends of the wings went out as in "anting" behavior. Scorpions were crushed or hammered at the head end, often until the tail dropped off (see also Haverschmidt 1977). Whip-scorpions were pounded until the long legs dropped off. Large beetles required much hammering and crushing; I once saw a scarab repeatedly pop from the beak and be recaptured in mid-air. These woodcreepers rubbed hairy caterpillars on trunks or leafy trash. One green caterpillar was rubbed under the tip of a wing several times. On another occasion, a bird capturing an ant with a larva, carefully dropped the ant and ate the larva. One roach was turned with the tongue so that it was head-first rather than tail-first before swallowing. Birds sometimes wiped their beaks after crushing large prey.

Black-banded and Barred woodcreepers thus foraged much alike at Manaus, except that the former were more regular at ant swarms and did more foraging near the ground. Both worked similarly near the ground, looking back over their shoulders from moderately large perches and diving rather clumsily to snap up prey fleeing the ants. They preferred fairly open understory, being larger and not so maneuverable as antbirds, and perched only with difficulty on slender growth. In dense undergrowth, both woodcreepers tended to cease foraging near the ground and to hitch upward. However, they were heavier and better able to

use large vertical perches than were crosswise-clinging antbirds.

Above the ground, both of these woodcreepers hitched short distances and waited for a few seconds to minutes looking for distant prey. They seldom examined the nearby trunk minutely or pecked at it, woodpecker-style. These woodcreepers tended to follow ant probes up trunks and to check certain types of sites where ants regularly flushed prey. They visited palm fronds and crowns (229 records in my notes), rotten snags or stubs (154), hollow "acariquara roxa" trees (128), slits or holes in trunks (75), liana-crowded trunks (70), and under or near epiphytes (55). Termite runways (30) or termite and ant nests (11) attracted them, probably because such runways are often on dead portions of trunks. Fluted trunks (13) and tree crotches (12) were visited. Occasionally one visited a treefall (6), but such sites generally had only horizontal and cluttered perches in which antbirds were more at home. I saw Black-banded Woodcreepers flying back and forth around such tangles, unable to enter. They infrequently foraged on logs (4 records), loose bark (4), and debris (2). One tore off a philodendron leaf plastered on a trunk and peered underneath.

Emergences of winged ants above the ground led to woodcreeper "circuses," with as many as seven species fluttering about actively. Black-banded Woodcreepers tended to rapidly replace low-foraging White-chinned Woodcreepers (*Dendrocincla merula*) and subordinate Barred Woodcreepers, but Black-banded and Plain-brown woodcreepers stayed even if Red-billed Woodcreepers scared them to the periphery. Chestnut-rumped Woodcreepers might hitch up to get prey on trunks, and Long-billed Woodcreepers (*Nasica longirostris*) might glean on limbs. Black-banded Woodcreepers mostly sallied downward for flying ants from near the

TABLE 4. Competitive interactions of Black-banded Woodcreepers over army ants.

Species	Number of interactions <sup>a</sup>				
	Sup-planting	Dis-placing	Fight	Re-turn	Ig-nore
<i>Dendrocolaptes picumnus</i>	312	33	11	2	1
<i>Dendrocincla fuliginosa</i>	151	30		1	5
<i>D. merula</i>	52	5		3	1
<i>Dendrocolaptes certhia</i>	32	27	2	2	
<i>Hylexetastes perrotii</i>	/44	/14			
<i>Xiphorhynchus pardalotus</i>	17/3	7/1			
<i>Nasica longirostris</i>	/3	/1	/4		
<i>Gymnopithys rufigula</i>	43	8			1
<i>Pithys albifrons</i>	21	1		5	2
<i>Pernostola rufifrons</i>	4	1			
<i>Cacicus haemorrhous</i>	5				
<i>Pharomachrus pavoninus</i>	/4				
<i>Trogon violaceus</i>	/1				
<i>Monasa atra</i>	1				
<i>Campephilus rubricollis</i>	1/1				
<i>Turdus albicollis</i>	1				
<i>Ramphocelus carbo</i>	1				

<sup>a</sup> Records alone or before / denote dominance by Black-banded Woodcreepers; records after / denote dominance over these birds.

exit holes. They then hitched rapidly up to just below the exit holes again, or as close to the holes as Red-billed Woodcreepers would allow them to come. Meanwhile, Plain-brown Woodcreepers sallied out from hiding places around peripheral vines and limbs. They and Black-banded Woodcreepers were often the last to leave such a site, and reaped the benefits of being the first at new emergences.

Between periods of watching or of activity at special sites, Black-banded Woodcreepers often wandered near swarms. They did not spiral around trunks as much as did Barred Woodcreepers, but otherwise similarly hitched up irregularly. Often they hitched up along the upper sides of canopy limbs, only to glide off with short bursts of flapping to other limbs or to lower trunks. Regularly, they came to any activity of other woodcreepers or antbirds. Their open-winged downward glides, preceded at times by heavy flutters, sometimes scared off small birds from such places. Meanwhile, Barred Woodcreepers wandered high and peripherally, and appeared mainly when a particular zone of activity became quiet. Both of these woodcreepers seemed the same size in the field, despite differences in weight, and the two overlapped greatly in foraging over ants.

*Foraging away from ants.* At Manaus, Black-banded Woodcreepers infrequently foraged away from ants. They usually stayed high in the canopy or in the forest mid-levels, where they wandered steadily as if searching for ants.

They rarely followed mixed-species flocks. Normally they hitched up tree trunks or major limbs, looked about at stops, and glided off in catenary curves to other trees. Sallying to foliage was recorded once.

#### COMPETITIVE BEHAVIOR

*Interspecific.* Black-banded Woodcreepers attacked a few birds over army ants, mostly woodcreepers, with a moderate number of attacks on antbirds (Table 4). I seldom witnessed other attacks: trogons attacked a few of these woodcreepers near trogon nests, and a woodpecker attacked one that chased it around a trunk away from ants. Shortly after this incident, the woodcreeper attacked several caciques (*Cacicus* sp.).

Attacks on antbirds were generally simple "supplantings" or replacement of one bird by another near the ground. Some Rufous-throated Antbirds chipped in alarm at sudden attacks, but normally I heard no sound. These woodcreepers sometimes attacked antbirds in food-catching attempts (six cases for *G. rufigula*, four for *Pithys albifrons*, two for *Pernostola rufifrons*). Antbirds often moved off, "displaced," at a slight lunge or stare by the woodcreeper. They usually stayed within a meter or two, even "returning" to the perch just vacated by the woodcreeper in the case of *P. albifrons* (a species that infiltrates persistently behind or near large competitors). Black-banded Woodcreepers near the ground occasionally grunted at the small antbirds swirling nearby. Large antbirds such as species of *Phlegopsis* in other regions seemed to be avoided, for Black-banded or Hoffmanns' (*Dendrocolaptes hoffmannsi*) woodcreepers usually foraged away from the ground whenever these antbirds were present.

Attacks by and on other woodcreepers formed a considerable part of competitive behavior. Gleaning trunk-foraging woodcreepers in the genera *Xiphorhynchus* and *Nasica* seemed pugnacious, and often initiated or received attacks. Chestnut-rumped Woodcreepers, the smaller species at Manaus, occasionally hitched rapidly along toward Black-banded Woodcreepers, pecking and dodging return pecks. The latter normally chased the former, rather than vice versa. Long-billed Woodcreepers, a large, limb-foraging species, initiated several attacks and fights with Black-banded Woodcreepers despite their rarity at Reserva Ducke (being mainly a bird of floodplain woods or varzeas). Away from Manaus, fairly large (60–65 g) Buff-throated Woodcreepers (*X. guttatus*) sometimes stopped their trunk- and epiphyte-peering long enough to attack, engage in a pecking duel, or drop in a fluttering aerial

duel with Black-banded or Hoffmanns' woodcreepers. The Buff-throated Woodcreeper usually won, but at times a Hoffmanns' or Black-banded woodcreeper snarled and jabbed back or supplanted the fast-climbing opponent. A Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*) was once seen to displace a Black-banded Woodcreeper at Diamantina. Medium-sized species of these trunk-climbing genera perhaps win at times over species of *Dendrocolaptes* because the latter cannot climb and dodge as rapidly, being adapted for salying rather than for trunk foraging.

Medium-sized (40–55 g) ant-following woodcreepers of the genus *Dendrocincla* were regularly attacked by Black-banded and Hoffmanns' woodcreepers. Uncommon low-foraging White-chinned Woodcreepers at Manaus were attacked about one-third as often as common, high-foraging Plain-brown Woodcreepers, even though Black-banded Woodcreepers spent only one-third as much time near the ground as high above it. (Low-foraging birds concentrate more than do high-foraging ones, however.) Attacks were usually simple, rarely with a gape or snap of the beak, and were usually without calls except for occasional chatters or "stieking" notes from the supplanted *dendrocincla*, or a grunt from the attacker. Black-banded Woodcreepers whirred their wings loudly in some attacks. Occasionally one hitched rapidly up a trunk after a *dendrocincla*. *Dendrocinclas* alighting near Black-banded Woodcreepers were likely to be driven off, as were those that tried for prey nearby (17 of 151 supplantings and 2 of 30 displacings for *D. fuliginosa*, plus 3 of 52 supplantings of *D. merula*, were in prey-catching attempts).

Black-banded Woodcreepers occasionally supplanted or displaced evasive Barred Woodcreepers, while Red-billed Woodcreepers, which were larger, regularly supplanted both. Small birds regularly avoided larger ones in this group of ant-following woodcreepers, reducing the number of confrontations. Attacks by Black-banded upon Barred woodcreepers were much less frequent than their intraspecific attacks, and tended to be quieter: a grunt, a growl, or rarely a squeal or two. Barred Woodcreepers often hid by hitching quickly around trunks. Red-billed and Black-banded woodcreepers sometimes did the reverse, suddenly lunging around a trunk at a surprised smaller woodcreeper. Favored sites, such as hollow trees, rotten stubs, holes in trunks or palm crowns, sometimes attracted first a Barred, then a Black-banded, and finally a Red-billed woodcreeper. One Barred Woodcreeper dropped 4 m at a look from a Black-banded Woodcreeper, then hitched slowly up toward

it. When attempting to feed, Barred Woodcreepers were sometimes displaced (5 of 27) or supplanted (1 of 32) by Black-banded Woodcreepers. The latter, when feeding, were sometimes supplanted (4 of 44) or displaced (1 of 14) by Red-billed Woodcreepers.

*Intraspecific.* Black-banded Woodcreepers lived in pairs, although male and female sometimes fed at different colonies of ants. The sleek-headed bird (female?) displaced or supplanted the ruff-headed bird (male?) when they were at the same ant raid, and the latter took whatever foraging sites were left. One evening, I watched a pair threaten each other and fight, tumbling fluttering to the ground before separating. Disputes between Black-banded Woodcreepers were relatively frequent, for the male and the female of a pair were antagonists, while boundary disputes and territorial trespassers led to other attacks. Only 8 of 312 intraspecific supplantings and 1 of 11 fights were connected with feeding chases. When neighboring pairs met over ant swarms, noisy chases with squealing usually ensued. Two pairs rarely stayed at a single ant raid unless they could forage over different branches of the raid. Wandering individuals, including immatures, were chased when encountered, but wandering birds often hid persistently at distant parts of a raid and hence followed jointly with territorial pairs.

Disputes between mates, or between parents and dependent young, normally involved simple chases, supplantings, or displacings with little display or calling; after head ruffing or sleeking and a grunt or squeal, the two separated. Young birds supplanted the ruff-headed parent in disputes but avoided the sleek-headed parent's lunges. One young grunted at the ruff-headed parent before supplanting it. At times, however, the sleek-headed parent fled from the young bird as it followed for food. Families often flitted their wings when together, perhaps a sign of low-intensity aggression.

Disputes between residents and nonresidents, or between wandering birds, were often vigorous and noisy. Squeals and songs, fluttering aerial duels or chases, and fights erupted when a new bird or pair appeared at an ant colony. The wrists and alulars were often spread, as were the body feathers. Sleek-headed birds never spread the head feathers, but ruff-headed individuals consistently did so. Ruff-headed birds often ruffed the throat and the breast feathers (i.e., all the streaked feathers) in and out. Only the back, breast and lower neck were ruffed out in sleek-headed birds (Fig. 3A, B). Birds of both types spread their tails and wing tips somewhat, and pushed the body out from the trunk. There was at times slow

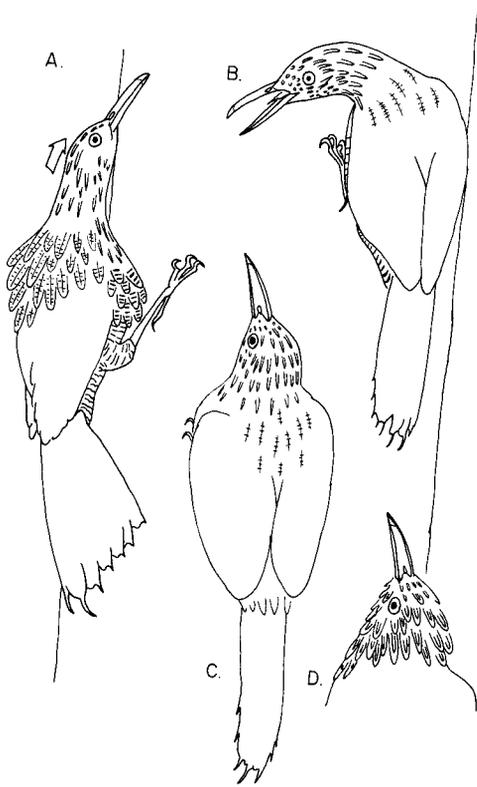


FIGURE 3. Disputing Black-banded Woodcreepers, from field sketches. A. Sleek-headed aggressive bird jabbing the head toward an opponent above. B. Sleek-headed bird threatening bird below. C. Sleek-headed submissive bird. D. Ruff-headed submissive bird.

forward and upward jabbing of the bill. Sleek-headed birds sang faintly, while ruff-headed birds sang and squealed noisily. In one case, two disputing ruff-headed birds gave only strangled snarls as long as a Black-faced Hawk (*Leucopternis melanops*) waited above, then flew back and forth past each other with piercing squeals from the losing bird. Submissive birds tended to retract the head and to cling close to the trunk (Fig. 3C, D).

I watched a dispute among three banded birds in tall second growth, peripheral to the forest zone that was the center of the pair's activities. One nearly-independent young (a sleek-headed individual) disputed with a wandering sleek-headed young while the ruff-headed parent foraged peripherally; when the intruding young supplanted him, he ruffed his head feathers and started singing faintly, then hitched up and fled. The resident young and the intruding one were silent except for a few sharp snarls at first, and ascended in displays until out crosswise on terminal twigs of the small tree. When on vertical perches, they pointed their sleeked and extended heads and necks skyward, but when on horizontal twigs

they bowed their heads at each other. Their backs and scapulars were very ruffed out, their breast plumage was expanded but rather flat (except for a central groove), their wingtips were out and were flitted, but their wrists were concealed in the spread body feathers. Finally, the intruding young started singing loudly and fled down to near the ground. The resident young followed, the intruder snarled, and both began to forage over separate parts of the ant swarm. Once the intruder tried to supplant the resident young, but it pecked back and stayed. The resident female was not present, presumably being at another ant colony.

On a later occasion, the same resident ruff-headed bird was more aggressive, snarling loudly and ruffing his head at a quietly singing intruder, then chasing the squealing bird about. Meanwhile, his sleek-headed mate flitted her wings and foraged; later she supplanted the intruder briefly. On another occasion, the same ruff-headed bird spread its head feathers at a trespassing ruff-headed bird, then hitched up and chased it.

In Barred Woodpeckers, males (ruff-headed birds) also feuded noisily on territories while females (sleek-headed birds) disputed quietly; females dominated males despite seemingly more vigorous display from males (Willis, unpubl.). My observations of Black-banded Woodcreepers suggest that even trespassing sleek-headed immatures seem capable of displacing ruff-headed resident adults at times.

Black-banded Woodcreepers, like other species of *Dendrocolaptes*, regularly sang at dawn and dusk. In 1972 to 1976, a pair of these birds roosted every night inside bromeliads 12 m up on a tree trunk outside the dining room at Reserva Ducke. Both birds sang as they approached the roost site at dark, occasionally even on the roost tree, before separately hitching up inside the bromeliads. At dawn, a few songs marked the departure of one or both. Probably territories are marked by these song periods near roost sites. Songs at other hours marked disputes, either over or away from ants, and were infrequent.

#### REPRODUCTIVE BEHAVIOR

The behavior of mated birds and of singing birds is described above, see Competitive Behavior, Intraspecific.

Salmon (Sclater and Salvin 1879) found two white eggs  $29 \times 22$  mm in a tree hole in northern Colombia.

I found several full-sized peepsinging young out of the nest between 6 July and early January at Manaus, and banded three of them. The single young bird in each family normally followed the sleek-headed bird of the pair, but

in one case a young bird received food from both birds. The young resembled the adult except for fluffier plumage. For several months, it peepsang repeatedly every 4 s or so as it wandered near the presumed female or on its own around ants. If the female captured prey and started to beat it on a trunk, the juvenile quickly flew over or hitched up to her. If she did not dodge away, it often fluttered its wings and gaped (Fig. 4A), then received the food as it hitched rapidly up past her. One feeding by a male was similar. The young then crushed and flailed the prey on its own, and swallowed it. Young birds sometimes pecked off and chewed bits of bark or leaves or stood on the ground (Fig. 4B), but gradually began to capture prey items. They apparently stayed with their parents for several (3–4) months. Occasionally two young were together, with or without parents, in November or January. Afterward, they wandered away from their parents and disappeared from my study area. Other birds, thought to be immatures, wandered into the study area at this time (Fig. 5). Some young peepsang after leaving their parents, as late as 21 January.

#### MAINTENANCE BEHAVIOR AND MOLT

Preening birds used vertical perches, although more perches were subvertical than in ordinary foraging (of 129 preening perches, 12% were 60–80° and 86% were 80–100°). Most preening perches were 1–10 m up, and few (10% of 129 records) were below 1 m. Perches 5–15 cm in diameter were used more often (42% of 121 preening records) than in foraging, while perches under 5 cm diameter were seldom used (8% of 121 records). Probably slender, low, and overhanging perches were used in foraging more than in preening because prey could be captured from them, while larger, higher, and subvertical perches were used in preening because they were safer and conserved effort. Birds preened in the open forest understory, and did not go to dense cover first.

The head, whether ruffed or not, was scratched over the wing (16 records). Once a bird wiped its head on a tree trunk. Resting birds clung close to the trunk, and body feathers were fluffed over the corners of the wing (Fig. 2B). After preening or resting, stretching motions were much as in other birds. When bathing in a cavity, one bird was seen to flutter, hitch upward to preen nearby, and then back down into the cavity to bathe some more. Another bird flattened out and “sunned” briefly when it hitched into sunlight on a tree limb. Normally these woodcreepers remained in the shade. Even so, they sometimes kept their beaks

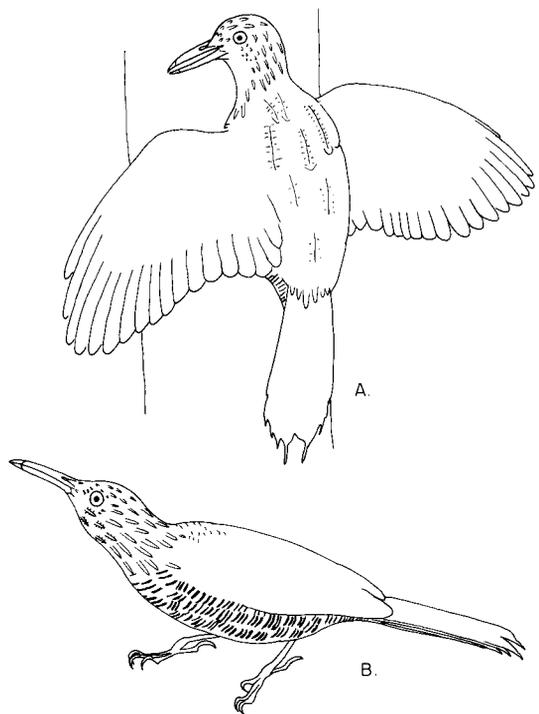


FIGURE 4. Young Black-banded Woodcreepers, from field sketches. A. Fluttering while begging from parent. B. Standing on the ground.

open in hot weather. In rain, an immature bird hitched up under a dead *Cecropia* leaf caught in a tree fork and clung close under it with head retracted, remaining for many minutes, until the rain ended.

One bird was seen to cough up fragments of insect exoskeletons. Excreta were ejected forcefully outward and backward as the tail was lifted well off the trunk for a fraction of a second (Fig. 2C). When army ants attacked them, these woodcreepers jittered back and forth from one leg to the other, pecked ants off their toes, or fled.

*Molt.* Remiges were molted from the innermost primary (no. 1) outward and rectrices were molted from the innermost pair outward. Wing molt in Central America took about five months, with birds starting molt noted from June to mid-July and ones ending molt from mid-October to mid-December. At Reserva Ducke, one presumed male molted two primaries in just over a month, and was in the middle of wing molt in mid-November. His mate was not so advanced in molt, for primary no. 3 was new on each side in early November (she was still feeding their grown young at this time). Another bird was ending molt in early February. Molt apparently followed breeding and was later than in Central America.

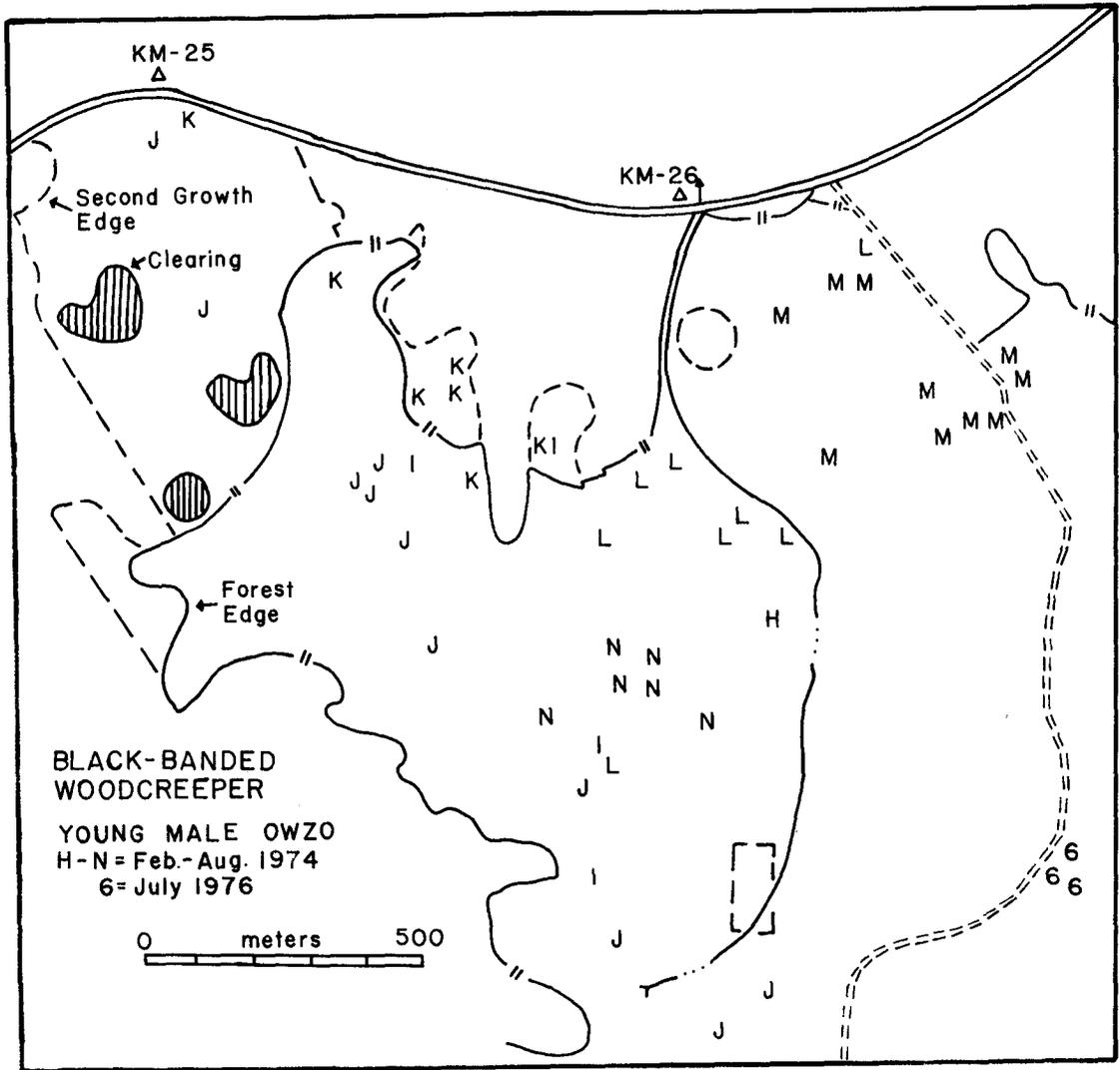


FIGURE 5. Wandering of an independent Black-banded Woodcreeper at Reserva Ducke. Kilometer posts along the highway from Manaus to Itacoatiara are indicated by triangles; a side road is indicated by a double dotted line; a stream is indicated by a line interrupted by dots.

*Temperatures.* Cloacal temperatures, not counting one bird at 41.9°C, varied from 43.0–44.0°C ( $\bar{x}$  = 43.3,  $n$  = 13).

**SPATIAL BEHAVIOR**

In the Amazon region, Black-banded Woodcreepers principally occupied upland forest and forest edge, where they ranged from large limbs near the canopy down to the ground—the last mainly when following army ants. At Manaus, they regularly wandered from the forest into plantations, orchards, and tall or even semi-open second growth. In northern Venezuela, I saw individuals (captured by J. Terborgh) in dense thorn woodland of the northern side of Rancho Grande National Park, and Paul Schwartz (pers. comm.) found them in tree-shaded coastal cocoa plantation and montane

forests as well. In Central America, habitats range from bromeliad-crowded montane forests to semi-open pine-oak woodlands (Land 1970).

At Manaus, pairs occupied different, somewhat overlapping areas that seemed to be territories (see Competitive Behavior, Intraspecific). In the best-studied pair (Fig. 6), the male, female, or both birds occasionally wandered well into the territories of other pairs for a few days when following an ant colony, but deserted the colonies after the local pairs moved in. The young bird wandered with the presumed female for several months, then wandered irregularly around the parental area. Other presumed immatures (Fig. 5) moved through the territories of settled pairs. One wandering presumed male gained a mate in

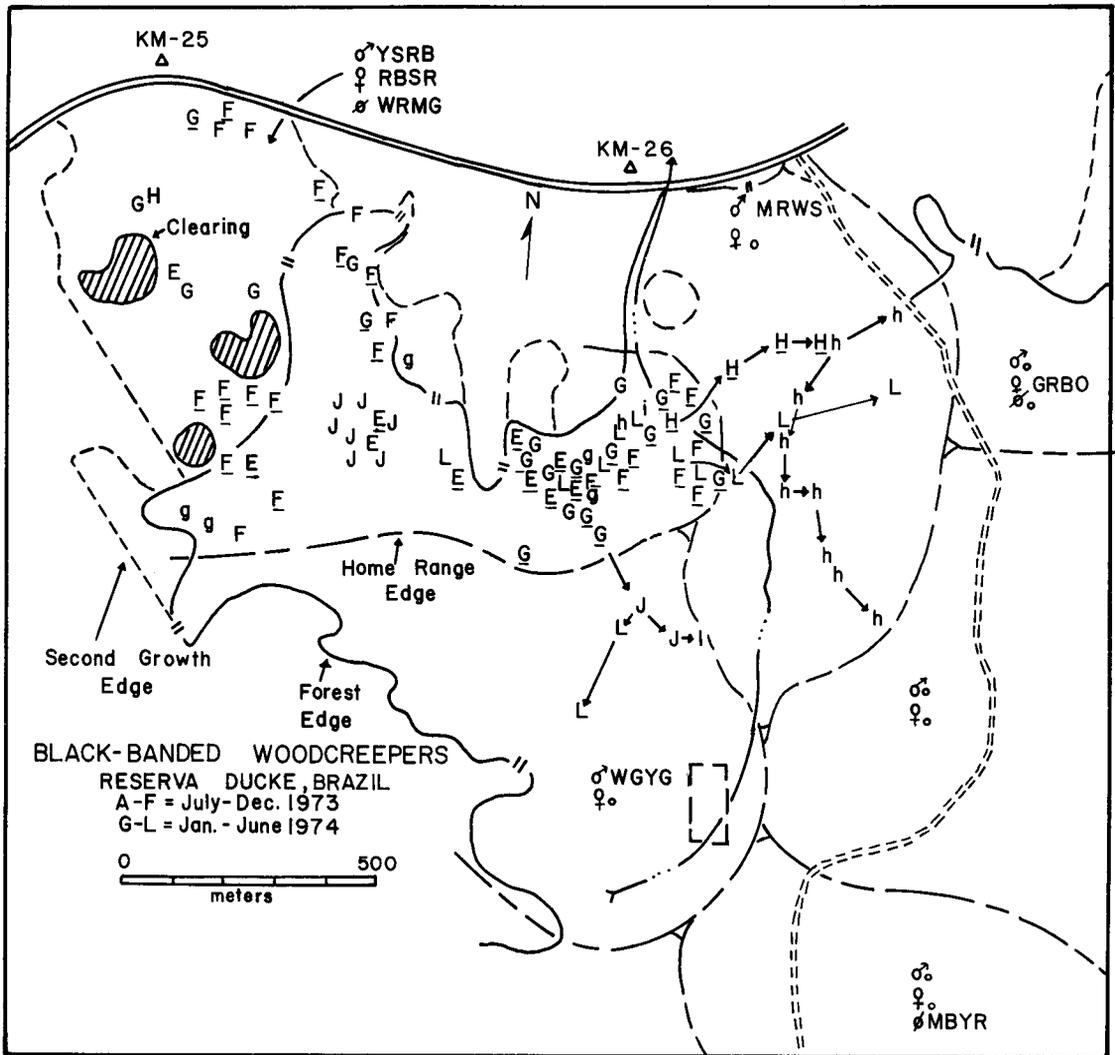


FIGURE 6. Home area of a pair of Black-banded Woodcreepers near Reserva Ducke, and early wandering of their young bird. Upper-case letters are records of a parent bird or pair; underlined letters indicate young and old bird(s); lower-case letters indicate records of the young bird alone. Approximate areas of neighboring pairs are indicated by "home range edge" lines.

June 1974 and became settled; it was noted singing on several occasions in June and July. Densities were low, being about five settled males, five settled females, and four wandering birds on 2.8 km<sup>2</sup> of study area, or some 4 g/ha, in May of 1974. Densities had been somewhat higher in July to November 1973, when several young birds were also present—over one per km<sup>2</sup>. Wandering birds were less numerous at that time, however, being about one bird/km<sup>2</sup>. I rarely found more than three Black-banded Woodcreepers at a single swarm of ants (Table 5).

#### BEHAVIOR OF RELATED SPECIES

Hoffmanns' Woodcreeper, a Brazilian species studied briefly at Maloquinha, Borba, Coatá,

Nova Olinda do Norte and near Tangará da Serra (Willis 1976), behaved like *D. picumnus*. It was usually in floodplain forests or varzeas, but probably occurs in upland forests of the region as well. Both forms of the snarling note of *D. hoffmannsi* were much like those of *D. picumnus*; I did not note other calls. The sneezing form of the call ("wh'kai") was associated with disputes, which the sleek-headed member of a pair always won; the sharp form of the call ("kaihh-jeep") was given in seeming alarm, with wing-twitching and with hitching upward. One sleek-headed bird ruffed the throat but not the crown. Of my 33 records of foraging, one was a sally to the ground, 11 were sallies to palm fronds, 8 to other leaves, 4 each to trunks and lianas, 2 to the air, and 3 to unre-

TABLE 5. Swarms of *Eciton burchelli* ants with given numbers of Black-banded Woodcreepers.

Month	Number of swarms with given number of birds					
	0	1	2	3	4	5
July 1973	3	3	4	7		
August	18	18	16			
September	61	22	7			
October	19	7	17	15		
November	36	12	18	11	4	
December	28	11	9	13	5	
January 1974	25	25	15	11	1	
February	7	15	8	10	2	7
March	11	16	9	9	4	
April	22	25	14	7	1	
May	23	27	9	1		
June	18	6	12	3		
July	40	7	18	5		
August	15	11	7	1		
Total (Sept.–Aug.)	305	202	159	86	17	7

corded sites. Of 12 records of gleaning, 4 were from leaves, 3 from lianas, 2 from trunks, and 1 each from a palm frond, twig, and debris. These woodcreepers competed with several large antbirds near the ground, and foraged near the ground less than did Black-banded Woodcreepers at Manaus. One bird, foraging away from ants at Nova Olinda do Norte stayed 20–30 m up on fairly large limbs. Another, at Coatá, while gliding down over ants and showing the yellowish wing linings, occasionally alarmed White-breasted Antbirds (*Rhegmatorhina hoffmannsi*). Extending the neck, as I saw in one bird that I alarmed (it sleeked its crown after and before ruffling the crown) and another that had supplanted a White-chinned Woodcreeper, may have been aggressive behavior. Hoffmanns' Woodcreeper supplanted or displaced White-chinned, Plain-brown, Elegant (*Xiphorhynchus elegans*), and Barred woodcreepers but fought with or was supplanted by Buff-throated Woodcreepers.

I studied Planalto Woodcreepers briefly near Marabá (Pará), Bacabal and Colinas and Serra Negra (Maranhão), and at many localities in southern Brazil west to central Mato Grosso (180 km W Barra de Garças). The average weight of these birds was 62.1 g in a sample of 14 specimens from northern Argentina. Most songs and snarling notes were like those of Black-banded Woodcreepers (Fig. 1). Regular singing by scattered birds at dawn and dusk revealed that more birds were present than I had suspected. Another song of pairs in Maranhão and São Paulo, a series of “yourit” notes, reminded me of Barred Woodcreepers in Panama. One Planalto Woodcreeper gave grunting “i-i-i” notes as attacked by another, then

snarled; another gave a series of squirrel-like grunts, then started rattling. Planalto Woodcreepers foraged like Black-banded Woodcreepers, but were more often away from army ants. Over ants, they often foraged low, sallying to the ground for prey, for the ant-following birds of most of their range were such small forms as fire-eyes (*Pyriglena* spp.) and tanagers (*Trichothraupis* spp.). I saw them supplanted by Buff-throated Woodcreepers (Marabá, Bacabal), while they supplanted Plain-brown Woodcreepers (Bacabal), Thrushlike Woodcreepers (*Dendrocincla turdina*), fire-eyes, and *Trichothraupis* tanagers. Occasionally, especially when wary of an observer, Planalto Woodcreepers foraged high above the ground. Away from ants, they hitched slowly upward or looked about from medium-sized trunks and limbs from near the forest floor to the sub-canopy, sallied for prey or pecked it from nearby lianas or leaves, and glided to low on other trunks. I watched one visit light poles at the forest reserve headquarters at Carlos Botelho Reserve (near São Miguel Arcanjo, São Paulo State) for insects in the early morning. Others wandered low on the trunks of “cer-rado” (savanna) trees in the early morning both in Maranhão and Minas Gerais (Brejo Januaria). In pairs, one bird ruffed the head while the other was sleek-headed; but birds were generally solitary. They sometimes followed mixed bird flocks, but not persistently.

It is possible that *D. hoffmannsi* and *D. platyrostris* are subspecies of *D. picumnus* (including the yellow-billed and as yet unstudied *D. p. pallescens* and relatives of western Brazil and Bolivia south to Argentina). None of these ecologically and behaviorally similar woodcreepers is likely to be more than marginally sympatric, perhaps in adjacent territories in differing habitats. The culmen and wing of seven museum specimens of *platyrostris* from Maranhão are longer than normal for that species, within the range of variation for *picumnus*. The *platyrostris* that I observed at Marabá and in Maranhão had pale-tipped bills, like *picumnus* rather than like dark-billed southern *platyrostris*. It is possible that *D. picumnus transfasciatus*, found from the Tapajoz River east to the Xingú River and close to Marabá, is more closely related to *platyrostris* than to *D. p. picumnus* north across the Amazon River.

## DISCUSSION

While only one species of large woodcreeper follows army ants in most neotropical regions, three large species do so over much of the central Amazonian region. At Manaus, these

species subdivided their niche of "large ant-following woodcreeper" by dominance: Red-billed chased Black-banded, which chased Barred woodcreepers. Black-banded Woodcreepers foraged low over ants less than did Red-billed Woodcreepers, but more than did Barred Woodcreepers. Causal relationships are not certain, for the last species differed little in behavior between Manaus and Belem (Willis, unpubl.), even though the other two did not occur at Belem.

In behavior, *D. picumnus* differs little from its closest relatives. It nevertheless conforms to the general prediction (based on ant-following antbirds) that, because social groups attract attention, subordinate ant-following species should be less social than dominant ones. Young *D. picumnus* stay with their parents three to four months, longer than subordinate *D. certhia* stay with parents but a shorter time than do domineering *H. perrotii* (Willis, unpubl.).

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