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DIVERSITY IN ADVERSITY:
THE BEHAVIORS OF TWO SUBORDINATE ANTBIRDS

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ABSTRACT

The main subordinate ant-following antbirds south of the eastern Amazon (White-backed Fire-Eyes, Pyriglena leuconota) *and north of the eastern Amazon (White-plumed Antbirds,* Pithys albifrons) *differ in many behavioral aspects despite their similar niches. They and other subordinate ant-followers studied previously are more diverse in behavior than are the dominant antbirds of the same guilds.*

The main foraging adaptation of White-plumeds is rapid flying, infiltrating among larger antbirds by being nonsocial and speedy. The main foraging adaptation of Fire-Eyes is rapid hopping around the periphery of dominant birds. Flying is most useful between vertical perches low inside forests, where White-plumeds are common; hopping is most useful where horizontal vines and twigs occur near the ground, as in the second-growth, swampy or dry forests where Fire-Eyes are common. White-plumeds therefore forage near the centers of forest swarms, darting to the ground for prey and fleeing instantly to escape attacks of dominant birds. Fire-Eyes forage more diversely, capturing food on the ground or on foliage, either high or peripherally, around woodland swarms. Fire-Eyes also forage away from ants whenever colonies are inactive.

Voice and aggressive behaviors are minimal in White-plumeds, probably so as to be inconspicuous when infiltrating among larger birds; the facial plumes may signal to other White-plumeds instead. Individuals wander widely between ant swarms and show little sign of territoriality, probably because their small foraging niches at a given ant swarm are easily closed off by dominant birds. Fire-Eyes are very vocal and aggressive, and pairs maintain dominance in their territories even though trespassing individuals are grudgingly permitted to stay. Probably the necessity of foraging away from ants makes it advantageous for Fire-Eyes to retain territories in which other foragers will not reduce food supplies irregularly. Territories plus relative safety from dominant birds at swarm margins favor aggressive behavior, in retaining foraging sites.

Both White-plumeds and Fire-Eyes, like the subordinate antbirds previously studied, have little intraspecific submissive behavior. Poor etiquette may be characteristic of subordinate species because they cannot associate in family groups without attracting dominant birds, and hence have little kin selection for intraspecific appeasement behavior.

Tendencies for subordinate antbirds to seldom use "keening" alarm calls may also result from lack of kin selection. When a subordinate species emphasizes chipping alarm to hawks or mobbing to mammals, it may be gaining in individual selection by scaring dominant competitors or by disturbing the possible predators. Fire-Eyes do not mob mammals as much as do most subordinate antbirds, perhaps because mammals are too dangerous in the cluttered undergrowth where Fire-Eyes normally live.

Courtship in subordinate antbirds depends less on courtship feeding of females and more on mutual grooming and special displays than in dominant antbirds, which probably get food for females more easily. An unusual wingwaving-zeesinging display in White-plumeds may be sexual, as may be a draping display in Fire-Eyes. Hypertrophy of courtship patterns may occur because pair bonds are somewhat unstable in Fire-Eyes and very unstable in White-plumeds. Fire-Eye pairs stayed together except when foraging at ant swarms, but separated readily when their woodland territories were cut. White-plumed pairs stayed together only for brief nestings, and females left males feeding single young to move quickly to new males for new nestings.

Because they show high divorce rates or repeat nestings throughout most of the year, Fire-Eyes and White-plumeds are relatively "r-selected" for high reproductive rates. The Spotted Antbirds previously studied, however, have undergone a demographic transition to short (6-month) breeding seasons despite subordinate sta-

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tus. Apparently long breeding seasons are linked with high adult mortality rates in wandering Fire-Eyes and White-plumeds, short seasons with low adult mortality rates in territorial Spotteds. Nest-success rates are low (10%) for Spotteds, moderate (20%) for Fire-Eyes, and higher in White-plumeds. It may thus be unusually expensive for Spotted Antbirds to rear young, contributing to deemphasis of repeated breeding as a path to genetic survival.

Sexual dimorphism is the rule in subordinate ant-following antbirds, perhaps because individuals forage far apart at swarm borders and females need not bluff males. Females may, by adopting dull plumage, reduce likelihood of male attack if birds are widely separated and attack therefore expensive. Relative lack of dimorphism in White-plumeds, as in most centrally foraging dominant antbirds, may be linked with tendencies to crowd together between dominant antbirds and hence greater female need or success in bluffing the relatively unaggressive males. Reduced dimorphism in some subspecies of Fire-Eyes may be linked with their tendencies to forage close together in certain environments.

Fire-Eyes have subspeciated repeatedly, while White-plumeds and Spotteds tend to show speciation instead. Attaining speciation may indicate more rapid evolution than does subspeciation, and seems associated with high-diversity habitats like the rain forest. Taxon flow of rapidly evolving forms from high-diversity habitats replaces species in lower-diversity habitats. Diverse form and behavior evolve in subordinate ant followers despite competitive adversity rather than because of it. Moderate diversity of opportunity, not the negative factors of competition or extreme diversity, seem to explain high rates of diversification.

INTRODUCTION

Natural diversity of form and behavior has long invited explanation, even before Darwin asked why species diverge. Evolutionary theory now suggests two causes: before or after reproductive isolation, mutations and selection pressures differ for different groups of individuals. In particular, it has repeatedly been suggested that competition between different forms is one pressure that produces differences: "competitive exclusion" will occur, or "ecological isolation," or "character displacement."

Competitive divergence has proved controversial, in part because it has rarely been proved that competition between two forms leads to more change than would occur for such other pressures as those for reproductive isolation. Grant (1975), reexamining a supposed case of character displacement between two species of nuthatches, found that differences said to be due to competition also occur in nearby regions where the two do not occur together. He concluded that factors other than competition between the two must explain their divergence. I have repeatedly shown (Willis, 1966, 1968a, 1972a) that direct competition leads to differences in foraging behavior in some birds that follow army ants. Competition can lead to evolution in certain cases.

A more serious criticism of the idea of competitive divergence is that it may occur only under certain conditions, which have to be delimited. Cody (1969) suggested that competition can lead to convergence, or "competitive mimicry" (Willis, 1976a), if a species reduces the territories of another by imitating it. Competition may also stop evolution ("stabilizing selection") or reduce diversity by elimination of forms. How can one determine the conditions under which competition favors diversity instead of convergence or stagnation?

Theoretically, one could look at forms occupying similar niches in the same region to see if certain degrees of competition (o any other axis of interest) produce divergence or not. In practice, one expects divergenc and thus rarely finds many forms occupying a given niche in one region. An alternative method is to look at forms occupying similar niches in several regions. One expects convergence, so that persistence or appearance of divergence is positive or direct evidence that the given level of the factor under consideration encourages evolutionary diversity. To reduce differences due to past history, it is best to have forms that are closely related; and if one wants to explore the competitive axis of divergence, he needs a range of competitive conditions with little change in other conditions.

These two requirements are reasonably well met by certain antbirds (Formicariidae) that follow army ants in tropical American forests (Willis and Oniki, 1978). Most of these antbirds are closely related; there are intermediate forms between genera and many questions about generic limits; hereditary reasons for diversity are minimal. Foraging reasons for diversity are also minimal: there are one important species of army ant, *Eciton burchelli,* and one less important one, *Labidus praedator,* from Mexico to Argentina. In all regions, overall behavior patterns vary little among the ants or among the birds that follow them to capture flushed prey. However, the Andes and major rivers of the Amazon basin separate different guilds of ant-following birds, so that one gets new competitive groups over the ants only a few kilometers apart. Each such guild occurs for hundreds or thousands of kilometers between rivers, reducing the possibility that conditions outside the guild (such as local weather, trees, or predators) are significant.

A range of competitive conditions occurs in each such ant-following guild (Willis, 1972a). There are dominant antbirds, which are just large enough to supplant other species, occupying the central and best zones over the ants. Subdominant antbirds and subordinate antbirds occupy successively more peripheral zones or rings about the swarm centers. It is thus possible to see if subordinate antbirds are more or less likely to be diverse than are subdominant or dominant ones, and hence to map one set of competitive conditions against diversity of morphology or behavior. For instance, I have found that dominant ant-following antbirds (Willis, 1973a, 1979) and a similarly foraging woodcreeper (Willis, 1979) converge rather than diverge in behavior. This paper compares the behavior of a subordinate Panamanian antbird studied earlier (Willis, 1972a) with the behaviors of subordinate White-backed Fire-Eyes *(Pyriglena leuconota)* south of the eastern Amazon River and of similarly subordinate White-plumed Antbirds *(Pithys albifrons)* north of the eastern Amazon. The question asked is: does the moderate competitive adversity faced by these interspecifically subordinate birds result in diversity of behavior?

THE BEHAVIOR OF WHITE-BACKED FIRE-EYES

Locally, among the commonest subordinate birds of ant-following guilds in southern South America are three species of red-eyed antbirds in the genus *Pyriglena:* the White-shouldered Fire-Eye *(P. leucoptera)* of northern Argentina north through Paraguay to Bahia in Brazil; the Fringe-backed Fire-Eye *(P. atra)* of central Bahia; and the White-backed Fire-Eye *(P. leuconota),* which occurs as isolated or semi-isolated populations from eastern Brazil across to the lower Amazon, thence southwest into Bolivia and northwest along the Andes to the coast of Ecuador and the Andes of Colombia. Some consider the three forms to be one species (Zimmer 1931); here I follow Meyer de Schauensee (1970). Males of *leuconota,* the species considered here, are black with concealed white back patches; females have concealed white back patches but vary in different regions from brown to black with brown mantles.

Study areas

I first encountered White-backed Fire-Eyes *(P. l. castanoptera)* following army ants in subtropical forests and woodlands at Paraiso (800-1100 m elevation, Caquetá) and San Agustín (1650 m elevation, Huila) in Colombia in April, 1962. In January, 1966, I briefly studied the subspecies *similis* in dry woodlands at Diamantina and Palhão near Santarém (Pará), Brazil. In August, 1967, I encountered the subspecies *leuconota* in forests and woodlands at Belém (Pará). Oniki (1972) studied it and other ant-following species at Belém from 1966 to 1968. I returned to Belém from 28 March 1972 to 26 May 1973, 28 September to 13 October 1974, and 3 to 4 August 1976 for extended studies of the subspecies. I encountered it in dry woodlands at Bacabal, Colinas and Fazenda Serra Negra in Maranhão in October, 1974, and the subspecies *interposita* at Marabá, Pará, in September, 1974. In July, 1975, I found the subspecies *maura* with army ants in sandy woodlands 40 km NW of Tangará da Serra, Mato Grosso (Willis, 1976b).

Novaes (1979), Oniki (1972), and Lovejoy (1974) describe the Belém study areas. The main study tract is the Aurá forest reserve, part of the "Area de Pesquisas Ecológicas do Guamá" (APEG) on the grounds of the Instituto de Pesquisa Agropecuária do Norte (IPEAN) at the edge of the city. The southern part of the Aurá reserve is "várzea", forest partially flooded twice a day by tides that run up ramifying channels from the Aurá River (a small branch of the lower Rio Guamá). With the highest tides of the year, flooding of nearly the whole zone can force ants and birds to climb in the vegetation. However, the flooding does deposit thin layers of sediment that make the zone highly productive. At the edge of the várzea are narrow zones of swamp forest of "igapó", flooded only by rain water or by streams coming out of the upland or "terra firme" forest. The upland forest in on flot or slightly dissected ground only a few meters above sea level, and has been extensively modified by removal of trees. Presently, it forms only a narrow band between the várzea or igapó and second growth ("capoeiras") of various ages. West of the reserve are pastures for water buffalo, and north beyond the capoeiras are pastures or plantations of rubber trees. Eastward, várzea forests are fairly continuous along the Guamá River.

Near the river, trails to marked rubber trees *(Hevea brasiliensis)* and extensive areas with cacao undergrowth *(Theobroma cacao)* hint at earlier use of the várzea. The açaí *(Euterpe oleracea)* palms common in the zone are still the object of fruit collection and,recently, cutting for palm hearts.

These and many other human activities (such as extensive collecting of birds in the area prior to 1967, bleeding of birds for arbovirus studies in parts of the area until 1972, and cutting of trails and placement of boardwalks and location stakes in parts of the area) seemed to have little effect on Fire-Eyes during my study. Two other scientific projects did cause important problems during the study.

At the north edge of the reserve, rubber plantations had grown up to second growth and were being used by Fire-Eyes and army ants when, in September 1972, agronomists decided to cut the undergrowth. The exodus and population shifts of Fire-Eyes are detailed below. A second source of disturbance was that workers on arboviruses regularly killed army ant colonies that entered their cabin just inside the entrance of the Aurá Reserve. This created a local ecological vacuum that led to proliferation of colonies of carpenter ants *(Camponotus* sp.*)* and to absence from the central Aurá Reserve of Fire-Eyes, which incidentally carry arboviruses. This disturbance also forced me to work mainly in three study areas on the south (I), northeast (II), and northwest (III) sides of the Reserve, rather than in the "Station A" central zone worked by Oniki (1972) and Lovejoy (1974) in their earlier studies of this and other species. Area I, my várzea area, corresponds to the várzea worked by both earlier workers; Area II, mostly in terra firme and capoeira, lies just northeast of Station A; and Area III, the rubber plantations cut over during my work, lies just northwest of Station A.

Methods of study

I observed behavior of Fire-Eyes from behind swarms of army ants with 8 x 30 or 10 x 50 binoculars. Birds accustomed to the observer become fairly tame and show relatively consistent behavior patterns, which were recorded in a notebook. At Belém, 114 individuals were color banded after capture in mist nets set ahead of ants. Some of the same birds had been banded in 1966-72 by Oniki or Lovejoy. Cloacal temperatures were taken with a Schultheis thermometer, weights with Pesola Scales. Recordings were made with a Uher 4000-Report S at tape speeds of 19 cm/sec; sound spectrographs were made with a Sona-Graph at the American Museum of Natural History. Color pictures, with Takumar 200 mm f 3.5 lens, required electronic flash units because of poor light in the forest. Birds were filmed with a Beaulieu R-16 movie camera and Angienieux 12-120 lens.

Maps are based on aerial photographs and maps at IPEAN.

Weights and temperatures

Weights of 41 adult males at Belém averaged 35.4 g (range 31.6-39.4 g), while 19 young males still following their parents averaged 32.7 g (30.0-35.8 g). Thirty adult females averaged 32.9 g (28.7-36.2 g), and 12 young females averaged 31.4 g (29.4-33.6 g). These were mostly well-fed birds caught in the late morning or early afternoon near swarms of army ants; birds caught away from ants, in the early morning, or held in sacks for some time before weighing (Oniki 1974) generally weigh less.

Cloacal temperatures of 61 birds ranged from 40.4°C to 44.1°C and averaged 42.7°C. Averages ranged from 42.9°C for 30 adult males to 42.4°C for 4 young females.

Molt

Even near the equator at Belém, Fire-Eyes have a fairly distinct molt season. Of 139 seemingly adult birds captured or recaptured in the field, 89 showed wing molt. Between March and July, 73 of 96 showed molt, but in November and December only 5 of 21. Two of these 5 were birds with dull plumages and dark eyes, perhaps birds of the year molting out of season.

A few nesting females and males did not start wing molt until April and May. They thus avoided molting when they had young birds in the nest.

Of 312 museum specimens from the region of Belém (east to Maranhão, west to the Xingu River, and south to Araguatins, Goiás), at least 136 were in wing molt. February to September were the main months of molt, but only in June and July were the majority of birds in molt (35 of 46 specimens). November to January birds were seldom in molt (13 of 58), and several of these were perhaps young birds molting out of the dull juvenal plumage.

Other populations near the equator also molt mainly from March to August. Of 43 specimens of eastern *P. l. pernambucensis,* 8 were starting molt in February and March and 2 ending molt in September. No others were in molt, but none were collected from April to August. In the central Amazon, between the Xingu and Tapajós rivers, 19 of 49 *P. l. similis* were in wing molt, including 12 of 19 collected July to September. From the Andes of northern Peru to Colombia, molt of *P. l. castanoptera* was noted in 16 of 34 May to September specimens but in only 8 of 29 November to April birds. In western Ecuador, 13 of 19 May-August specimens of *P.l. pacifica* were in wing molt, but only 2 of 21 specimens taken September to March.

Races farther south molt successively earlier in the year, as Snow (1976) noted for Cotingidae. In the central Peruvian Andes, 7 of 10 March-May specimens of *P. l. picea* were in molt but only 1 of the 8 other specimens, taken July to December. In the southern Peruvian Andes, one February and one March specimens of *P. l. marcapatensis* were in wing molt, but none of the 16 taken May to October. In the Bolivian Andes, 10 of 18 *P. l. hellmayri* taken December to May were in molt, but only 3 of 67 June to November birds. From lowland Bolivia into western Mato Grosso, 12 of 23 December to May *P. l. maura* were in molt, but only one June and one November birds of 28 specimens taken the rest of the year. Farther south, *Pyriglena leucoptera* is in molt mainly November to April, except for a few birds from Bahia in molt in June. Collectors obviously avoided the rainy and hot summer months, when southern-hemisphere birds are generally in molt; only 177 of 493 *leucoptera* specimens were taken October to April, while *maura and hellmayri* collections peak May to October.

Some of the birds trapped at Belém were retrapped later in their molt cycles. Adult individuals molted about two primaries per month, indicating a duration of four to five months for completion of primary molt (starting with primary number 1 near the wrist and finishing at number 10 at the tip of each wing). Some males, known to be wandering birds low in peck orders, molted much more slowly, at times less than one primary per month. These males all started with dull eyes and dull plumages, and presumably were first-year birds.

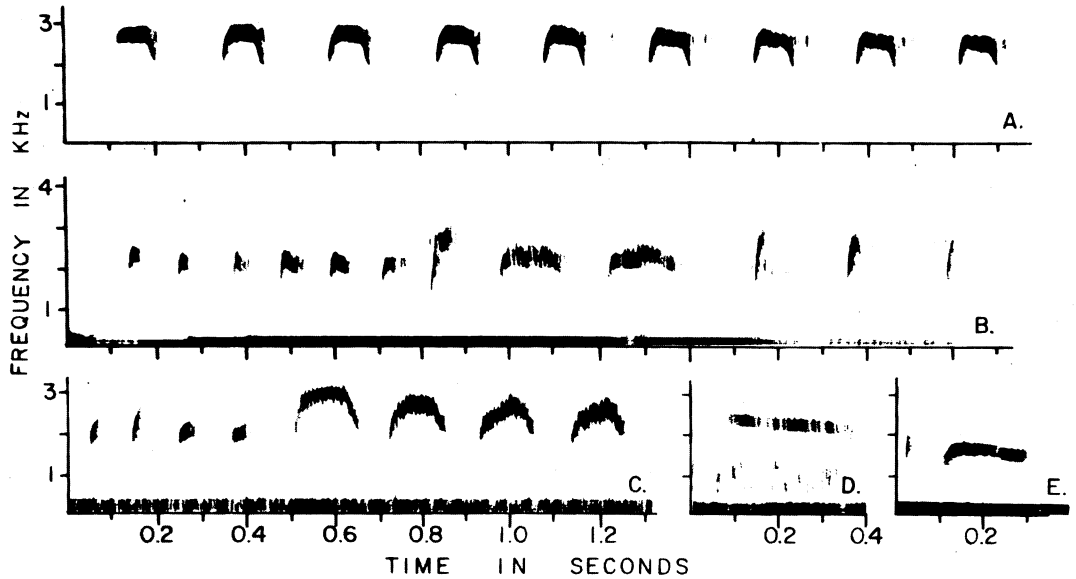

Figure 1. Sound spectrograms of calls of White-backed Fire-Eyes. A. Loudsong B. Serpentine or bubble song C. Bubblesong D. Keening E. Grunt and "eu", perhaps form of booing.

Zimmer (1931) erred in reporting a separate "1st annual" plumage in Fire-Eyes; specimens he attributes to this plumage are birds that were finishing the postjuvenal molt and starting to lose juvenal tail and wing feathers. His suggestion that the juvenal female resembles the juvenal male is also incorrect, as reexamination of his specimens indicates differing plumages. Young *P. leucoptera* of southern Brazil do molt into the adult plumage shortly after leaving the nest, their first fall; therefore they do not retain the dull juvenal plumages as long as do young *P. leuconota.* This difference between species could have led Zimmer to err.

Voice

White-backed Fire-Eyes have 16 or more distinct calls and songs. Fire-Eye calls that seem similar to those of Bicolored Antbirds (Willis, 1967) or of Chestnut-backed Antbirds (Willis and Oniki, 1972) are here given the same names as for those species. Faint chirps are also heard at times but are not listed because it is difficult to establish that they are not forms of bubbling.

Songs. As in Bicolored Antbirds, there are loud-songs, faint-songs, and serpentine-songs. The loud-song of Fire-Eyes is a descending series of several loud and clear "Peef" notes (Fig. 1A). The notes are given about 4.6 times per second in Belém, but at a faster rate at Marabá and in Mato Grosso. The songs are used mostly in agonistic behavior and are given with tail and head-pumping movements. Faint-songs are weak descending series of four or so "wheef" notes (Fig. 1C), given as birds wander near each other. I rarely noted songs intermediate between the two extremes. Serpentine-songs are series of faint-songs punctuated by chirping or bubbling notes and used when calling for young or mates (Fig. 1B). One common type, the "bubblesong", is a series of bubbling notes followed by a faint-song (Fig. 1C).

Screaming. A bird in the hand gives squalling rasps or "wah" noises.

Keening. At distant danger, Fire-Eyes freeze and give a thin, faint "tooooh" or "teeeeee" (Fig. 1D).

Rattling. Toward humans or in alarm, Fire-Eyes give a loud rattle (Fig. 2A), "di-i-i-i-i-i-ih!" The call may be homologous to chirring in Bicolored Antbirds, but unlike it is much slower and does not resemble the growl of a carnivore.

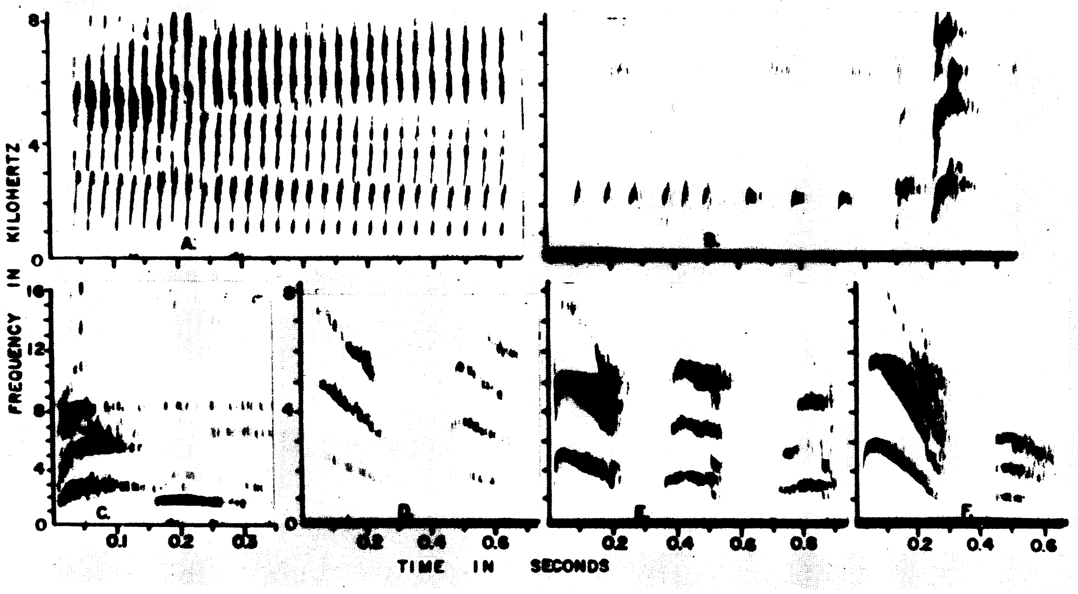

Figure 2. Sound spectrograms of calls of White-backed Fire-Eyes. A. Rattle B. Bubbling and chip C. Chip-boo D. Double boo E. Triple boo F. Double boo.

Chipping. In fights, when supplanted, or in alarm, a sharp "wheek!" or "peet!" is often heard (Fig. 2B, C). A faint version, "preet", seems intermediate between chipping and bubbling (Fig. 3C).

Booing and chip-booing. In circling disputes or while traveling, a loud chip followed by one or more loud and low-pitched "boo" notes (Fig. 2C) is often heard: "peet-boo". A single or double (rarely triple or quadruple) "boo" occurs in disputes (recorded as "groo" in my field notes, possibly a different call) but more commonly in alarm situations (Fig. 1E, 2D, E, F). The first boo of a double to quadruple-boo generally differs in pitch from the others: "pew-boo". At times the boo seems to resemble a loud form of keening, at other times it becomes a guttural growl (Fig. 3B). Double to quadruple booing or chip-booing is absent from *Pyriglena leucoptera* and rare in *P. atra*.

Snapping and puffing. Supplantings are usually silent, but at times the attacking bird snaps the beak or one bird (attacked?) gives a brief sound much like screaming.

Bugling. In fights, there is sometimes a short and rattly buzz or snarl (Fig. 3A), "garrr!", somewhat like the bugling of antbirds of the genus *Rhegmatorhina* (Willis, 1969).

Grattling. Females chased viciously by males give guttural rattles, "gra-a-a-a-a-a-ah!". At times a male or female gives a guttural growl to an antagonist, "raah", rather like the last note of some double-boos (Fig. 3B) or like the growling of a female accepting food from a male (see below).

Bubbling (or grunting). A faint "prit", like a soap bubble breaking, is common when birds forage near each other or when tame birds pass the observer (Fig. 3E). Often there is a rapid series of bubbles or chirps, "rapid-bubbling", sometimes followed by a faintsong as a "bubblesong". The sound is used much as "grunting" is in Bicolored Antbirds (Willis, 1967).

Whimpering. In the hand or when threatened by a Fire-Eye higher in the peck order, males sometimes give a faint high "pee-pee-pee-pee".

Chirping. A male dropping to his belly before a female or showing a possible nest site gives a fast series of faint "ē" notes (Fig.

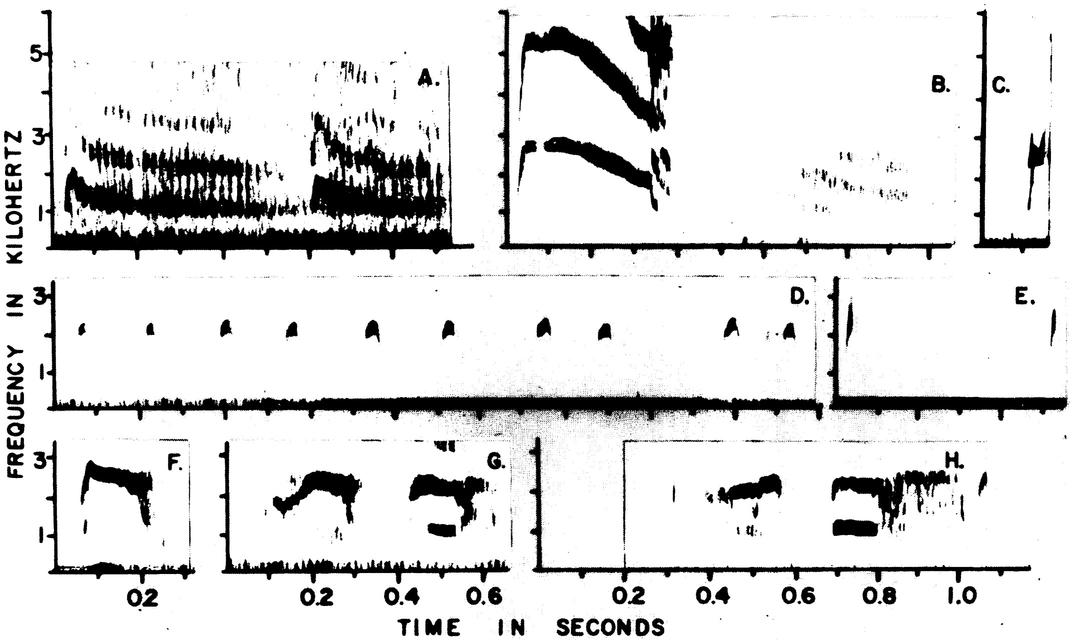

Figure 3. Sound spectrograms of calls of White-backed Fire-Eyes A. Bugling B. Boo-growl C. Preet note D. Chirping E. Bubbling or grunting F, G, H. Peeping.

3D). Similar notes are given in some serpentine-songs by males and females.

Growling. Faint rasping noises, "scahhh" or the like, sometimes come from a female accepting food from a male or approached by a male. At times, however, both birds rapidly bubble or are silent during feedings. This sound and the probably related grattling were not heard from males, except for a growl of indeterminate nature.

Peeping. Young birds out of the nest give faint or moderately loud single to multiple peeps, "pew" or "pe-her (-her)", every 3-5 seconds as they follow their parents (Fig. 3F, G, H).

Squeaking. Young hiss roughly several times when fed, "chiahhh" or the like.

Basic postures and movements

The basic or "standard" posture for White-backed Fire-Eyes of the Belém subspecies is much as in Fig. 4A or D. The fairly long tail points in much the same direction as the body, at about 20°from the horizontal, and is closed at times to the extent of being slightly notched. The bill and head are more or less horizontal. The bird stands high on long legs. The wings are closed, the wrists not exposed. A white triangle shows on the back in this subspecies but not in the subspecies *similis* or *castanoptera.* Much of the white area is hidden in the standard posture even in Belém birds.

Fire-Eyes cling to slender vertical perches much as do other ant-following antbirds; the lower leg is extended, the upper one flexed. The upper toe of the lower foot (toe II) is held apart from the others and nearly horizontal, while toes III and IV remain together and point obliquely in much the same direction as the lower leg.

Fire-Eyes perch rather briefly compared with other ant-following antbirds; instead, they hop or bound about constantly. They are very good at bouncing along fallen lianas or through dense tangles, common in the second-growth or somewhat open dry-forest habitats favored by the species whenever competing antbirds are present. At times, one hops to the ground in traveling between vertical saplings, rather than flying di-

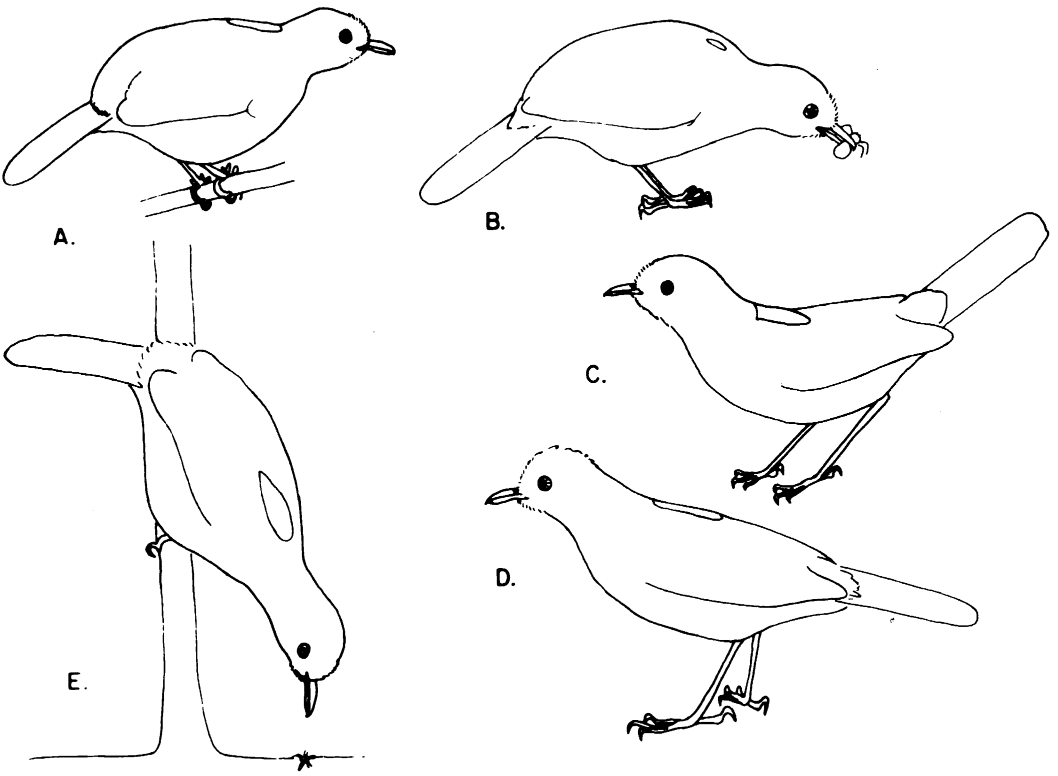

Figure 4. Foraging postures of White-backed Fire-Eyes. A. On horizontal perch B. Eating on ground C, D. Waiting on ground E. Gleaning from vertical perch.

rectly from one to the other. Hopping is the major foraging adaptation of the species.

The tail is often raised as Fire-Eyes hop about, and at the slightest excitement is "pounded" rapidly downward. The return movement is less rapid, seemingly a passive return rather than an active movement. They thus belong to the genera of hop-foraging antbirds *(Percnostola, Myrmoborus, Myrmeciza, Rhopornis)* that "pound" the tail rather than to the group of stand-foraging genera *(Gymnopithys, Rhegmatorhina, Hylophylax, Phaenostictus, Phlegopsis, Skutchia, Pithys,* and even *Thamnophilus* and some *Myrmotherula* and *Myrmeciza)* that drop the tail slowly and "flick" it upward rapidly. (The *Myrmeciza* in the last group perhaps belong in other genera.)

Flights are usually short and fluttery, rounded wings beating rapidly. The birds move at less than 3 m above the ground most of the time and take advantage of every tangle enroute to hop on low perches rather than fly long distances. Vertical perches are rarely used enroute. Small rivers and roads are crossed easily, but wide open areas are avoided.

Alarm behavior

As in previous studies of antbirds (Willis, 1973a, 1979), I divide behavior into six units: alarm behavior to large negative factors; maintenance behavior to small negative ones; foraging behavior to small positive factors; agonistic behavior to medium sized negative ones; reproductive and social behavior to medium-sized positive factors; and spatial behavior to large positive ones. Words in common use for these behaviors in ecological publications are predation, pollution, growth, competition, reproduction, and dispersal.

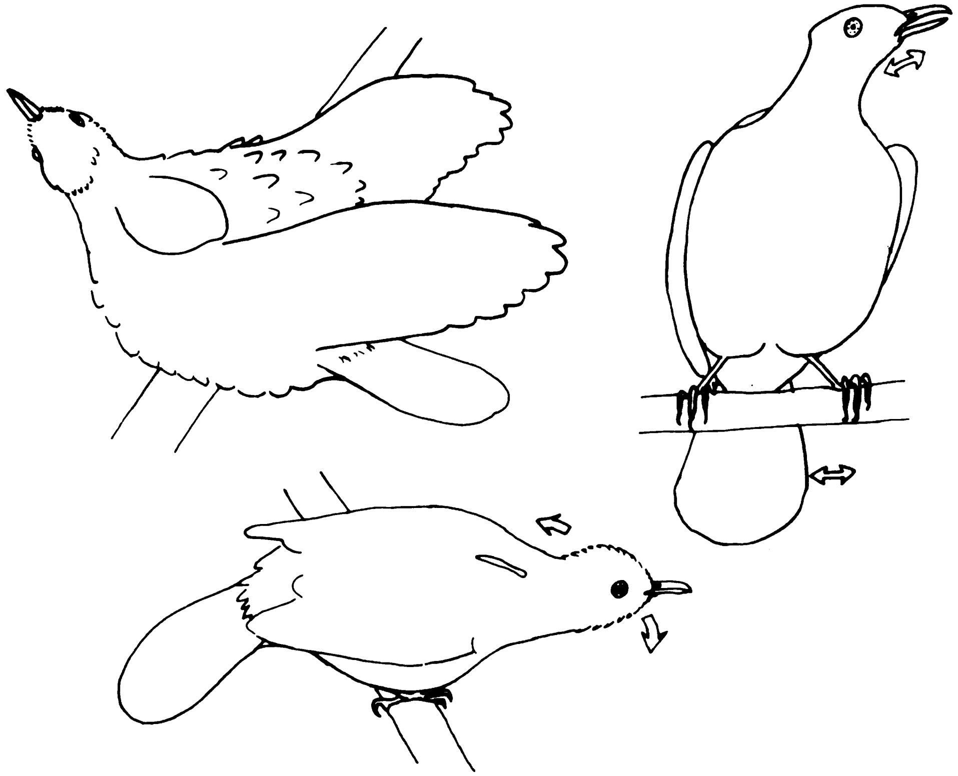

Figure 5. White-backed Fire-Eye postures. Above left, sunning. Above right, loudsinging. Below, alarm.

Alarm behavior in Fire-Eyes is rather like that in antbirds previously studied: freezing and keening to distant danger, various types of panicking and chipping or booing to closer danger, and mobbing with rattling to humans. Taming (habituation) is, as in other animals, a loss of alarm behavior.

Freezing and keening. At distant alarm calls of other birds or the appearance of hawklike objects, Fire-Eyes freeze or crouch immobile; they sometimes keen as well. Ducking the head, or extending it while the neck is flexed toward the body, is common. The tail often closes as do the legs and the wings. At times the bird looks up or around (Fig. 5). In one instance when an *Accipiter bicolor* attacked a group of birds near a stream bank and then waited nearby for a few minutes, one Fire-Eye remained frozen without any head movement in a bush below the lip of the bank. It resumed movement only after other birds started alarm calls, a minute after the hawk left. When the hawk attacked, none of the birds present called; all dashed for cover and froze.

Keening was recorded as a response to alarm calls of birds *(Dendrocincla fuliginosa,* 28 times; chipping of Fire-Eyes, 4; *Monasa morphoeus,* 1; *Formicarius analis, 1; Attila spadiceus,* 1; *Ramphocaenus melanurus,* 1; unidentified species, 2), to sightings of distant hawks *(Leptodon cayanensis, 2; Leucopternis schistacea,* 1; *Micrastur semitorquatus,* 1) or flying birds *(Ramphastos* sp., 3; *Coragyps atratus,* 1; *Geotrygon montana,* 1; small bird, 1; unidentified, 4), and once to my swinging a notebook at mosquitoes.

Freezing or ducking the head without keening was recorded in many of the same circumstances: in response to alarm calls *(Dendrocincla fuliginosa,* 15 times; booing of Fire-Eyes, 2, chip of Fire-Eye, 1; *Myrmotherula hauxwelli,* 2; *Piaya cayana,* 1; *Thamnomanes caesius,* 1; *Pygiptila stellaris,* 1;

Manacus manacus, 1; Querula purpurata, 1; *Cacicus cela,* 1; *Eucometis penicillata,* 1) and hawks *(Accipiter bicolor,* 1; *Harpagus bidentatus,* 1*)*. Once a Fire-Eye hid in a treefall and froze silently when the wind blew.

Freezing occurred concurrently with foraging or other behaviors at times. In very open açai *(Euterpe oleracea)* swamps, Fire-Eyes often seemed half frozen as they foraged. Activity was often inhibited when other birds were alarmed, when cover was lacking, or when I was near half-tame birds.

Panicking, with chipping or booing. Various degrees of movement or flight also may occur at the approach of danger. The movements seem more diverse than in certain other antbirds (e.g. Willis 1967) and calls are certainly more diverse, but for the present all will be grouped as forms of a single display.

The simplest movements, or low-intensity ones, involve pounding the tail downward or down and slightly to one side, raising the head while flexing it on the neck so as to maintain a level position, and standing somewhat higher on the long legs than in the standard posture. The body and head feathers are somewhat sleeked, but the tail is spread. Between pounding movements, the tail is lifted wrenlike. The bird may flit its wings as the intensity of the display rises. It may turn the head rapidly or yaw one way and then the other, or it may reverse ("about-face") on the perch.

Finally, it leaps away from the source of the stimulus or toward dense cover. Rapid hopping about, or dreads of flushed birds when attacked by a hawk, are even more complex forms of panicking.

Booing and chipping, or combinations of these calls, are common during panicking and fleeing. Booing, at low intensity, sounds somewhat like a loud short form of keening. Single boos at low intensities sound like "proo" and may be a different call; the note varies a great deal. Single boos are especially characteristic of parents when the observer approaches a young bird. Such adults boo even when accustomed to the observer. Booing and multiple-booing are somewhat more closely associated with alarm than is chipping or the chip-boo, which often are given as well in excited chases in agonistic behavior. (Boos and multiple-boos were noted in agonistic behavior only as "groo" calls, possibly a different note.) More significant is the association of chipping and chip-booing with flights, especially in the first movements of flights, while booing and multiple-booing were associated with an alarmed bird in cover, staying in place but making panic movements. Morton (1977) associates low-pitched notes like the boo with tendencies for a bird to stay in place, while notes that rise in pitch as does chipping are associated with tendencies to take flight or escape.

Often a bird traveling to or from a nest or antswarm chip-boos or double-boos repeatedly. It is very hard to see or follow such birds, so I do not know the meaning of their calls.

Booing and double-booing were directly associated with predators *(Micrastur ruficollis,* 8 times; *Harpagus bidentatus,* 1; *Buteo nitidus,* 1), alarm notes of other birds *(Dendrocincla fuliginosa,* 3; *Xiphorhynchus guttatus,* Fire-Eye rattle, 1; *Thryothorus genibarbis,* 1), my presence (10 times), very open undergrowth lacking cover (2), and travel through the forest. Chipping or chip-booing was associated with predators *(Micrastur ruficollis,* 2: *Harpagus bidentatus,* 2; *Mustela frenata,* 1*)* or their calls *(Micrastur ruficollis,* 7*)*, passing small or large birds *(Celeus elegans,* 1; *Ramphastos* sp., 1; unknown, 2), a falling leaf (1), alarm calls of other birds *(Dendrocincla fuliginosa,* 2), attacks by other birds *(Phlegopsis nigromaculata,* 1; Fire-Eyes, often), my presence (3), and travel through the forest. In one case, chipping of one Fire-Eye attacked by another caused distant Fire-Eyes to dart to cover.

Alarm notes and fleeing to cover were the usual reactions to the distant "kimp" calls of *Micrastur ruficollis.* I found no evidence to support the theory of Smith (1969) that calls of forest falcons help them to catch alarmed birds.

Silent fleeing or panicking movements were responses to possible predators *(Accipiter bicolor,* 1; *Micrastur ruficollis,* 1; *Chondrohierax uncinatus,* 1; *Mustela frenata,* 1; *Saimiri sciureus,* 1; humans, 7, alarm notes

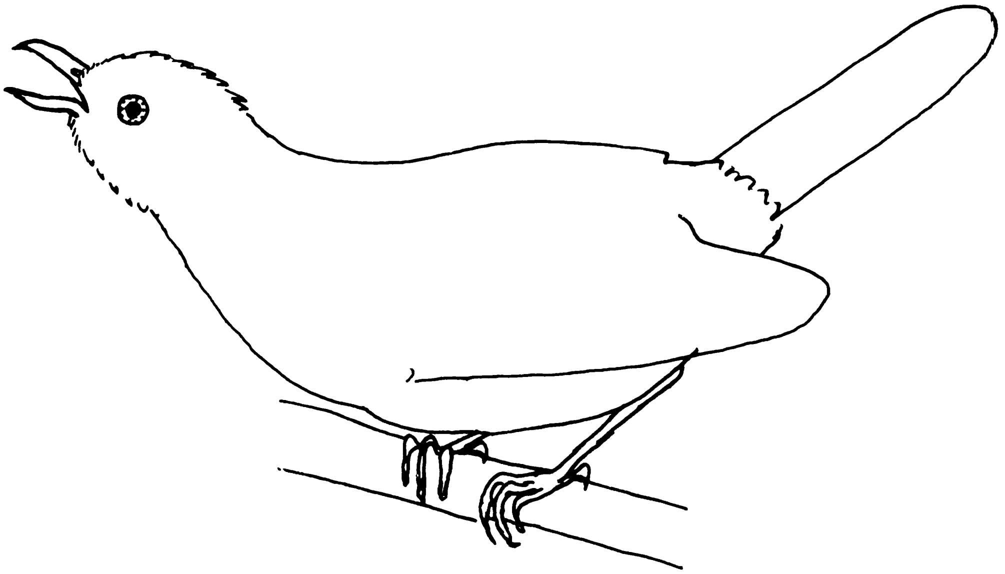

Figure 6. Rattling White-backed Fire-Eye.

of other birds (chipping or chip-booing Fire-Eyes, 7; rattling ones, 3; keening or booing ones, 1 each; imitations of the chip-boo by *Cacicus cela,* 1; *Dendrocincla fuliginosa,* 7; *Querula purpurata,* 2; *Formicarius analis,* 1), an exposed position on the edge of the forest, and the sudden sight of a bird's own reflection in a pool of water.

On several occasions, a bird fleeing me or a hawk darted into a very dark place under a log. The dark plumage should protect the bird in such situations. Even the white back is not conspicuous, at least not in the dark forests at Belém; it looks like a tiny sunfleck on the forest floor if the bird stays still. However, many other races close the back patch unless fighting, suggesting that predators can see it.

The great development of calls and activities of fleeing and panicking in this species is probably related to its subordinate role in interspecific groups of birds over ants; the same correlation was noted for Spotted Antbirds in Panama (Willis, 1972a) and for White-plumed Antbirds at Manaus (below).

In the hand or mist net, Fire-Eyes occasionally scream and kick-flutter, and are very good at escaping. The kicking sometimes disjoints a leg in immature birds. Persons capturing them should be careful that their feet do not grasp the fingers or other objects and hence will lack purchase for damaging kicks. The excessive kicking is probably related to frequent hopping during foraging.

Screaming in this species is probably just a method of startling the predator; the continuous squalling used by some species as an inducement to relatives to mob the predator is not heard. This correlates well with theories that squallers have relatives nearby, for Fire-Eyes are rather nonsocial birds because of their low positions in peck orders.

Unlike Bicolored and similar antbirds that fly horizontally and low through the forest, Fire-Eyes bound and fly to 4 to 10 m above the ground, circle about and evade mist-nets persistently. Probably, moving vertically is an adaptation to avoid mammal predation in the thick understory of woodlands and second growth where most subspecies of the genus reside. It is difficult to drive Fire-Eyes into a mist net, unless one rushes at them suddenly when they are next to it. By contrast, alarm calls often send Fire-Eyes down to thick cover, indicating that the calls are correlated with danger from above.

When three men passed on one occasion, all the Fire-Eyes sleeked their bodies and flew up high, silent except for faint grunts at each other. Once, when the rare weasel *Mustela frenata* wandered past, a male Fire-Eye flew upward. He then flew after it, peering at it; after a few faint-songs he gave a few chips and chip-boos, and returned to the ants.

After an alarm, movements and calls of alarm gradually slow, and Fire-Eyes return one by one to forage over the ants. Usually the birds lowest in the intraspecific peck order return first, perhaps because they are the least well fed. This should result in a higher mortality rate for such birds. Fire-Eyes return before species dominant to them.

Fire-Eyes often moved up to 2-4 m above the ground before crossing a small road, then dropped at a 30° angle with tailpounding flight as if to gain advantage of gravity for a more rapid crossing.

Mobbing and rattling. A sharp rattling, like a slow version of the "chirring" often heard as a response to mammals in some other antbirds (Willis, 1967, 1972a, 1973a), is a moderately common reaction when one approaches Fire-Eyes closely. The sound is rather like rattling in *Myrmeciza exsul* (Willis & Oniki, 1972), and similar notes occur throughout the genera *Myrmeciza, Percnostola,* and *Rhopornis* when a human or other mammal scares the birds.

Other than opening the beak widely for the call-showing the yellow gape-none of these birds seems to adopt strong postures for mobbing. However, the slight crest and perhaps head are often ruffed up, as in most mobbing antbirds (Fig. 6). The tail can be spread but is pounded slowly rather than rapidly as in panicking behavior.

Mobbing and rattling are usually brief reactions in Fire-Eyes, not extended behavior patterns as in ant-following antbirds of deep forest. Ordinarily, Fire-Eyes turn to panicking or flight rapidly. However, if one stays still on arriving at an antswarm, the whole group of Fire-Eyes may approach and rattle repeatedly, staring at the strange object, before dispersing to return to the raid.

Birds rattled toward me (many times), humans (9), *Eira barbara,* and *Dasyprocta agouti.* Twice rattling was a reaction to *Micrastur ruficollis* and once to a flushed *Otus choliba.* Once a rattle followed the alarm call of *Dendrocincla fuliginosa,* and once the sudden loud song of a *Laterallus viridis.* One bird rattled when supplanted by a *Phlegopsis nigromaculata.*

Habituation and displacement activities. Fire-Eyes come to ignore or even investigate animals that pose little danger for them. *Micrastur ruficollis,* a forest-falcon that often follows ants for insect prey, causes alarm when it arrives suddenly but may be almost ignored after some time. Fire-Eyes in one case watched the falcon fly in directly under them. Flocks of caciques *(Cacicus cela)* in the treetops are usually ignored, as are passing bands of squirrel monkeys *(Saimiri sciureus).*

Habituation to me was quite evident. Rattles and then fleeing greeted me the first time I encountered individuals; but after a few weeks they foraged fairly close to me with only some tail-pounding and bubbling. Even when chased for netting, they circled and hid in low tangles rather than leaving.

Some displacement activities were observed when I approached half-tame birds, apparently as results of conflicting tendencies to flee and forage: brief preening, yawning, wiping the bill, looking at the toes, turning back and forth with bubbling notes, scratching the head over the wing.

Maintenance behavior

Maintenance behavior, or reactions to small or polluting nuisances, includes preening, bathing, sleeping, reactions to army ants, and similar activities. I include also reactions to mosquitoes, though in a sense such reactions are antipredator or alarm behavior. I also include sunning even though it may be a type of foraging behavior (input of energy) as well as a way to dry feathers. Foraging behavior, sometimes considered maintenance, is discussed later.

Reactions to mosquitoes, a common nuisance in the second growth and swampy

Table 1. Characteristics of perches of preening White-backed Fire-Eyes

Ht.(m)	*No.*	%	*Angle(°)*	*No.*	%	*Diam. (cm)*	*No.*	%
0-1	98	30	0-20	156	69	0-1	52	24
2	133	41	40	44	19	2	123	56
3	50	15	60	20	9	3	23	10
4	21	6	80	6	3	4	11	5
5	16	5	100	1		5	8	4
7	5	2				7	1	
8	1	1				10+	2	1

forests at Belém, include much head-shaking and twitching. Occasional tail-twitches also mark the path of a hovering mosquito.

Army ants at times attack the feet or even the back of a Fire-Eye. Responses were much as in other ant-following birds: quick shakes of the foot or tail; "jittering" back and forth from one foot to the other; quick pecks at the foot or back to toss the ant in the air; and fleeing. One male on the ground did several fast hops, so that ants fell off; his white back was spread by the end of the series of hops.

Bathing in small pools in the swamp, or in water in fallen palm sheaths, was often observed. The bird hops into shallow water, sits and fluffs the underparts into the water, flutters the wingtips, and dips the head and foreparts so that water droplets cascade over the back. The flutter-dipping is repeated a few times. Often the bird alternately hops out of the water and returns for several short baths. It may shake or preen in intervals and always does so after bathing. Commonly birds of a family bathe together or in sequence, at times several families do so in a fairly orderly fashion. Pecks enforce order at other times.

At times the bird hops onto a submerged twig or is in such shallow water that it does not touch the water when dipping for a bath; it goes through the motions of dipping and shaking in the air anyway.

When it rains, the birds stand under leafy cover looking about, and wander off as soon as the rain slackens slightly. Birds become quiet at the sound of approaching rain.

Between bouts of foraging, Fire-Eyes often preen in protected sites, such as tangles of vines or in the lower petioles of a clump of açaí palms. Perches selected are generally nearly horizontal and higher than those used in foraging (Table 1). Preening is much as in other antbirds, with the bill passing from base to tip of each feather cleaned. The head is scratched over the wing (23 records).

After preening, the bird may sit and rest, fluffing out the body feathers. Perches for resting are always near the horizontal and commonly are from 1 to 5 m above the ground as in preening rather than near the ground as in foraging.

During or after sessions of preening or resting the bird may stretch in one of the ways common among birds: yawning with or without stretching the neck forward; a stretch of wing, leg, and tail on one side of the body only (lateral stretch); standing very high on the legs (toestanding) or repeated pushups on the legs. I did not record double flexing of the wings above the back. Once a bird stood on one leg during foraging, possibly resting.

Sunning is an unusually frequent activity in these Fire-Eyes, recorded more times (24) than for any other antbird I have studied. It was recorded equally often for males and females, so that the black color of males is not the only factor involved. (Black-bodied *Phlegopsis nigromaculata,* in the same area, sun rather infrequently). The feathers are fluffed, especially those on the side toward the sun. The wing on that side is often raised vertically, so that the flank is exposed to the sun's rays. One bird held up both wings briefly (Fig. 5). The tail is spread and may be tilted toward the sun. The head is often ruffed up, and one side faces the sun so that the eye shines brightly. The birds usually sits or half-crouches. After sunning, the bird usually preens.

Foraging behavior

Fire-Eyes follow army ants for much of their food, but regularly capture arthropods and other small prey away from ants when no swarms are available. They are, therefore, not as dependent on army ants as are some antbirds (Willis, 1967, 1973a). However, they move between ant colonies more readily than do such antbirds as *Hylophylax naeviodes* (Willis, 1972a), and hence are more regular at ant-following than some species. I doubt that they can survive indefinitely without the ants in most regions, and class them as "professional" ant-followers within the guilds of birds that follow army ants.

Drinking. One Fire-Eye pecked water from the tip of a leaf; drinking water is perhaps unnecessary, since prey items are generally very juicy.

Foraging away from ants. I have not extensively investigated foraging behavior away from ants. Individuals or pairs wander low on near- horizontal perches in patches of dense undergrowth, especially tangles in second growth or along creek borders. They pause only rarely for preening. Faint bubbles, rarely a loudsong or chip-boo, mark their courses. They move rapidly and with double-boos or chip-boos high (2-4 m up) through vertical saplings of open undergrowth between the patches.

Heights of foraging range from near the ground to 3 or 4 m up, rarely higher; much of the time they hop near the ground like a *Myrmeciza exsul* (Willis & Oniki, 1972).

Fire-Eyes infrequently join interspecific bird flocks (other than the type noted below) away from ants, and even then seem to wander widely around or behind the flocks. Other species of Fire-Eyes are similar in this respect. A bird flock near an inactive ant bivouac is likely to attract Fire-Eyes briefly, but they leave after seeing that the army ants are not present.

Foraging with ants. One or more Fire-Eyes commonly wander by themselves or with other ant-following species *(Phlegopsis nigromaculata, Dendrocincla fuliginosa, Eucometis penicillata).* Often the birds sing loudly as if for other birds or come to calls of Fire-Eyes. Individuals and groups separate and rejoin irregularly. When a colony of ants stops swarming, or fails to swarm one day, the Fire-Eyes circle and wander persistently in the vicinity of old and new bivouacs and in places where the raid was the previous day. Statary or sedentary colonies often fail to swarm in the morning, or swarm only on alternate days; by watching near an inactive bivouac, one can quickly verify that single birds or pairs visit it throughout the day. It is rare for a swarm that starts in the afternoon to lack Fire-Eyes for more than the first hour or two. (One would generally count such birds as being away from ants if he did not know of the inactive ant colony nearby). Fire-Eyes follow trails of army ants until they encounter a swarm; they give grunts or excited faint chips and may spread the white back. One even followed the line of the previous day's trail, missing the swarm of the day.

Fire-Eyes are commonly at nomadic raids before 7 am; at times they arrive before the ants start raiding at 6 to 6:30 am. An arriving group of birds often gives excited chips as it spreads out over the new ant raid, but faint grunting is the rule thereafter. When a raid folds, Fire-Eyes follow the retreating line of ants and find other forks in this manner. However, they cut across the angle between forks if they hear or see other birds over the active fork. One pair detoured to follow the ant trail in to the swarm even though another Fire-Eye was perfectly visible over the swarm.

Fire-Eyes usually shift rapidly from an inactive or statary colony of ants to an active and nomadic colony of ants, as long as the latter continues to raid every day. Individual birds move about from colony to colony, according to opportunities in a given area. Often birds alternate between two colonies of ants that are out of phase in their nomadic-statary cycles.

Eciton burchelli, which forms large swarms and raids nearly every day in predictable patterns, is the main ant species followed. The smaller and straggling raids of *Eciton rapax* and the unpredictable raids of *La-*

Table 2. Characteristics of perches used by foraging White-backed Fire-Eyes

Height(m)	*No.*	*Height(m)*	*No.*	*%*	*Angle(°)*	*No.*	*%*	*Diam.(cm)*	*No.*	*%*
Ground	146	0-1	3310	50.9	0-20	856	42.5	0-1	800	41.8
-0.1	434	2	1681	25.9	40	364	18.1	2	607	31.8
0.2	731	3	768	11.8	60	206	10.3	3	230	12.0
0.3	713	4	372	5.7	80	169	8.4	4	105	5.5
0.4	411	5	131	2.0	100	414	20.6	5	57	3.0
0.5	291	6	104	1.6	120	3	0.1	6	10	0.5
0.6	191	7	45	0.7	140	1	0.0	7	12	0.6
0.7	130	8	33	0.5		2013		8	6	0.3
0.8	84	9	21	0.3				10+	86	4.5
0.9	80	10	17	0.3					1913	
1.0	99	11	7	0.1						
	3310	12	5	0.1						
		13	7	0.1						
			6501							

bidus praedator are used mainly when the local *burchelli* colonies are inactive. The larger colonies of *burchelli* are favored, so that up to 20 birds can occur at one colony and almost none at nearby small ones.

When there are few competitors or many places for birds, Fire-Eyes wait or move about quietly low over the ants (Fig. 4). Horizontal and slightly inclined perches are favored, but vertical perches are common in open undergrowth and are used regularly when little competition from other antbirds or woodcreepers exists. Slender perches are favored. Perches 10 cm or more in diameter rarely (10 of 86 cases) were inclined more than 45°. In one such case the bird fluttered for balance and quickly moved to a perch 5 cm in diameter. Table 2 indicates perches used by birds foraging alone or in various competitive situations. Fire-Eyes competing actively tend to hop about rapidly, move to high or peripheral perches, use tangled vegetation, etc.

Even when alone and unperturbed, their long-legged hopping about is obvious; they do not wait stolidly like dominant species. They are even less phlegmatic than is *Myrmeciza exsul*, a bird which also seldom seems to stop. They hop long distances for few prey items when foraging peripherally to dominant antbirds; one records many perches without prey for each perch with prey. The birds look actively in all directions, not just toward the ants or ground, and move vertically as well as horizontally.

Activity seems to attract them, resulting in local concentrations of birds that shift individually or as groups. One female feeding a noisy young bird attracted four hopping males and then a *Phlegopsis nigromaculata*. The jump of another female for prey attracted a male, who watched her eat and then turned away. In other cases, the attracted birds took the place of the forager. At times Fire-Eyes move to activity of other species, even woodcreepers *(Xiphorhynchus guttatus* and others) foraging several meters above the ground. As a result, at a swarm with several individual Fire-Eyes, a given perch is used in a musical-chairs fashion, though it would seem more efficient for each bird to stick with its own perch. However, the pattern is not arbitrary, as is detailed below under "competition".

Fire-Eyes do not wait on the ground very often. When one does so, it frequently holds the head high as if for better vantage (Fig. 4C, D). Ants often attack such birds.

The commonest foraging method, as in other ant-following antbirds, is a quick jump to the ground to capture fleeing prey, followed by a quick return to the same or another perch (Table 3). It is common for a bird to hop or spin in a brief chase of prey during such a sally to the ground, or even to stay pecking at the prey despite ant attacks. Prey also may be pecked from the ground, without leaving a safe perch just above the ant hordes. At times a bird tosses fallen leaves, grasping each between the mandibles and

Table 3. Foraging sites and methods of White-backed Fire-Eyes[a]

Site	*Method*				
	Sallying	Gleaning	Leaftossing	Unrecorded	Total
Ground, log, root	2365	352	83	11	2811
Leaf, epiphyte	120	122		2	244
Dead leaf	37	29		2	68
Debris	14	33	1	2	50
Stem, liana	9	76		2	87
Trunk, buttress, stilt	22	62		1	85
Limb	4	6			10
Twig	1	25			26
Petiole, palm sheath	2	12			14
Air	19	7			26
Not recorded	59	24			83
	2652	748	84	20	3504

[a] 30 March 1972 to 12 October 1974, Belém

flicking the head sideways, until a fleeing prey is uncovered. A bird may wait near a spot where prey has hidden, watching closely. Sallying to snap prey off foliage or other objects above the ground is rather clumsy and is used mainly for prey on leaves or dead leaves. For other prey locations, hopping up or down to peck the prey is more common than is sallying. Short flights to snap prey from the air are rare, being used mainly at termite emergences and for other slow-flying primitive insects, though at times a moth is taken in the air. The maximum distance recorded for a sally was 2 m horizontally and 3 m vertically, or nearly 4 m; most sallies are far shorter (Table 4).

Most food comes from the ground (Table 5), where the ants flush most prey. Perches taken before attempted captures of prey (Table 6) are lower than perches taken by foraging birds (Table 2), mainly because Fire-Eyes spend much time hopping around high perches for little prey when *Phlegopsis nigromaculata* or other domineering competitors usurp the lower levels over ants. Fire-Eyes often wait successfully next to a tree trunk or palm clump or under vine or debris tangles above the ground, and they peer and poke in epiphytes, tangles, or palm sheaths at times. Fire-Eyes use low, dense carpets of *Selaginella stellata* for foraging, but flee for tangles at any alarm.

At times a young bird or one low on the peck order steals booty from a returning army ant.

Spiders, roaches, grasshoppers, crickets, katydids, and other orthopterans are favorite prey. Moths, caterpillars, beetles, and other higher insects seem less frequently taken; beetles are hard to identify, however,

Table 4. Distances of food capture, White-backed Fire-Eyes

Distance(m)	*Ground Records*	*Above-Ground Records*
0-0.1	64	
0.2	51	11
0.3	26	8
0.4	5	16
0.5	9	9
1.0	11	22
1.5	2	7
2.5		7
3.5		2
4.0		1

Table 5. Heights of food capture, White-backed Fire-Eyes

Ht. (m)	*No.*	*Ht.(m)*	*No.*	%
0-0.1	2826	0-1	2993	86.7
0.2	33	2	212	6.1
0.3	21	3	137	4.0
0.4	13	4	70	2.0
0.5	20	5	13	0.4
0.6	26	6	14	0.4
0.7	18	7	4	0.1
0.8	14	8	4	0.1
0.9	7	9	2	0.1
1.0	15	10	3	0.1
		11	1	0.0

as they resemble roaches. One bird peered at a fly on a leaf but did not try for it. Certain ants that race upward with larvae on the approach of army ants are pecked rapidly, the bird grabbing each larva and tossing away the adult. Millipedes are rarely taken and arouse bill-wiping and head-shaking reactions. Various other small prey seem distasteful and are chewed in the tip of the beak with much shaking of the head and ruffling of the crown. Fire-Eyes low in the peck order take such prey more often than do adults high in the peck order. Centipedes are eagerly caught and battered, except for the very largest individuals. One bird pecked at a small várzea crab, which raised its chelae and was then left alone.

Very large food items, such as huge bird-eating spiders or scorpions, are sometimes left alone after a tentative peck or two. However, slightly smaller bird-eaters or scorpions are taken to a peripheral spot on the ground, pecked to death and torn apart; and very large katydids or grasshoppers seldom escape. Dissection often seems irregular and unsystematic, but at times birds grab a leg and twist it off by slamming the body of the prey on the ground or other substrate. Dropped parts may be eaten or left. One moth was shaken so that scales flew. One bird with a 6-cm scorpion chewed the cephalothorax. A herculean dissection of one 5-cm grasshopper took 12 minutes. Often the back patch is closed when the bird is dissecting prey on the ground, so that hardly any white shows.

"Anting" was noted on several occasions; the bird chews a small prey in the tip of the bill and swipes it through the tips of the primaries or under the tail. The body is sleeked and the wrists out. At times the prey was eaten afterward. Commonly, crest-raising, bill-wiping, head-shaking, and other signs of discomfort attend eating. Series of anting incidents, involving several birds, seem to result from emergences of social or locally distributed insects. As in other ant-

Table 6. Characteristics of perches used before food attempts by White-backed Fire-Eyes

Height(m)	*No.*	*Height(m)*	*No.*	%	*Angle(°)*	*No.*	%	*Diam.(cm)*	*No.*	%
0-0.1	59	0-1	234	73.4	0-20	88	39	0-1	95	47
0.2	67	2	54	16.9	40	39	17	2	59	29
0.3	51	3	15	4.7	60	24	11	3	22	11
0.4	23	4	7	2.2	80	17	7	4	9	4
0.5	14	5	3	1.0	100	58	26	5	8	4
0.6	7	6	4	1.3	120	1		6	1	1
0.7	7	7	1	0.3				7	2	1
0.8	1	8	1	0.3				10+	7	3
0.9	2									
1.0	3									

Table 7. Types and sizes of prey taken by White-backed Fire-Eyes

Food	*Number of Prey of Given Length (mm)*													
	?	0-5	-10	-15	-20	-25	-30	-35	-40	-50	-60	-70	-80	+
Unidentified		44	24	33	1	9	2		1					
Scorpion										1	2,1[a]	2[a]		
Spider	10	1	1	16	5	4	4	1	1[a]		1[a]	1[a]		
Centipede	1								1	6	1		1	1,1[a]
Termite	9													
Roach	7		1	31	8	11	4	1						
Cricket	1		1	9	1									
Grasshoper	8		1	15	2	9	4		2	6	2,1[a]			
Katydid	1						2							
Beetle				1			1							
Caterpillar							1				1			
Moth	2			2										
Ant or larvae	3	32												
Wasp-like	1		1	1										
Lizard	1					1				1				
Total	45	77	29	108	17	34	18	2	4	14	6		1	1

[a]Number of prey items abandoned. All other numbers refer to prey that were eaten.

Table 8. White-backed Fire-Eyes and interspecific attacks[a]

Other Species	*Supplantings*	*Displacings*	*Returns*
Black-spotted Bare-Eye	2/1028	/300	/24
White-chinned Woodcreeper	2/26	/8	
Plain-brown Woodcreeper	4/10	1/3	
Gray-headed Tanager	2/7	/1	
Barred Woodcreeper	/1		
Black-faced Antthrush	/1	1/6	
White-lined Tanager	1/4	/1	
White-ruffed Manakin	4/	1/	
Buff-throated Woodcreeper	/2	/2	
Band-tailed Antbird	2/	1/	
Cocoa Thrush	1/	/2	
Pectoral Sparrow	2/	1/	
Greater Ani	/2		
Smooth-billed Ani	/2		
Plain-throated Antwren		2/	
Great Antshrike	/1		
Lined Antshrike	/1		
Bright-rumped Attila		/1	
Fuscous Flycatcher	1/		
Nightingale Wren	1/		
White-necked Thrush	1/		
Silver-beaked Tanager	/1		
Buff-throated Saltator		/1	

[a]Names follow Meyer de Schauensee (1970). Attacks by Fire-Eyes are above diagonal lines; attacks on Fire-Eyes are below diagonals.

birds, the pattern seems a method of treating distasteful prey items rather than a behavior related to molt or other maintenance activities.

One bird gaped and regurgitated a fragment of exoskeleton.

Agonistic behavior

Agonistic or competitive behavior involves in White-backed Fire-Eyes five main activities: aggressive display, submissive display, flight, attack, and fighting. The resulting patterns of dispersion of Fire-Eyes around army ants are in fact spatial behavior, but they will be considered here as results of competition interacting with foraging behavior.

Interspecific agonistic behavior. Interspecific agonistic behavior includes mainly flight and attack, for Fire-Eyes rarely display at other species. A bit of pecking, pointing the bill, or spreading tail or back feathers, can sometimes be seen as a weak form of aggressive display. In one case a Fire-Eye spread its tail and wings in aggressive display at a *Phlegopsis nigromaculata,* which supplanted it. Table 8 lists supplantings or attacks (one bird flies at another and takes its perch, sometimes with pecking or a brief fight), displacings (one bird points the beak at another or moves toward it, but it flies before actual attack), and returns (one bird watches until another leaves, then takes its foraging position) for Fire-Eyes in relation to other species.

Among the professional ant followers (Species 1-5 in Table 8 plus Fire-Eyes), the Fire-Eyes are clearly number 6 in the peck order. The rare small antbird *Hylophylax poecilonota* should be number 7 at Belém; it is commoner in extensive upland forests not far from Belém, where Fire-Eyes are uncommon either because they do poorly on the vertical perches common near the ground in tall forests or for some other reason. Occasionally a Fire-Eye attacks a White-throated or Plain-brown Woodcreeper or a Gray-headed Tanager, but these species generally dominate it. The last two species generally forage above Fire-Eyes, the tanager on horizontal limbs and the woodcreeper on vertical saplings. The woodcreepers tended to avoid perching near me, and at times the Fire-Eyes took advantage of this by moving upward over me. Once a Fire-Eye at 6 m up dropped a prey, which a woodcreeper caught before it hit the ground. One Tanager pounced on and then pecked at a Fire-Eye; and one Plain-brown Woodcreeper spread its wings at a Fire-Eye to supplant it.

White-throated Woodcreepers forage aggressively low over the ants but are rare in the second-growth and várzea areas where Fire-Eyes are most common; the woodcreepers seem to prefer the vertical saplings of upland forests and to avoid aggressive Black-spotted Bare-Eyes *(Phlegopsis nigromaculata)* of várzeas. Fire-Eyes can vary their foraging from low to high, from horizontal to vertical perches, in cluttered second growth and várzeas, and thus can evade Bare-Eyes in ways impossible for the specialized Woodcreepers, which keep to low vertical perches.

Fire-Eyes suffer many attacks (Table 8) from large but phlegmatic Bare-Eyes. A Bare-Eye moving to the center of a group of Fire-Eyes causes them to disperse radially. Occasionally a Bare-Eye tramples a screaming Fire-Eye in the leaves. However, in the understories of várzea and second growth there are enough horizontal perches near the ground for Fire-Eyes to hop around their larger relatives like Indians circling a fort. Bare-Eyes stand quietly near the center of the swarm, low over the ants, in the best positions to capture fleeing arthropods, but the peripheral zones belong to the Fire-Eyes. Even when 15 to 22 Bare-Eyes swirl around the swarm center and young or subordinate ones ascend high over the ants, there are usually a few Fire-Eyes high or peripherally: the Bare-Eyes simply are slow at attacking them.

I recorded locations of Fire-Eyes circling around Bare-Eyes by using terms like "left", "right", "behind", or "ahead" of the swarm "center". (Records of Fire-Eyes at swarms without Bare-Eyes are not tabulated, because nearly all records were for center locations except for birds low on the Fire-Eye peck order.) The data (Table 9) must be interpreted with caution: the lower number

Table 9. Interspecific attacks on Fire-Eyes using various locations at ant raids

Location	Perches Used		Attempts at Prey	
	No.	Attacks[a]	No.	Attacks[a]
Central	405	128	75	8
Left or right end	3253	199	489	24
Ahead of ants	1397	41	139	5
Behind ants	2128	48	361	8
High over ants	493	55	2	0
Near me	153	18	92	1

[a]Mostly by Black-spotted Bare-Eyes; rarely by White-chinned Woodcreepers.

of records ahead than behind reflects the fact that I normally watched from behind the ants and hence scared timid dominant species ahead; there are few records for "high" over the ants because I normally recorded exact heights rather than use a word; and the original data records of "left" are more numerous than those for "right", because I normally watched from left of the ants and scared dominant species to the right. (A table similar to Table 9 for White-chinned Woodcreepers shows a surfeit of right and ahead records). However, the data do indicate that few Fire-Eyes infiltrated into the central part of the swarm, and that those that did were very likely to be attacked by Bare-Eyes. Open undergrowth, where the Bare-Eyes could see distant Fire-Eyes, led to long-distance supplantings and to an increased central zone vacated by Fire-Eyes. Moving high over the ants also led to attacks rather frequently (although not so frequently as near the ground; Bare-Eyes were somewhat wary when high, and often ignored Fire-Eyes close to them), as to some extent did use of the ends of a swarm. Fire-Eyes were less likely to be supplanted when behind or ahead of the ants. Sites near me were not especially safe, since young Bare-Eyes bounced from the swarm center by their elders often moved near me.

In one case, a Fire-Eye supplanted a surprised Bare-Eye that was tossing leaves on the ground. Another Fire-Eye flew up and pecked a fledgling Bare-Eye in the back, forcing it to fly, but a second fledgling Bare-Eye pecked back. One Fire-Eye, upright and spread-tailed, challenged a Bare-Eye but was supplanted by it.

Fire-Eyes, especially young ones low in the peck order, tended to forage at a waning swarm or return to a swarm in situations of alarm when Bare-Eyes had already deserted. Fire-Eyes must gain some food in this way, perhaps at the expense of a higher mortality rate than that characteristic of Bare-Eyes.

Grunting (bubbling) was once used as a Pectoral Sparrow hopped up nearby on the ground. Grunting may be used against other interspecific competitors, but it is normally difficult to tell if the sound is directed to other Fire-Eyes or to other species.

Intraspecific agonistic behavior. Fire-Eyes follow well the rule that underprivileged antbirds (low on peck orders interspecifically) are intraspecifically very aggressive but show little submissive behavior (Willis, 1972a). Noisy arguments are constantly erupting among the circling Fire-Eyes. Fights, supplantings, and displacings are common (Table 10); returns were rarely recorded, mainly because Fire-Eyes rarely stopped long enough to obviously wait for a dominant bird to leave, so that I could not be sure whether a given bird was returning or just moving.

Aggressive display, or "challenging", occurs in various forms or degrees. The locally dominant males frequently take conspicuous perches 2 m or so above the ground, and assume "hulking" or "patrolling" postures: tails, and body feathers spread but heads sleeked, arched, and snakelike. The bill points down when an opponent passes (Fig. 7C). Bill wiping, common after patrolling, is natural because the bill is already down. The hulking bird may toelook, too, or preen after the other bird passes. The lower

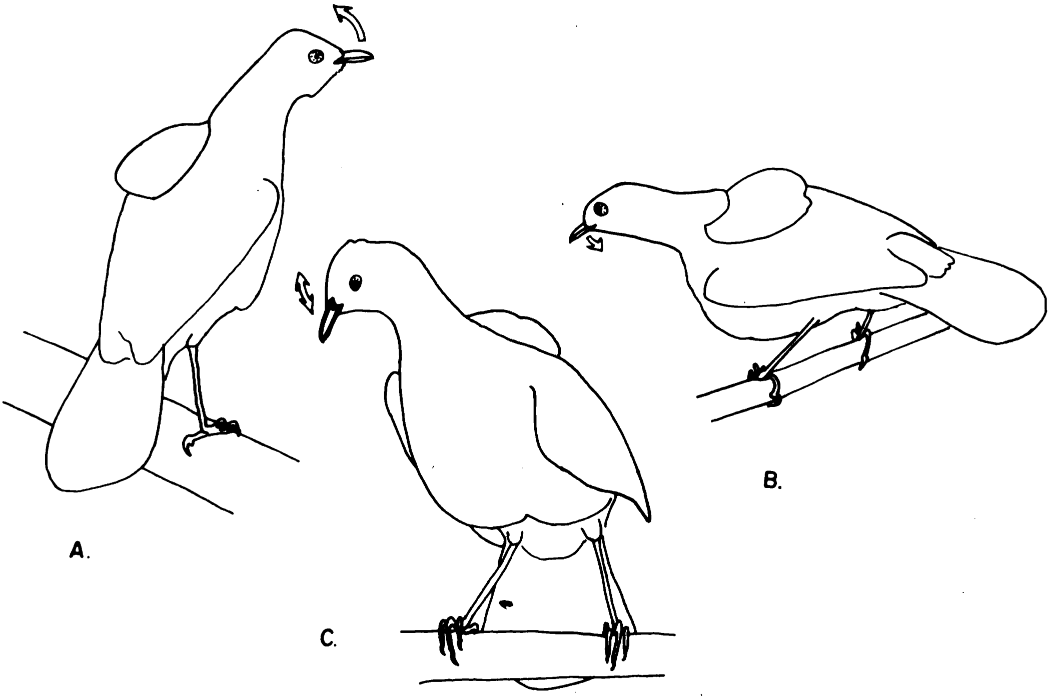

Figure 7. Aggressive White-backed Fire-Eyes. A. Upright challenging. B. Horizontal challenging. C. Hulking bill-down challenge.

neck tends to be fluffed, and the breast may be so fluffed that its feathers shield the abdominal ones.

Sleeking the head exposes the red eyes prominently under beetled brows and a flattened crown; this display presumably is the main reason for the bright color. The pupil of the eye becomes smaller in challenging, exposing the red color even more. At times the eyes bulge prominently upward like the eyes of a crocodile.

At higher intensity, the hulking or challenging postures become more upright (Fig. 7A), the feathers of the tail and white back patch spread even more widely (the latter until there is a hollow in the center), the legs are splayed, the corners of the wings come out (in the southern *Pyriglena leucoptera,* white shoulders are displayed by this movement), and the bird either arches the head more to a bill-down posture or stabs it upward as a bill-up posture. The neck is extended. At times the bill-up challenger sways back and forth snakelike, emphasizing the display. Snarling may accompany a sky-stabbing motion from the challenging position; the head position for interspersed chipping or booing notes during challenges was not noted.

Except when in the bill-up posture, the challenging bird follows the "rule of angles" noted for other antbirds (Willis, 1967, 1972a, 1973): angles near the center of the body are opened while angles at the periphery are closed (head, toes, etc.). Presumably closing the peripheral parts of the body protects them from attack while spreading the central ones gives the impression of large size.

Challenging at high intensities usually ends quickly in vigorous attacks or fights. The attacker points toward the other (Fig. 7B) and lunges or flies at it, and may peck at it. Attacks are normally quiet and simple supplantings or displacings (sometimes with snapping, huffing, or growling notes), but the attacker may chase the other bird around

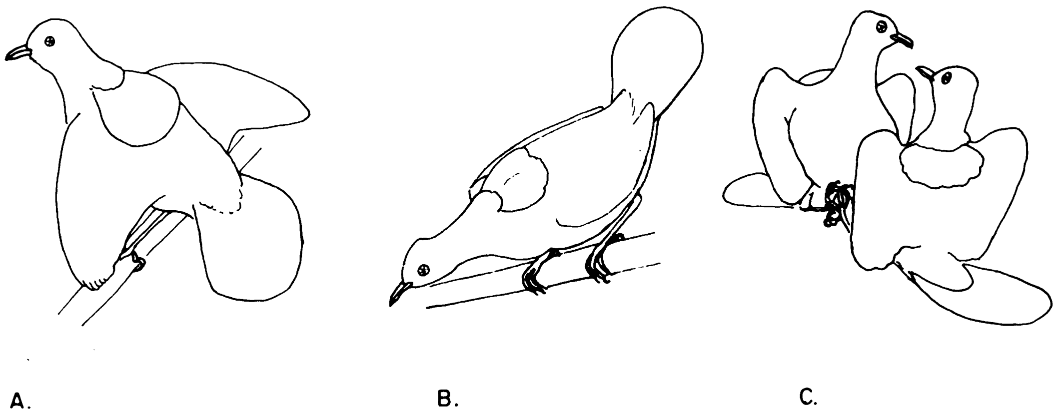

Figure 8. Fighting White-backed Fire-Eyes. A. Wings spread after fight. B. Tail spread and up before attack. C. Fight on ground.

or away through the under growth with chipping notes and snarls. The wings whir unusually loudly in some rapid attacks, but slow parachuting or "butterflying" was used by some attackers. At times the attacker hops forward slowly, then rushes suddenly at the opponent with a whir of wings in a kind of bum's rush. A bird that is trapped may almost be murdered by its attacker. A male at times pursues a female viciously persistently, finally forcing her to grattle as she dodges him. Occasionally the female turns on her pursuer and fights (gaping, pecking or challenging) briefly as they reach places far from the swarm, and the male may cease attack or even be repulsed; of course, he no longer has evident reason to continue the attack, for neither bird is now in a good foraging place. In one case, the dominant male watched another male chase his mate about, but only opened his white back and continued to forage.

Attacks sometimes resulted in the winner stealing food that the loser dropped.

Males attacking males, or females attacking females, often cause brief fights and sometimes cause extended ones (Table 10). With chipping, bugling, booing, the two glaring birds (Fig. 8B) attack back and forth until one flees. There may be a rapid chase to and fro, or screams or booing from an attacked bird. Exchanges or pecking occur at the start of fights and during aerial fluttering, but fights on the ground are usually grappling matches with the feet (Fig. 8C). In ground fights, the wings may stay spread (Fig. 8A), and one bird being chased by another threw its wings up at each stop.

Commonly loudsongs erupt from both birds after a fight or series of challenges, especially when the subordinate bird stays. A bugled gargle may introduce each song (the beak stabs forward for bugling). Songs may spread to several birds, generally including the locally dominant male (on territory) and his mate.

At times two to four other pairs from nearby territories add to the loudsinging din. Loudsinging birds take an upright posture (Fig. 9) in which the raised or horizontal head stabs forward prominently at each note (Fig. 5, above right) while the spread and lowered tail pumps forward slightly earlier (?) than each note, so that the bird seems to ride an invisible galloping horse. The bird is upright even when the opponent is below. The corners of the wings (wrists) are out and pump outward with each note, the white back expands with each note and hence seems to wink repeatedly, the body is fluffed, and the head is sleeked. The back of the neck, sleeked when bugling, is spread for loudsinging. Irregular outbursts of songs often lead the observer to a swarm of ants; they must announce the location of a bird-crowded colony of ants to other birds as do

Figure 9. Loudsinging White-backed Fire-Eyes (above). Foraging bird (below).

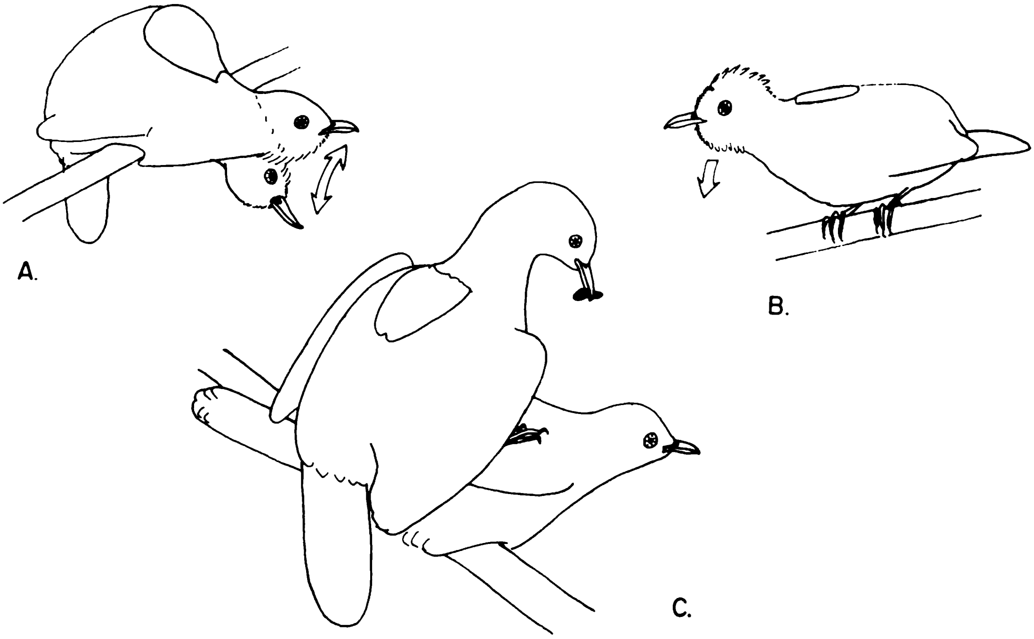

Figure 10. White-backed Fire-Eyes. A. Draping display. B. Submissive cringing. C. Copulation, the male still with food.

similarly loud songs of fighting Bicolored Antbirds (Willis, 1967). Other Fire-Eyes, and even Bare-Eyes, have been seen to come to noisy fights of Fire-Eyes. It is, however, not certain that the singing birds benefit by attracting others. Possibly related birds may be attracted and therefore find ants more easily, so that loudsinging is favored by kin selection. More probably, the loud songs are just part of the general aggressive repertoire necessary for individuals to retain their statuses. Birds on their territories also loudsing early in the morning, as do wandering or territorial birds hunting ants. When one such bird sang near the distant nest of one male, the latter gave chip-boo notes and went toward the songs. More often, the resident pair fly up and loudsing at approaching songs of another bird or pair. Distant songs tend to be ignored, except for faint comments.

Submissive display is infrequent and simple in Fire-Eyes, as is generally the case for species of antbirds low on the interspecific peck order. Fluffing the head and body feathers, crouching slightly on the perch, ducking or retracting the head, opening the toes, and closing the tail were low-intensity movements of the humble "cringing" display widespread in antbirds (Fig. 10B). The wingtips may droop, too, and the beak may open. At times, cringing females wingfluttered as well. Subordinate birds usually close the white back patch to some extent; dominant birds of the Belém subspecies do so only when dissecting prey on the ground. Insubordination is common, for subordinate birds often challenge slightly. One subordinate male spread his white back on seeing a dominant male capture an insect, then closed it again.

Also present and effective in subordinate birds were various evasive or escape behaviors, from turning the head or body away from the dominant opponent to rapid hopping or flight. Neither Fire-Eyes nor other species were fast enough to really chase Fire-Eyes, which were very good at evasive hopping at any attack. At times fleeing birds show aggressive display. Whimpering or brief squeaks were recorded mainly from

Table 10. Intraspecific agonistic interactions of White-backed Fire-Eyes

Winner		*Loser*					
		Ad. Male	Ad. Fem.	Imm. Male	Imm. Fem.	Unknown	Imm.
Adult male	1.[a]	29	2			1	
	2.	637(26)[b]	478(24)	97(6)	45(1)	35	1
	3.	294(9)	137(11)	19(2)	15(7)	9	
	4.	2	2				
Adult female	1.	1	6			1	
	2.	32[c]	116(8)	6	23(3)	1	
	3.	25[d]	86(2)		19(3)		
Imm. male	1.		1	1			
	2.	3	34(3)	5	6		
	3.		3	1			
Imm. female	1.				1		
	2.	2			1		
	3.			1	3		
Unknown	1.					16	
	2.	19	13	9	2	269	1
	3.		2			1	

[a] 1. Fights; 2. Supplantings; 3. Displacings; 4. Returns. Numbers in parentheses represent cases of the preceding number that followed a try for food by the loser. [c] 15 of 32 were supplantings of a male by his mate, and 3 others were cases of a female successfully repulsing a male's attack. [d] 17 of 25 were displacings of a male by his mate.

young males (but at times from adult males or from a female) trying to forage near attacking older ones. After fleeing, the bird may toelook, scratch the wing, stretch, or wipe the beak as a displacement activity; bill wiping and toelooking were recorded from winners as well.

Birds often grunt or bubblesing as they forage near social inferiors. At times the bubblesongs were given by a weakly challenging (slightly spread tail and body) female evading a dominant female, however; it may be that the sounds express mild aggressivity in foraging contexts whether the bird is dominant or subordinate. A group of busily foraging Fire-Eyes keeps up a constant patter of grunts to bubblesongs; but single birds are generally silent as are young birds and others low in the peck order. (The sound is also used against the observer when birds are accustomed to him.)

Male Fire-Eyes ordinarily dominate females other than their mates (Table 10). Adult males are more aggressive than adult females, in general. Young males also attack more than do young females; young males even attack adult females more than adult females attack them. One young male supplanted an older one from behind, but the older one supplanted him the moment he looked back to see the young male. Male Fire-Eyes tend to take the best foraging positions near the swarm center, but the most dominant males waste much time patrolling; females and young males come next, above or around the swarm; and young females are low on the peck order and keep to the outskirts of the swarm. As a swarm approaches and passes a given perch, it often is occupied in regular sequence: young female; adult female or young male; adult male; *Phlegopsis nigromaculata;* adult male; adult female or young male, and finally young female again. Very young birds are quite foolhardy at venturing near adults or Bare-Eyes and suffer many attacks; older young seem less silly.

Territoriality also determines which Fire-Eye dominates an encounter, as is generally true in ant-following birds. The male and female of the local territory sing most loudly and dominate the other birds. As the ants move into another territory, the neighboring pair become dominant. However, the transition zones between territories seem very diffuse, compared to Bicolored Antbirds (Willis, 1967). It is often difficult to tell in the confusion who is dominant, for birds that are similar in dominance may avoid or sing at each other rather than resolving issues with direct attacks. Subordinate birds mute their disputes, however, rather than loud-singing or fighting noisily. The birds often seem "too busy" foraging to waste time with equals. Subordinate birds often are chased when equals are not confronted; this may be a type of "redirected aggression" that has the population-control effect of eliminating subordinates (Rohwer, 1975). Much of the attacking of females by males seems of this type, for the females stay peripherally and rarely occupy foraging sites worth usurping. However, rival males often stay well apart or hulk at each other from well above the ants, so that females and young birds get good foraging positions and then have to be expelled vigorously by the returning dominant males.

The female Fire-Eye of the local territory sings and displays at trespassers when her mate is on the nest but often is subordinate to trespassing males if they call her bluff. Arriving birds are especially subject to challenges from the resident male, female, or both.

Cooperative agonistic behavior is uncommon in Fire-Eyes, except when a supplanted female moves to near her mate as if for protection or to exploit his foraging place. Now and then, a male and female stand together when loudsinging or displaying against others. Also, a female commonly moves with her mate so that he sweeps away at least some males or females that she could not displace by herself. Fighting can attract other Fire-Eyes, and at times noisy 3 or 4-bird melées erupt. Possibly the others move in to establish their own dominance rights, or interpret concentrations of birds as signs of good foraging areas.

Commonly, Fire-Eyes forage a meter or two apart with only faint challenging or cringing movements, but at times a bird flies 3-5 m horizontally especially to attack another. Preening birds dispute at times; often birds passed preening ones less than a meter away without obvious interactions.

Reproductive behavior

Reproductive and social behaviors of White-backed Fire-Eyes are generally similar to those of other antbirds. Courtship involves feeding of females, mutual grooming and association of pairs for long periods. A special display by the male, "draping", seems associated with showing possible nest sites to a female. Nesting is the task of both male and female, and young remain with their parents only while being fed.

Courtship. As in other antbirds, courtship feeding occurs in White-backed Fire-Eyes. However, it is not as common for male Fire-Eyes to give food as it is for well-fed males of dominant species to do so, and it took me several months to establish that it occurs in Fire-Eyes. The male chews a prey, looks around, serpentine-sings, and wanders about. The female flies up and grabs the food quickly, sometimes growling or bubble-singing a bit, and hops away to eat or dissect it. The male often bubbles rapidly at the same time as the female.

She may follow him as he prepares a large prey at several places on the ground. The male is often hulking with sleeked head and neck as he presents the food, and both birds may spread the tail and white back; he may peck at her as she flees. Birds mated for long periods manifest less aggression than do birds that are pairing or have paired recently. Following feeding, both birds champ the beak and hop apart.

Mutual grooming or brief copulations followed some feedings, the male hopping onto the female's back and fluttering rapidly; but the females often hopped out from under their males. At one feeding a few hours after a case of attempted copulation, the female crouched as she accepted food. In two copulations, the male held the food in his beak, and the female took it only afterward (Fig. 10C). He held the bill down and the head arched during the copulation. After another copulation, the male hopped off beside the female and arched his ruffled head as if for mutual grooming.

Mutual grooming occurs at times. Either or both birds freeze with heads arched and ruffed after an approach, and finally one nips and eats small objects from the feathers of the head of the other. The nictitating membrane is closed on the side being groomed. The legs splay, but the birds are crouched near the perch rather than high as in agonistic splaying. They may nibble with beaks together, or even nibble the toes. The pair groom each other only briefly, for male and female in this species are not very social. However, the two often hop up near each other for short periods or preen close together.

A special display, "draping", sometimes occurs when a female approaches her mate or an unmated male. The male drapes himself over the perch like a limp, black dishrag, spreads his back patch prominently, and gives "chirping" calls (Fig. 10A). One male pointed the bill up before draping be fore his mate. The head is low and ruffed (including cheeks, crown, and throat) in some cases but sleeked in others. The neck is elongated. The male recovers quickly when the female hops away. Draping commonly occurred in low, dense vegetation of a type suitable for a nest and in several cases was definitely the display of a male showing possible nest sites to his mate as they wandered. The male builds much of the nest alone, and may display to get her favorable response or interest before he starts to build. The female sometimes drapes, chirps, or sits in good sites, and in some cases the male comes up and chirps near her.

Pair bonds and "divorces". Both at and away from swarms of ants, male and female of a pair commonly preen together but forage and wander somewhat separately (rarely less than 10 cm apart, but at times much closer together than unmated Fire-Eyes). Serpentine songs keep the two in touch at times. The female is likely to retreat to her mate if attacked by other Fire-Eyes, but attacks by other species easily separate the pair. The female responds, albeit rather tardily at times, if her mate loud-sings. Dominant or subdominant pairs may loud-sing near each other in disputes, but locally subordinate birds are less responsive to their mates. It often took me much time to discover who was mated to whom among subordinate pairs.

In several cases, mates were somewhat antagonistic to each other, grunting and toe-looking when they foraged together. At times, a female dominated her mate and supplanted him to take his foraging position. However, males often followed their mates or serpentine-sang for netted mates. The general lack of attention between mates in this species is probably a result of low status on the interspecific peck order, forcing mated birds to forage peripherally and separately, for the same phenomenon occurs in other low-status species (Willis, 1972a, 1972b).

Pairs often stayed together for the 14 months of my study, although male or female remated rapidly if the partner disappeared. At times a male fed another female or a female accepted food from a bird not her mate, especially if the mate disappeared for a few days. When agronomists cut the understory of rubber plantations at the northwest corner of the study area, the homeless pairs of Fire-Eyes did not always remain together. One pair separated, the female taking a new mate to the south and the male taking a new mate to the east. Other females also took new mates (in one case after being without a mate for a month), but I do not know what happened to their males. However, one pair from within the cleared zone shifted their territory into uncleared woodland and stayed together (Fig. 11).

Nesting. I saw males carry material and build nests, but I watched only at nests which were later abandoned. I suspect that males start building and females aid in later stages, especially the nest lining, at nests that are used. After nest-site showing and draping at several locations over a few days, the male begins to carry material. He takes the material to several sites in brush or *Selaginella* on or near the ground, often a site near the ant swarm of each day. One such site finally had a leafy ball with nearly covered top and was visited by the male over several days but never lined. The female visited the nest with him a few times but did not stay long. He chirped as he carried dead leaves to this nest from less than a meter away, sitting and placing each leaf in the site. The pair nested within the month, but I did not find their nest. Young males, not yet mated, sometimes carry and then drop material without definite directionality.

The nest, a leafy ball with side entrance, is set in dense material on or near the ground. It is lined with slender strands. I

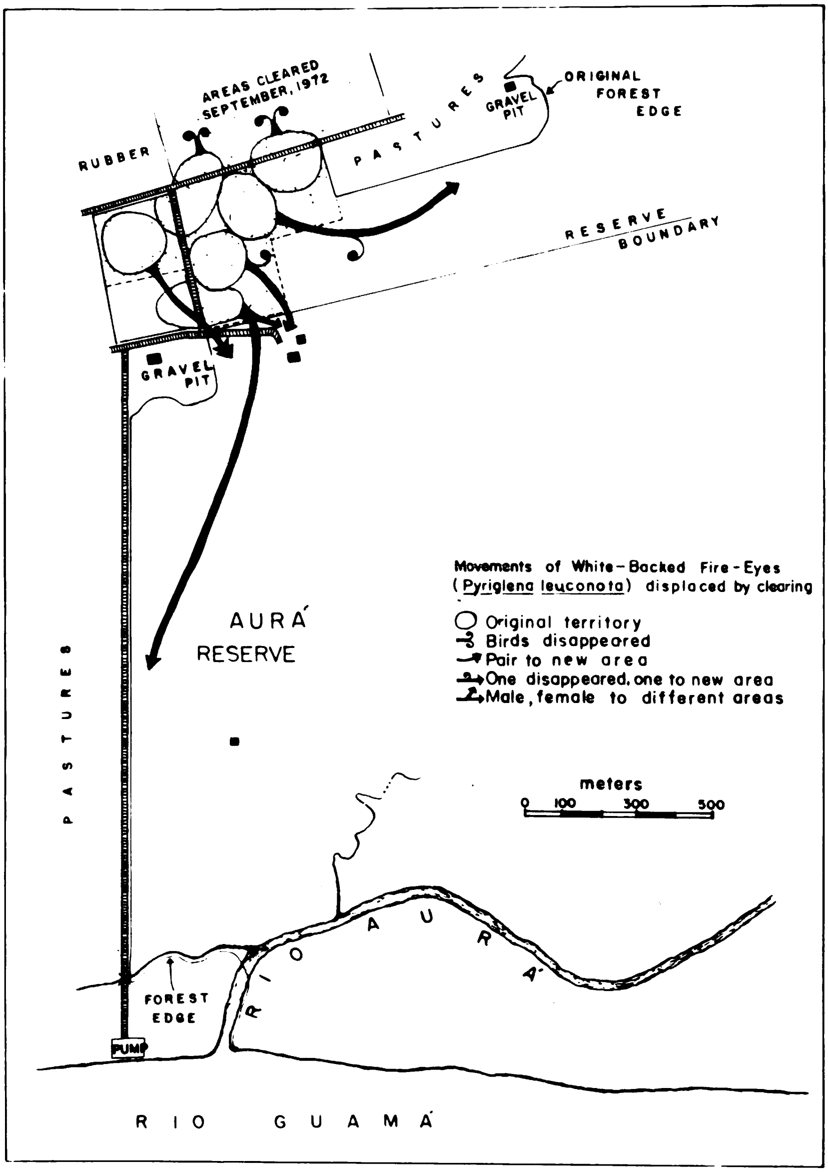

Figure 11. Results of clearing of Study Area III (second growth) in September, 1972.

found only one nest at Belém and one at Colinas, Maranhão, but Snethlage (1935), Pinto (1953), and Y. Oniki (pers. comm.) have recorded several others of the same type. The nest resembles the leafy ball of *Percnostola rufifrons* (at Almeirim, Pará), one of the few other antbirds with an oven-shaped nest.

Eleven clutches of two eggs and two of one egg have been recorded at Belém. The eggs are white or pale pink with dark blotches.

Male and female incubate alternately during the day, as in other species of antbirds. At swarms of ants, one sees that the male or female leaves with faintsongs and after two hours or so returns with loudsongs or chip-booing. The mate meets and returns to the raid with it. The returning bird preens and forages energetically while the mate rests and preens. Soon, the mate leaves with faintsongs. During incubation, the male occasionally appears at the ant swarm between 06:00 and about 07:30, but often does not appear at all until 09:30 or 10:00. The female disappears in the late morning to early afternoon, while the male disappears in the afternoon before or after she reappears. Y. Oniki (pers. comm.) found females incubating at night and at midday, while males incubated in the early morning and in the afternoon. At ant swarms, absence of the male and female alternately was a good sign of incubation or of brooding the young.

A helper and I watched 5-8 June 1972 at the Belém nest, until one young (the other had disappeared) was eaten by a *Pseustes* snake at 10:30 on 8 June. The two young had hatched on 3-4 June from eggs found 2 June. The female evidently brooded at night, as she came in without food and sat on the nest at 18:20 on 5 June and at 18:17 on 7 June, when it was nearly dark in the tall second-growth. The female was on the nest at 06:10 on 7 June and left 06:29. She often brooded the young after feedings, as did the male; the brooding bird turned so that its head was low in the entrance. Occasionally it rose and pecked down as if removing parasites from the young.

Normally, the male or female fed the young when it arrived. Feedings were 2 to 125 minutes apart ($\bar{x}$ = 46.2 min.; n = 31); the male fed 12 to 182 minutes apart ($\bar{x}$ = 84; n = 16) and the female 13 to 223 minutes apart ($\bar{x}$ = 112; n = 11). Often the adult arrived with grunts or bubblesongs, hopping from perch to perch; feedings were rapid, and faint bubblesongs caused the young to rise. When one adult left the nest as the other arrived, there were exchanges of faint bubblesongs. Loud double-boos or chip-boos sometimes marked the approach from a distance.

June 4 (08:55) the two young weighed 4.2 and 3.5 g, and were naked. June 5 they weighed 6.0 and 5.6 g, and one disappeared. On 6 June, the other young bird weighed 10.3 g and the longest primary pinfeather was 1 mm long; the next day it weighed 12.1 g and had a 6-mm long primary. It squeaked or hissed in the hand, then peeped. Feathered male nestlings are black and female nestlings brown (Y. Oniki, pers. comm.).

At swarms, one occasionally sees an adult carry food off toward a distant nest. The male no longer feeds his mate during incubation or care of the nestlings.

Care and growth of fledglings. Fledglings have short tails, about 10-20 mm long, and fly weakly when they first appear near swarms. They are rather well feathered in black (males) or brown (females) of soft and dull tones: but the beak is small and has pale enlarged gape angles. The white back is small compared to adults and is closed much of the time. The underwings and large thighs are bare. Young weigh about 30 g, close to adult weight, and are probably a few days out of the nest. They hide in low tangles some 10-100m from the swarm and loud-peed at times. Probably they are about one month (30 days) old, counting from the date of the start of incubation.

Adults bubblesing to lead the young birds to distant cover when the observer approaches. Each adult cares for one young bird and ignores or supplants the young bird of the mate. If only one young survives (as was the case in 11 of 14 broods watched from soon after fledging), it usually stays with one parent although it sometimes begs from or is fed by the other parent. At times the male feeds the female, and she gives the food to her young bird. In 12 cases when only one young survived, a female was the principal guardian of a young bird, in 3 cases the male. The male may, perhaps, be more occupied with territorial matters and leave the female to care for single young. The female cared for a young male in 6 cases, for a young female in 9; the male cared for a young male in 6 cases, for a young female in 3. For one other young male, I was unable to determine which parent was the main guardian. There is thus little suggestion of sexual favoritism by adults of either sex, and which young bird goes with which parent is likely to be an accident of which parent happens to be bringing food when a young bird first leaves the nest (as in Spotted Antbirds, Willis, 1972a).

The young bird peeps faintly or loud-peeps when the parent bubblesings, and hops or flies toward it. The parent bubblesings and feeds it rapidly; the young squeaks, crouches with bill up or gaping but head retracted, and may flutter the wings. If the young drops the food, the adult flies down, gets it and (perhaps with shaking and chewing) feeds the young again. If the parent stays nearby instead of hopping or fluttering off, the young may squeak in its ear or hop persistently around it, gaping.

By 45 or so days of age, the tail of the young bird is full length. The young is likely to hop and forage clumsily near the ants rather than wait in tangles away from the swarm, but it receives most of its food from its parent, which it follows with loud-peeps or faint peeping. Both young males and females peck at bits of debris, small or large leaves, and other objects and may champ them briefly before dropping them. The dark chests of young females are mottled with light hues similar to those of adult females.

By 60 days of age, the young bird sometimes receives pecks or chases as it follows its parent, despite its squeaks. Still, its hesitant or backpedaling parent sometimes feeds it or loses food to it. It captures much of its own food as best it can, and peeps only when with its parent. At times, however, the young is still being fed at 75 days of age, or 45 days out of the nest. Rarely a young bird stays with its parents a week longer but forages separately from them.

Older young wander independently of their parents, and at times were recorded up to 2 km away in my other study areas within a month or two after leaving their parents (Fig. 12). When they encountered their parents again, there was no sign of association or recognition, other than a tendency for parents to ignore rather than supplant them.

Immatures are very low in peck orders, and evidently have difficulty with maintenance. I often saw spider webs plastered over the head or bare patches on the head. They are dark-eyed and have pale gape angles and dull plumages for some months. Wing molt was near the middle of the primaries in one young female about 6 months old. Most young birds of about this age seemed in molt, leading to the glossy black plumage of the adult male and lightening the hue of the females slightly. I have little definitive information because most birds banded as young disappeared while other young of unknown age wandered in from outside. One young male rediscovered when less than a year old was in glossy adult plumage and had bright red eyes. He seemed to be unmated like some other younger males in wing molt into adult plumage. Males may seldom gain mates before their second year (as in Bicolored Antbirds, Willis 1967), though one young male paired his first year.

The age of first breeding for young females was not established, but probably is about one year; breeding may at times follow the first molt, in August of the first year. In several cases, subadult (molting) females established temporary bonds with subadult (molting) or seemingly adult (red-eyed) males, preening or mutual grooming and staying with them, even though the pair seemed not to be dominant nor to have a definite territorry. One such recently-adult male quickly deserted his young female when an adult female in the area lost her mate, and soon was on territory and nesting with the adult female. The young female soon gained another subadult mate, however, and they eventually settled on a marginal territory near where the first young male had been trying to create a dominance area.

Renestings, nesting seasons, and nest success. By time the young are 75 days old, their parents are courting and investigating nest sites again. In some cases, the parents were already incubating when the young birds were about 80 days old. The interval between loss of a nest and the start of incubation in another nest was about 10 days in two cases, perhaps more in others, judging from the behavior of adults when they were at swarms of army ants (method of Willis, 1973b).

Nesting at intervals of about 50 days between nests (when the first nest is success-

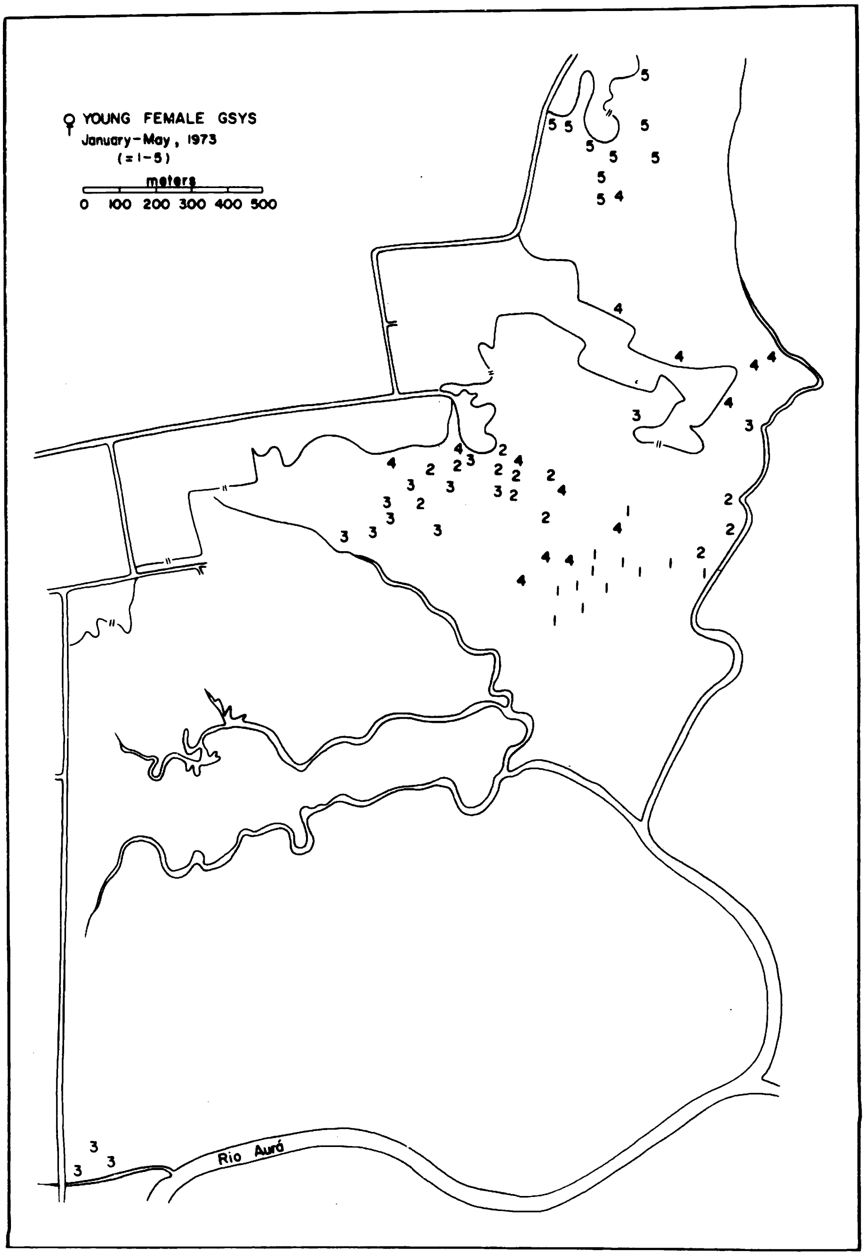

Figure 12. Locations for young female GSYS in her first five months after leaving the nest. January and February records (1,2) are mostly within the territory of her parents, as she was just becoming independent in late February.

ful) or 10-plus days (when the first nest is unsuccessful) seems to continue much of the year. Figure 13 shows records for a few of the better-studied pairs. From May 15 to August 15, however, hardly any egg laying was recorded. The only exceptions were the nest I found at Belém, in which eggs hatched June 3 after a presumed incubation period of 15 days, an unsuccessful nesting in June of 1972, and a small young bird out of the nest

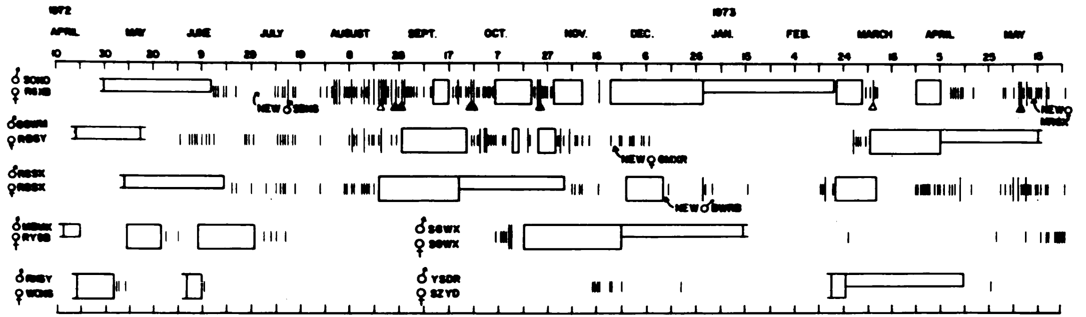

Figure 13. Reproductive activities of several pairs of White-backed Fire-Eyes. Short vertical lines, no reproductive activity. Long vertical lines, courtship feeding. Open triangles, attempted copulations. Closed triangles, copulations. Rectangles, nests. Slender rectangles, dependent young out of nest.

in the Mocambo Forest in August of 1967. May to August are the months of molt, and perhaps it takes precedence over nesting during those months.

When one assigns each nest to the month in which the last egg was laid in it, I recorded the following numbers of nests from Belém (numbers in parentheses refer to 11 nests in Pinto 1953 and Oniki MS): April 1 (1), May 3, June 1, July 0, August 3 (1), September 3, October 4 (1), November 5 (1), December 2, January 3, (3), February 1 (2), March 3 (2). Four other nests had received eggs in March, two in February, and one in January before I arrived in 1972. Nestings in which I was actually watching the parents at the start of incubation (and did not just estimate the start of incubation from observations of adults or young later) were these, from April 1972 to March 1973: 1,3,1,0,3,1,4,3,2,0,1,2. I was absent from 17 January to 12 February in 1973, and may have missed nestings. Nesting is frequent in the August-November period of relatively dry weather and little molt, at the same time as the peak of nesting for other species at Belém (Pinto 1953); but nesting continues well into the rainy January-May period. Many individuals started molt while feeding fledglings, and a few started molt while nesting. There was no evidence that any adult females were long without nests or dependent offspring during any months other than June and July. Adult males, however, at times lack mates and are not nesting.

Oniki (1979) found low nest-mortality rates in forest birds at Belém, and the forest-living Black-spotted Bare-Eye there seems to have high nest success (Willis 1979). However, Fire-Eyes seem to have rather low nest success despite their oven-shaped nests (Fig. 13 shows that many nests never produced young). Counting only nests for which I was watching the adults both at the time of egg laying and enough time later to establish whether young had left the nest or not, 4 of 19 nests (21 percent) succeeded. Probably a few unsuccessful nests were missed because they were destroyed during egg laying or before the parents settled into an incubation routine. Other nests may have been successful after I lost track of the parents, evening out matters. A success rate of 20% implies losses of 5.5% per day ("m" of Ricklefs, 1969) if the period from first egg to last young is 29 or 30 days as in related antbirds of similar size. Oniki (1979) did record low nest success for birds of second growth and open areas at Belém, and most Fire-Eyes were birds of second growth. I was unable to follow pairs long enough in the várzea part of my study area to establish if the success rate of várzea Fire-Eyes differed from that of second-growth birds.

Social and spatial behavior

Other than loose pair bonds, rapidly broken bonds between adults and offspring, and argumentative aggregations around ant swarms or in search of ant swarms, Fire-Eyes are not very social birds. They show none of the clan formation or tendencies to

Table 11. Numbers of White-backed Fire-Eyes following ant swarms at Belém

Month	*Number of Swarms with Given Number of Individuals*																				
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
May, 1972		1	3	3	3	1	4	5	8	3	3	3	2	1	2	1		2			
June		1	1	1	2	2	5	1	4	2	2		4	5	2	2	2	1	3		
July	1		2		3		2	2		4	4	1									
August			1	1		3	1	4		4	4	3	2								
September								1	1		1	3	2								
October	1	1	1	2	6	3	5	3	2	4	4	6									
November			8	7	1	4	4	3	2	2	2	2	2	2	2	3	2		1		
December	1	2		5	1	1	3	4	3	6	4	3	1	1	2	1		1	2		1
Jan., 1973		2	1	1			3	2	1	1	7	2	1	2							
February	1				1	4	3	1	6	1	2	1							1		
March				1		3	2	1	3	4	1	2	4	1					3	1	1
April			1	2	2	1	2	6	3	4	7	3	1	5	2	1		1			
Total	4	7	18	23	19	22	34	33	33	35	41	29	19	17	10	8	4	5	10	1	2

form family groups noted in dominant antbirds (Willis 1973a, 1979).

Table 11 lists numbers of Fire-Eyes at swarms of army ants (*Eciton burchelli*) in different months at Belém. These were aggregations of disputing pairs, young birds, and wandering birds and not social groupings though birds parasitize each other by following successful birds to good foraging places over the ants. It is possible that birds avoid ant colonies with few birds, for hawks may catch birds more easily when fewer birds keep watch, but Table 11 indicates that few swarms of ants lacked Fire-Eye attendants. Six to eleven birds were commonly encountered at each swarm, with the large colonies and nomadic or unusually active ones attracting more birds.

In the past, it was often assumed that persistent aggregations of this type could not occur with the simultaneous presence of territoriality. (Brown 1975 still accepts the old assumption, but his reasoning is primarily an appeal to convention.) Willis (1967) showed this assumption to be incorrect for Bicolored Antbirds, and later for other species of ant-following birds, which aggregate but show territoriality via dominance hierarchies: the bird on its own territory dominates others. This is apparently the case for Fire-Eyes, as explained under "agonistic behavior." Pairs tend to separate out on their own territories and usually wander in their own territories when not following ants or a recently visited colony. In the evening they are usually on territory, and the songs at dawn usually come from birds on territory. In most antbirds of this type, nests usually occur on territory, but information is lacking for Fire-Eyes. Home ranges of pairs sometimes overlap, even if territories do not (Figs. 14-16).

Habitat selection is an important aspect of spatial behavior for Fire-Eyes. At Belém, they were most common in second growth, common in várzea, and less common in tall forest (Table 12). In August to November, when numbers are low, densities ranged from 23-58 birds per km^2. Independent young birds were more common in várzea (Area I) and capoeira (Area III) than in terra firme (Area II) due in part to the movement of several young birds from the terra firme zone to capoeiras. (One young female moved to várzea but later returned to terra firme; transfers were about equal between Areas I and II.) From April to August, 1972, I encountered six young in the terra firme area, or one per pair; in capoeira, only two young were encountered for five pairs of birds. The young birds thus moved in the directions of higher adult densities, from the terra firme zone that produced more young per pair than did capoeira. Várzea pairs seemed to produce about as well as did terra firme pairs, between September, 1972, and May, 1973; i. e., five young for six pairs in Area II, five young for seven pairs in the western 56 ha of Area I. It seems that nest success

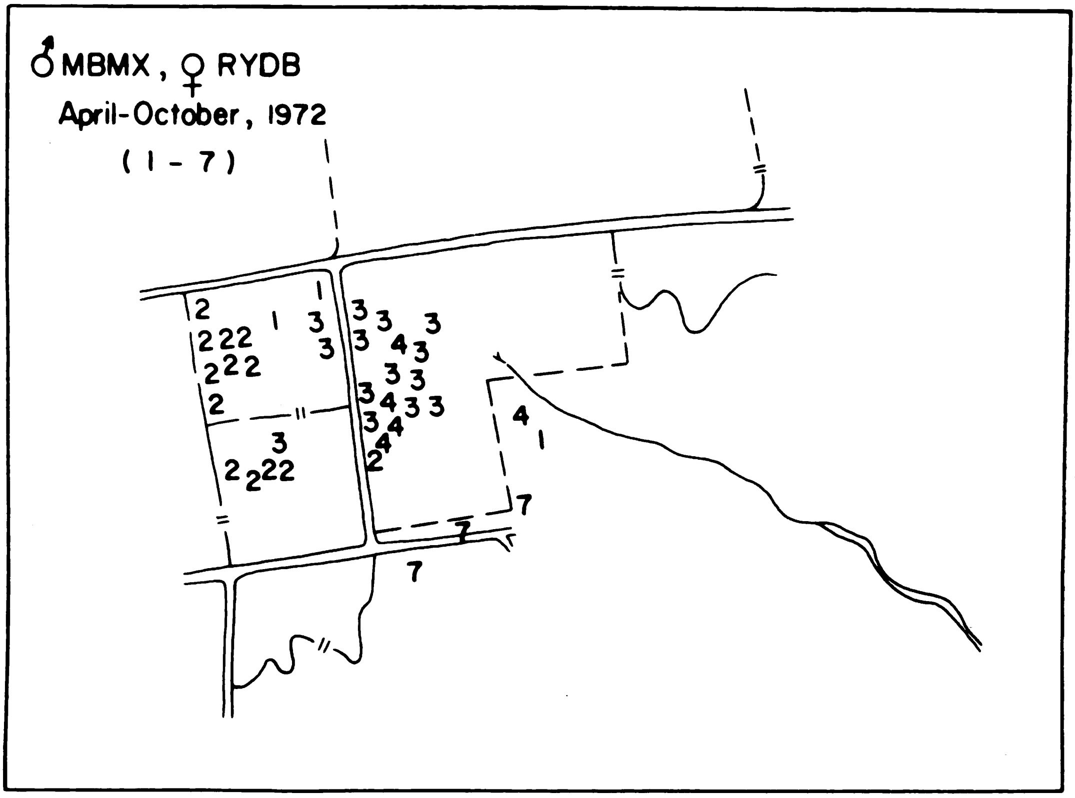

Figure 14. Locations recorded for a pair of White-backed Fire-Eyes of Study Area III.

may be higher in terra firme and várzea even though (or because?) adult densities are higher in capoeira; but direct confirmation is lacking. A major factor promoting high densities in capoeira may be that *Phlegopsis nigromaculata* rarely forages there; but it and Fire-Eyes were both more common in várzea (Area I) than in Area II.

At Santarém, Fire-Eyes occur only in borders of forests and not within extensive upland forests, where *Rhegmatorhina gymnops* (Willis, 1969) seems to occupy their niche. Southward, they live mostly in second growth and vine-tangled dry forests, and westward they are restricted to tangled montane forests along the Andes, avoiding the tall Amazonian and Colombian-Pacific lowland forests occupied by antbirds of the genera *Rhegmatorhina* (Willis, 1969), *Gymnopithys* (Willis, 1968a), and *Pithys*. They extend into scrubby forests, such as sandy woodlands at the base of cliffs in the headwaters of the Paraguay River (Willis, 1976b) but do not occur in cerrados, caatingas, chacos, desert scrub, or other semiopen forms of vegetation. Thus, they occupy the center of the habitat gradient from tall tropical or subtropical forests to open pastures, fields, or páramos - except when, as near Belém, there are not other competitors to keep them out of tall tropical forests.

They avoid following army ants out into open pastures, but forage from the edges of the woods or in piles of brush as long as there is shade. I have not seen them stay in sunlight long except when sunning. Brushy pastures are used at times, as long as there is fairly continuous cover. Birds may cross wide roads or rivers, but I have no evidence of their crossing open zones wider than a few meters. Even the lower Aurá River was never crossed while I was watching, although the

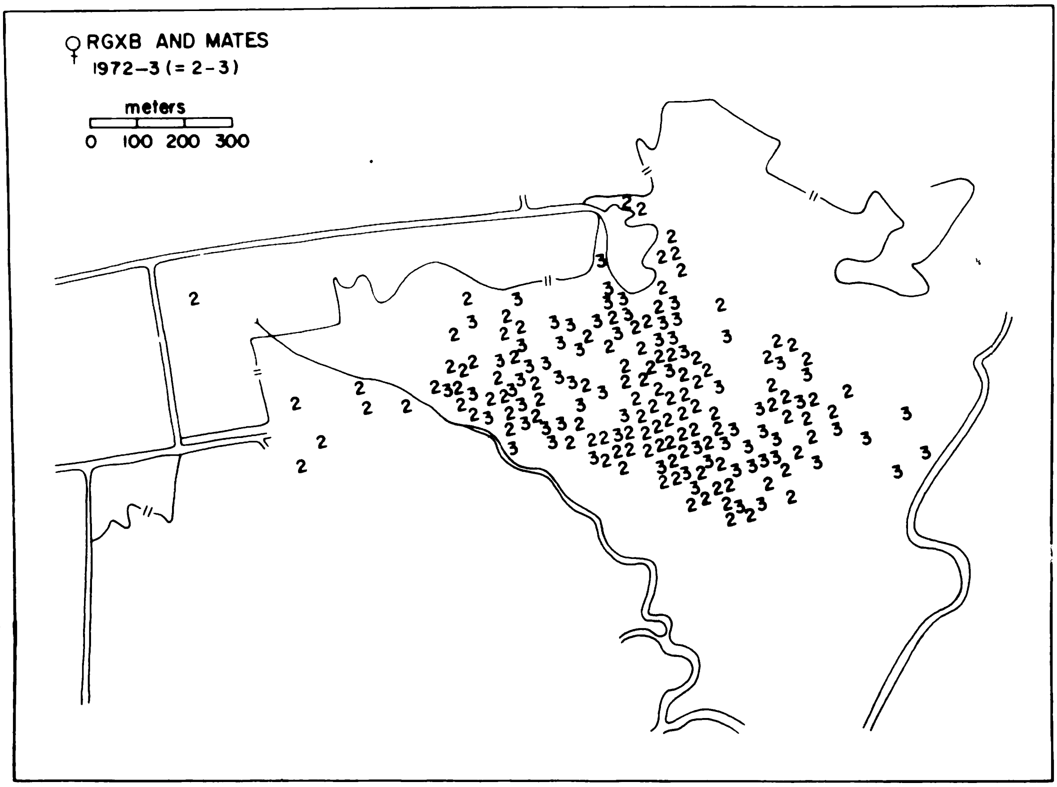

Figure 15. Locations for a pair of White-backed Fire-Eyes of Study Area II. The male was still present in 1976.

smaller branches of the river were readily crossed.

Mortality rates seemed moderate to high among adult and subadult Fire-Eyes at Belém. There were several cases where a female or male lost the mate and gained a new one during the fourteen-month study period. In the south central part of the terra firme area, 3 of 6 adult territorial birds were replaced between May, 1972 and April, 1973. The capoeira area was cut in September, 1972, so information is lacking. I worked the várzea area only from October, 1972 to May, 1973, and observed little mortality. When I returned in October, 1974, few banded birds were left in the terra firme area but fair numbers survived in the várzea area. Seven of 10 birds in the western várzea were still banded, 3 of 7 in the southern terra firme, though 9 of 10 were banded in both areas in May, 1973. In the northern terra firme, only 3 of 10 were still banded, but in this area no more than 7 of 10 had been banded in May, 1973. In August, 1976, I returned briefly to the southern terra firme area and found 3 of 12 or so birds still banded (all banded birds were adult males).

Thus the data suggest that mortality rates of adults are lower in the várzea than in the terra firme areas, where they seem near 50% per year. The várzea and terra firme both produce many young, and hence birds accumulate in the várzea areas but population levels remain low in terra firme. However, the equal movement of young birds between these areas suggests that both areas are about equal in feeding opportunities despite density differences. The situation in capoeira is uncertain but may well involve high adult and high nesting mortalities. In this case, the high population densities there may involve immigration from the várzea and terra fir-

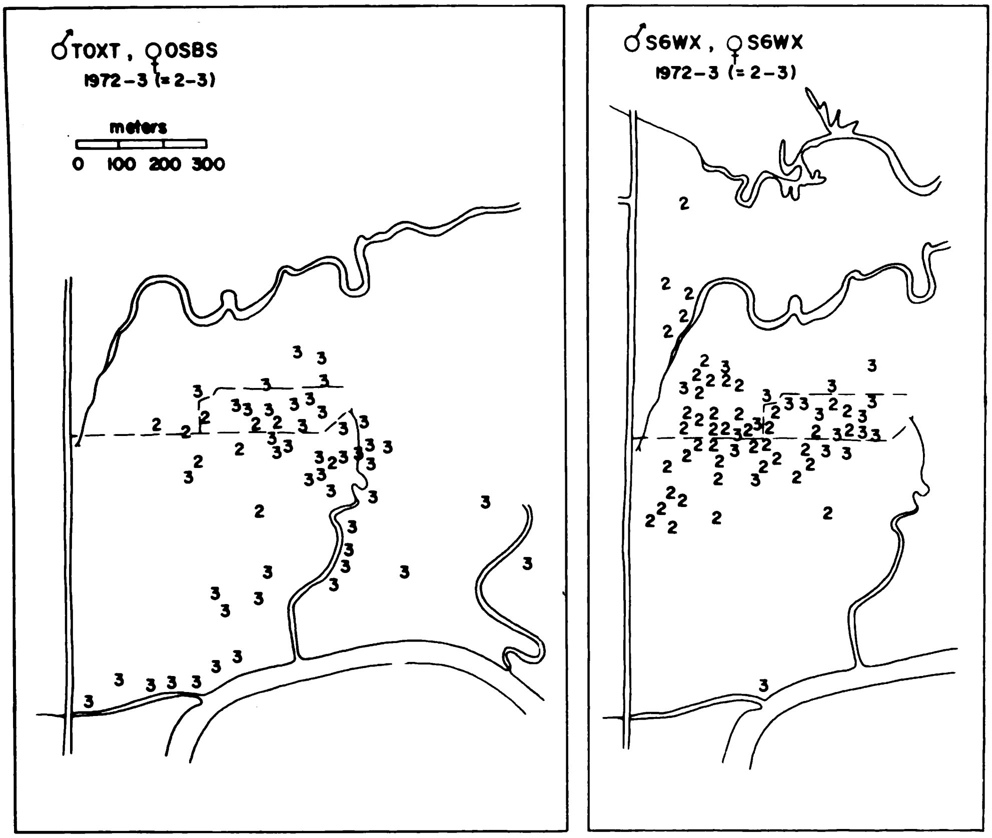

Figure 16. Locations for two pairs of White-backed Fire-Eyes in Study Area I.

me. The possibility of variation in mortality rates from year to year should be kept in mind, however; Black spotted Bare-Eyes in terra firme had high survival 1972-1974, then very poor survival 1974 to 1976 (Willis, 1979), One hawk arriving in an area can cause sudden changes in mortality, as Brown (1974) found for banded jays in Arizona.

Despite high mortality rates, some Fire-Eyes live for several years. Male MBMX, banded on 5 October 1967, was still alive 13 October 1974, even though he had been forced to move out of his rubber plantation territory when it was cleared in September, 1972. Male SBXG, banded 2 July 1971, was still alive in early August, 1976 and on his terra firme territory.

Table 12. Densities of White-backed Fire-Eyes at Belém

Area	*Habitat*	*Size*	*Densities per km²*				*g/ha*
			Ad. Male	Ad. Fem.	Yg. Male	Yg. Fem.	
I	Várzea[a]	78 ha	12.8	12.8	10.7	7.7	14.7
		56 ha	12.4	12.4	10.7	7.1	14.2
II	Terra firme[a]	77 ha	8.2	8.2	4.5	1.9	7.7
III	Capoeira[b]	24 ha	20.8	20.8	12.5	4.2	19.6

[a] November 1972. [b] August 1972.

THE BEHAVIOR OF WHITE-PLUMED ANTBIRDS

André (1904), Haverschmidt (1968), Oniki & Willis (1972) and others have noted that one of the most attractive members of the guilds of ant followers in northern Amazonia is the small White-plumed Antbird *Pithys albifrons*. Here I report on its behavior as a species low in the interspecific peck order, for comparison with White-backed Fire-Eyes and Spotted Antbirds (Willis, 1972a).

Study areas

For periods of a few days to a few weeks in 1961 and 1962, I observed the behavior of White-plumed Antbirds at Nappi and Bartica, Guyana (Willis, 1972c; Oniki & Willis, 1972) and at Tres Esquinas and Umbria in Colombia. In 1965 and 1966, I studied the species briefly at Zatzayacu and Yaapi in eastern Ecuador, at Leticia and Mitu in Colombia, and Reserva Ducke near Manaus, Brazil. In 1972-1976 I studied it in Brazil near Serra do Navio, various places near Manacapuru, and at Km 60 (the biological station is at 60º 03'W and at 2º 36'S) on the road from Manaus to Caracaraí. The main studies, however, were done at Reserva Ducke (headquarters at 59° 59' W and about 2º 56' S; described in Willis, 1977) from 1-14 September 1972, 3 July 1973 to 27 August 1974, and 21-28 July 1976.

At the Reserva, the two main habitats used by White-plumed Antbirds are a tall and diverse forest on yellow soils of flat upland areas (at about 100-120 m elevation) and a somewhat lower forest with many palms in sandy soils of valleys of small creeks (at 60-80 m elevation). Stemless tufts of palm leaves are common in the understory of upland forest, and offer nesting sites. The undergrowth is otherwise rather open, with many vertical saplings, as in many other tropical forests. Patches of dense grasses occur in swampy areas along creeks, however.

Near the main highway, open zones border on second-growth areas of various ages. Forest reaches the road only as a narrow peninsula at the reserve entrance. Along the side dirt road to the headquarters of Reserva Ducke are various types of experimental forest plots: forest patches with the undergrowth partly or wholly cleared or in various stages of dense regrowth; "forests" with various percentages of the upper-story trees removed; and tree plantations with or without large trees left for cover. Outside the boundary of the reserve, occasional cutting of trees for lumber and palm leaves for thatch modifies the peripheral 1-2 km of the forest considerably. Even the forest of the reserve has logging roads, hunting and forestry trails, and some extensive zones of what seem to be old second-growth woodland. Such man-modified areas, capoeiras, and forest borders were used by White-plumed Antbirds, but nearby semiopen or open zones and orchards near houses were not.

Methods

Methods of study were similar to those for studies of Fire-Eyes. The army ants at which I observed White-plumed Antbirds were mostly *Eciton burchelli;* once each at Km 60 and Tres Esquinas and twice at Mitu, pairs were at swarms of *Labidus praedator;* at Umbria, some followed a raid of *Eciton rapax.* 83 White-plumeds were captured one to several times for banding, weighing, etc, in mist nests set near swarms of army ants. Maps are based on compass and pacing and on foresters' maps at Reserva Ducke.

Characteristics, taxonomy and distribution

The White-plumed Antbird is unusual among antbirds in having long white forehead and chin plumes, which frame a small black bill and form a white "arrowhead" (Fig. 17). The head is otherwise blackish, except for a white stripe behind the dark eye in the nominate subspecies. The back and wings are blue-gray, with slightly darker feather tips. The tail and rump are rufous, as are the underparts and a collar around the neck. The legs are orange. The head plumes of the species are often illustrated incorrectly, sleeked close to the head as in specimens or when the bird is dissecting prey (Me-

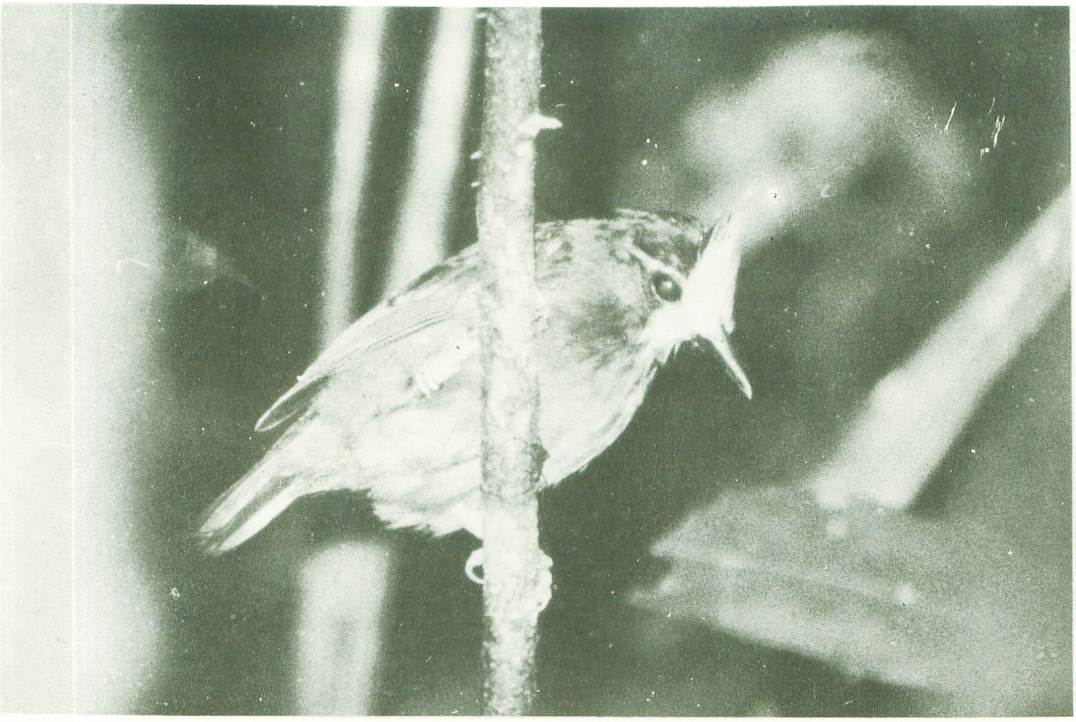

Figure 17. White-plumed Antbirds. Above, foraging adult. Lower right, foraging young bird. Lower left, male 8 months old sitting in possible nest site.

yer de Schauensee 1970, plate 36; Grzimek 1973, opposite page 127) or expanded in an unnatural way somewhat like aggressive threat (Haverschmidt 1968, plate 25). Young birds have rufous tips to the secondaries and have grayish heads without white head plumes or rufous collars (Fig. 17). Birds keep the rufous tips for some time after they otherwise seem adult.

White-plumeds range in forested regions north of the Amazon from Amapá and Cayenne westward to the bases of the Andes from southern Venezuela to northern Peru. The greatest recorded elevations are 2250 (meters?) on Mt. Duida, Venezuela, and 1800 m in the Cordillera Cutucu, Ecuador. On the lower Andean slopes, the species ranges south across the upper Marañon to the Apurímac River (Hacienda Luisiana) in Peru. The only other species of the genus, the White-masked Antbird (*P. castanea*), is recorded with *P. albifrons* at Andoas, Pastaza River, northeastern Peru.

A record from the Arapiuns River, south of the central Amazon (Pinto 1947: 474), is probably incorrect. The specimen (in the Museu de Zoologia, São Paulo) dates from June, 1936, in the middle of a six-month period when the collector, Lasso, was working near Macapá, Amapá, and not south of the Amazon (Pinto 1947:312). Two other Lasso specimens from "Rio Arapiuns" (in the Museu Goeldi, Belém) date from June, 1937, when the collector was indeed south of the Amazon. Possibly 1936 or 1937 is correct for all three specimens, but I hesitate to base records on Lasso specimens. These specimens were numbered and labels added later by a museum assistant (F. Novaes, pers. comm.), a practice which has led to such anomalies as a southern subspecies of *Pyrrhura picta* within the range of a northern subspecies and north of the Amazon (Novaes 1974:45). I have expressed doubts about a Lasso specimen of *Phlegopsis nigromaculata* north of the eastern Ama-

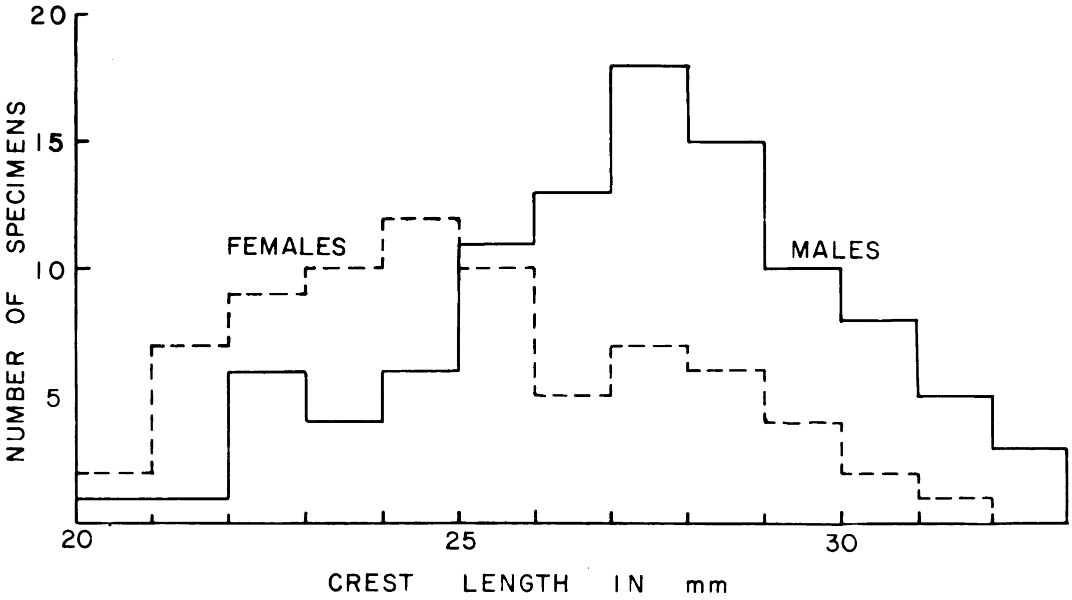

Figure 18. Crest lengths of specimens of male and female White-plumed Antbirds.

zon, and conclude that the *P. albifrons* and *P. nigromaculata* records of Lasso should not be used to prove Amazon crossings as Sick (1967:500) and others have proposed. Known cases of Amazon crossings involve mostly swamp-forest and open-country or treetop birds, not birds of the upland forest interior.

Weight, temperature, molt, and sexual dimorphism

Weights of 76 White-plumed Antbirds ranged from 18.8 to 24.9 g ($\bar{x}$ = 21.5 g), with adults and independent juveniles averaging about the same. Seven Peruvian birds (P. Wyrwich, Rio Pachitea) and 12 Surinam ones (F. Haverschmidt) averaged the same weight, but 10 other Surinam birds (G. Mees; $\bar{x}$ = 20.5 g) and 56 Cayenne ones (J. Dorst collection; $\bar{x}$ = 19.8 g) weighed less, probably because they had lost weight in mist nets before collection. Cloacal temperatures of 59 Manaus birds ranged from 40.5° to 43.7°C ($\bar{x}$ = 42.5°C).

Juveniles molt the wing feathers soon after they become independent. Adult wing molt is quite variable, slow, and irregular, especially in birds that are breeding; some individuals apparently interrupted or slowed molt for a month or more during nesting periods. Some breeding males showed irregularities in molt, with inner primaries molting after outer ones. Other irregularities included widely separated primaries in molt equally on both wings. Wing molt of birds in adult plumage did not seem restricted to any particular part of the year, being recorded in every month but February and March (I examined only one bird in those months); in nearly every other month, birds in molt slightly outnumbered those not molting.

Wing molt in the individual apparently takes six or seven months, as determined by recapturing a few birds. Of 603 seemingly adult specimens in museums, 335 were in wing molt, indicating that the average individual spends 5/9 of its adult life in wing molt and independently confirming the estimated time of molt. This also indicates that the birds are molting every 12 months rather than on some other schedule, or there would be too many or too few specimens in molt.

In September to December, 147 of 219 specimens were in molt, indicating extensive molt in the drier months of the year in most of

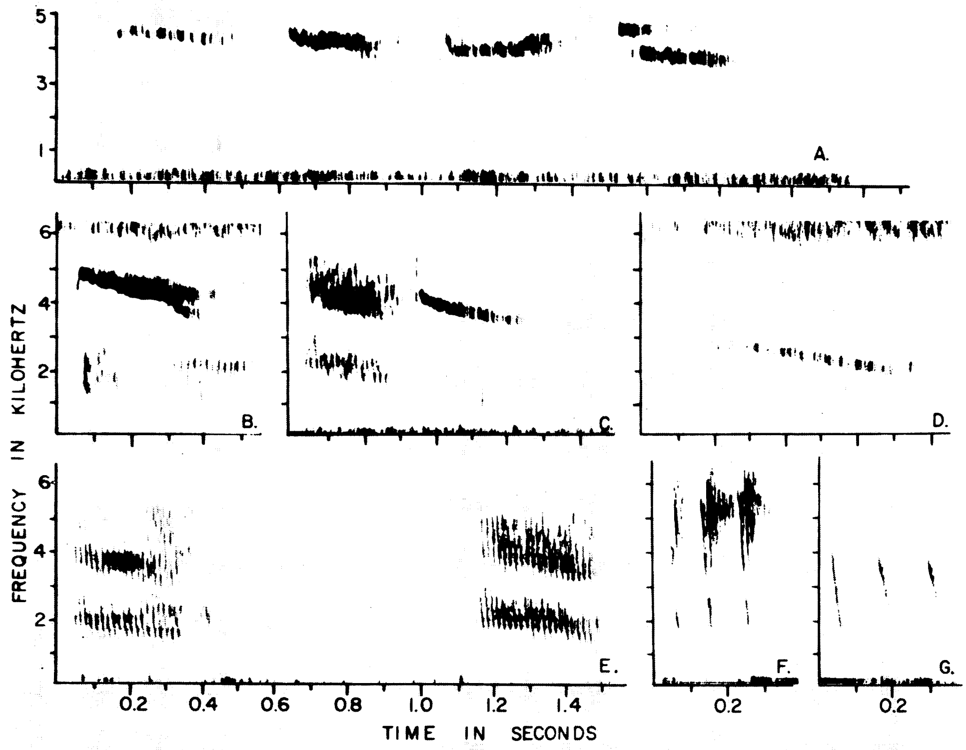

Figure 19. Sound spectrograms of calls of White-plumed Antbirds. A. Four-noted loudpeep of immature trying to find place over ants. B. Loudsong. C. Chirr and loudsong. D. Snarl. E. Two chirrs. F. Three chips. G. Tweeting ("si-si-si").

Amazonia (in months of slightly lowered reproductive activity at Manaus). Included, courtesy of J. Dorst and C. Erard, is a recent September collection from Cayenne with 24 of 36 birds in molt. In January to May, 107 of 234 birds were in wing molt. Some of the peak late in the year and of a minor peak in June and July is caused by molt of young birds hatched in the breeding peak of January to March.

I did not find any certain method of sexing birds, except by noting courtship feeding of females by males and wingwaving displays by a few males. Commonly the female of a pair had a shorter crest than her mate. Males molting the longest crest feathers, however, become as short-crested as females. Crest lengths (measured from the base of the culmen to the tip of the longest feather) of 176 specimens indicate much overlap between males and females, but the mode of male crest length is about 3 mm greater than that of females (Fig. 18). Slight bimodalities of measurements of both male and female crest length suggest that some specimens were sexed incorrectly; certain collectors were especially likely to label short-crested birds as "males" and long-crested birds as "females", as if missexing or mislabeling.

Voice

Some eight calls of White-plumed Antbirds are enough like those of Bicolored Antbirds (Willis 1967) to use similar names, but three others are different. The species is very quiet, with most calls short, simple, and dif-

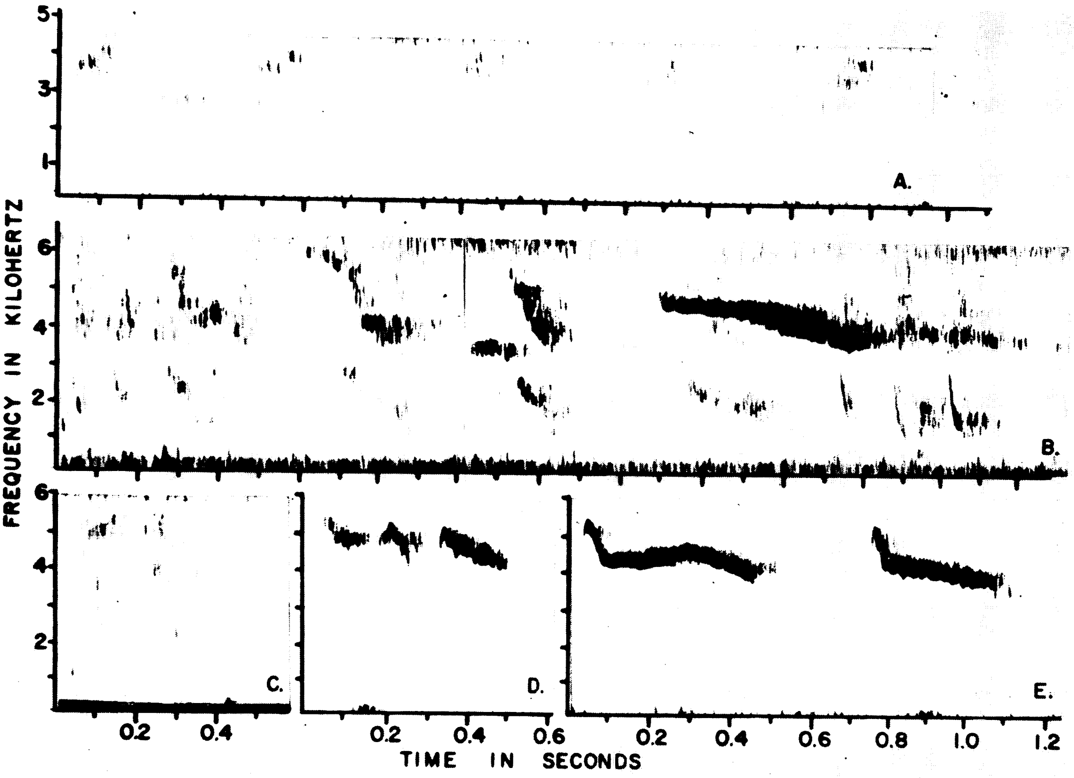

Figure 20. Sound spectrograms of calls of White-plumed Antbirds. A. Zeesong. B. Twitters and loudsong of bird attacked by *Gymnopithys rufigula*. C. Squeaks of young. D. and E. Loudpeeps of young bird.

ficult to locate compared to dominant antbirds. It also has few kinds of calls (9 adult, 2 juvenal) compared to other species.

Song. White-plumed Antbirds give a single thin note, "pseeeeeeeeeeeeeh!" (Fig. 19B), that apparently corresponds to the loudsong of related antbirds. It is similar to the double-noted song of Pale-faced Antbirds *(Skutchia borbae)*. As in related antbirds, songs are used between mates and young separated by vegetation, and by individuals searching for ants; use in agonistic or territorial contexts was not noted with certainty for White-plumeds (but, see "chirring" and "loudpeeping," below). Faint versions of the song are commoner than are loud ones.

Tweeting. A series of three or so short, soft notes, "see-see-see" (Fig. 19G, Fig. 20B) is given when an adult leads or searches for a young bird or mate. Tweeting sometimes alternates with faint squeaky "beie, beie, beie" notes as a continuous sinusoidal serpentine-tweeting when the young or mate does not appear rapidly.

Zeesongs. The strangest vocalization of any antbird known to me, completely different from any call of related species, is a series of buzzy calls (Fig. 20A) that can be approximated by whispering "Z" over and over at somewhat less than two times per second for up to 186 seconds (over 300 calls!) The zeesong often begins with a rising series of 5 to 10 soft "wherr" notes, and may slow and fade until nearly inaudible after sharp noises only to return to the original volume and speed each time. Males give a wing-waving display as they zeesing far from other birds.

Chipping. A short "chip" is a common alarm note, much as in other species of ant-following birds (Fig. 19F).

Chirring. A buzzy "chirrr," much like that of related antbirds, is a response to humans and other nuisances (Fig. 19C, E). Short chirrs at times follow a long chirr: "chirrr, ch-ch-ch." If keening exists as a third alarm call in this species, it would be hard to distinguish from a weak or soft song.

Squealing. Short "chieh" or "squeeh" cries are sometimes given when a human or a clawing Rufous-throated Antbird *(Gymnopithys rufigula)* captures a White-plumed. Squealing differs little from a faint song or snarl and may be a form of one or the other.

Snarling. A very faint and low-pitched "wrieehh" in aggressive threat (Fig. 19D), barely but consistently distinguishable from a faint version of the regular song, seems to correspond to snarling in related antbirds.

Puffing and Snapping. Attacks on other White-plumeds are usually silent, but at times there is a sudden faint vocal "sniff," much as in louder attacks in related species. Snapping of the bill is a rapid, high "snip-snip-snip" or the like.

Trilling. A rapid faint "tree-e-e-e-e-e-e-e-e-e-e" series, varied at times with double notes, is given when a male feeds a female. The notes may be rapid tweeting rather than a separate kind of sound.

Loudpeeping. As in related antbirds, the young bird gives loud songlike notes, e. g. a very loud "pseeeeh," louder but shorter than the adult song, when still dependent on the parent, and loud series of 2-5 notes, "pseeeee, seeh, hee-hee-heet", when forced to forage among hostile birds of other species as its parent begins to desert it (Fig. 19A, 20D, E).

Squeaking. Rough "squahh" and other notes, as in other young antbirds, mark feedings (Fig. 20C).

Postures and movements

The "standard" posture of White-plumed Antbirds on an inclined perch is much like the posture of the adult in Figure 17. The crest and beard form an arrowhead. The tail is slightly below the line of the body as in most related antbirds. To perch on a vertical sapling, the bird extends the lower leg and flexes the upper one; details of the posture are much as in Bicolored Antbirds (Willis, 1967). Toes II and III of the lower foot are inclined and together.

The most characteristic movement, as in Bicolored Antbirds and unlike Fire-Eyes, is "flicking" the tail, i e., the tail drops slowly and then jerks back to the line of the body. In this and other movements, the bird seems very light and quick. The head flicks back and forth, flashing the head plumes in a winking fashion that makes the bird hard to see. However, a tame bird can remain immobile for long periods with only slight head and tail movements.

Movements on the perch include swinging around it (pitching), turning to right or left (yawing) or completely about (reversing), and to a lesser extent inclining the body (rolling). Movements tend to be abrupt and rapid. A bird sometimes jumps from one perch to another or hops on the ground, but most movements between perches are short, rapid flights. Erratic, sudden zigzags often occur, the bird alighting on one perch only to leap or fly to another at the same instant. In flight, the white head plumes make the dark bird hard to see; a fast-moving small white spot, like a disembodied white arrowhead, darts through the forest understory and disappears or stops, and one has to focus carefully to see that a dark bird is attached.

As in related antbirds of the forest undergrowth, flights are usually short (up to 50 m each) and 1-3 m above the ground. Flight is direct and fast, with rapidly beating wings. Alighting is abrupt, without gliding, as is jumping from a perch.

Alarm behavior

The alarm behavior, or antipredatory behavior of White-plumeds, involves 1) freezing, 2) panicking and flight, and 3) mobbing.

Freezing and immobility. Foraging White-plumeds sometimes remain almost immobile for long periods, a behavior that reduces chances of attack by larger antbirds and also must reduce predation. (Scale-backed Antbirds, *Hylophylax poecilonota,* use this technique almost to the exclusion of others and are much more persistent at it

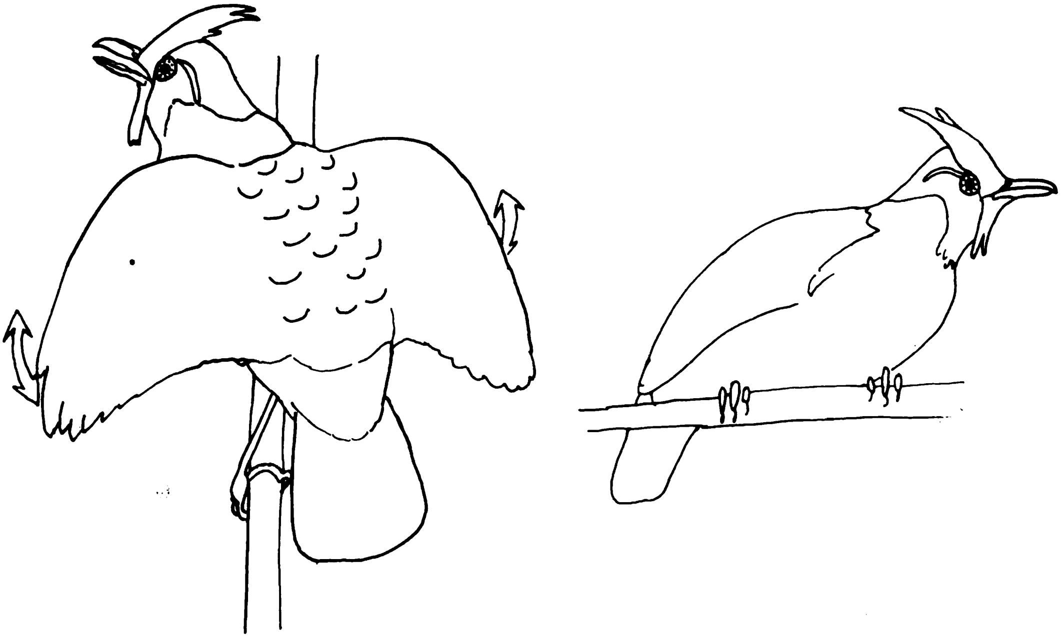

Figure 21. Postures of White-plumed Antbirds. Left, wingwaving while zeesinging. Right, crouching and freezing.

than are White-plumeds.) Probably, as a subordinate that often stays at the edges of competitive aggregations of birds, it would otherwise be in great danger of predation. It is difficult to say if this immobility becomes a distinct display upon the appearance of possible danger, for the faint high notes of "songs" in the species are almost exactly like the alarm calls of "keening" used by related antbirds when freezing. The songs themselves are also difficult to locate, for the reasons Marler (1955) noted for "hawk-alarm" calls of many passerine species. Faint notes given in immobile positions often resemble faint versions of songs and may serve to warn other individuals of the species, but I do not know if others interpret the faint song-like notes as warnings. In general, freezing and related calling seem not to be well developed, at least not in any altruistic or display form.

Ducking the head and crouching (Fig. 21, right) were twice recorded as reactions to alarm calls of *Dendrocincla fuliginosa*. Short songlike notes, perhaps keening, were given on one other occasion each in response to alarm notes of woodcreepers and to songs of a distant forest falcon, once in response to a forest-falcon *(Micrastur ruficollis)*, once at alighting hawklike Red-fan Parrots *(Deroptyus accipitrinus)*, and on various occasions to general alarm. It is likely that individuals regularly freeze or crouch at distant alarm calls, but immobility does not seem a major antipredatory strategy.

Panicking and chipping. Panicking, fleeing, and chipping seem very well developed, even hypertrophied, in contrast to freezing. At the slightest sign of danger, freezing is quickly replaced by rapid darting back and forth with chipping notes - a "chip and zip" syndrome. Spread tails flick rapidly. Birds dash hurriedly for last prey items, so that I often wondered if increased nervousness in situations of little danger might not help them scare dominant competitors into hiding.

White-plumed Antbirds are very light, large-winged, and fly well; they are thus well adapted to create confusing movements. Their white-plumed heads probably help serve as "disruptive coloration", breaking the pattern of the dark body with a white and very unbirdlike arrowhead, during the sudden and unpredictable movements back and forth.

White-plumeds commonly travel very rapidly between swarms of army ants, so that they are difficult to detect unless an adult is leading a young bird and tweeting ahead of its loudpeeps. When arriving behind me enroute to the ants, the bird often whirred in, reversed instantly, fled to the rear 10 m or so, and then circled in to the ants. In dashing about in situations of alarm, a common stratagem was to fly several meters and alight only momentarily on the perch that seemed the goal; the bird at once fled a short distance backward or to the side to another perch, in a zigzag with a long zig and a short zag. Sequences of these hooking zigzags made a very confusing pattern.

The movements of the feathers and other parts of the body in panicking are similar to movements of body parts in related antbirds. The flicking tail is commonly spread. The wingtips periodically flit out rapidly. The head jerks one way and then the other, flashing the white plumes confusingly but prominently. When the white plumes turn away, the bird seems to disappear. I did not note sleeking or spreading of the white plumes, though sleeking of head occurs in panicking relatives. A bird crossing a road had the crest plumes sleeked back, possibly for flight.

Chipping or fleeing was recorded 22 times in response to *Micrastur ruficollis*. Large birds gliding past or flying past caused chipping at times *(Dendrocolaptes picumnus* passing or fighting, 4 times; *Dendrocincla fuliginosa,* 1; *Ortalis motmot,* 1). Attacks by competitors *(Gymnopithys rufigula,* 2; *Pithys albifrons,* 1) or ants (1), falling fruits (1) or branch (1), a brocket *(Mazama americana)* racing past, and large Saturniid moths waiting immobile near the ground also caused chipping or panicking. Alarm notes of other birds *(D. fuliginosa,* 4; *Dendrocincla merula,* 2; *Dendrocolaptes picumnus,* 1; *Monasa atra,* 1) caused chipping at other times.

Although chipping and panicking are well developed in White-plumeds, the call is usually single rather than double (as in *Gymnopithys rufigula* and other moderately dominant antbirds) or triple as in *Dendrocincla merula* and other very dominant antfollowers, such as Ocellated Antbirds (Willis, 1973a).

Mobbing and chirring. Reactions to humans, as in many other ant-following relatives, are chirring and mobbing behaviors. Naturalists often think chirring the characteristic call of such birds, not realizing that tame birds seldom chirr. Chirring was also a reaction to tayra *(Eira barbara),* peccary *(Tayassu tajacu),* big Saturniid moths waiting on the base of a palm tuft, to *Micrastur ruficollis* (5), to a canopy hawk *(Leucopternis kuhli,* 1*),* to attacks by competitors *(Gymnopithys rufigula,* 1; *Pithys albifrons,* 1*)* or close approach or prey captures by them *(Dendrocincla fuliginosa,* 1; *D. merula,* 1; *Hylophylax poecilonota,* 1; woodcreeper, 1), to a dispute between two *Dendrocolaptes picumnus,* and to repeated alarm notes of a *Myrmotherula gutturalis* near its nest. Nuisances that interfere with foraging and other activities are thus the main stimuli for chirring and mobbing.

I did not note spreading of the head plumes in mobbing, but related antbirds commonly ruffle head feathers when mobbing. Other movements of the feathers, such as spreading the tail and raising it to horizontal, were much as in related species. Swinging back and forth to show the face, a common mobbing pattern in bare-faced species of antbirds, was not noted. Chirring and mobbing are common in the species, even more so than in dominant antbirds, in contrast to relative infrequency of mobbing in Fire-Eyes. It does have the problem that a passing mammal can easily usurp its foraging sites, for it depends on narrow areas remaining between dominant birds over ants, and these birds shift about when a mammal passes. Chirring, chipping, mobbing, and panicking often mix in birds forced to forage near the observer. Songs often mark movements of birds hunting mates or protected places to forage. On various occasions, mobbing or other alarm notes of timid birds of this or other species caused tame birds foraging near me to look my way and chirr or move away.

Habituation to hawks and humans. I found it unusually difficult to tame White-plumeds, mainly because they are adapted for traveling to distant swarms when expelled by dominant antbirds, and hence often left for another swarm when I appeared. Spotted Antbirds (Willis, 1972a) were also somewhat slow to tame because individuals often foraged away from me and ants; Fire-Eyes became tame when they had to forage near me, but not as tame as dominant antbirds in the same area. Eventually some White-plumeds became tame, losing mobbing and panicking behavior. No adult bird ever became curious enough to fly up to me and investigate me at close range. One young bird at Umbria in Colombia flew over and peered at me, giving loudpeeps now and then as it waited for its parent. Few used me as a foil against domineering antbirds when foraging, partly because tamer subordinate or young birds of larger species normally took that niche.

Some habituation to Barred Forest-Falcons was observed. The sudden dash of a forest-falcon to the center of an antswarm usually scattered chipping White-plumeds and other ant followers in all directions, even if repeated several times a day. If, however, the falcon stayed over the ants and began to hunt insects with short flights to the ground or by running along the ground, White-plumeds usually began to chirr in concealment, sing and regroup, and move closer to the ants. Finally the braver individuals, tails flicking nervously, began to forage at corners of the ant swarm away from the falcon, watching it silently and scattering quickly if it flew in their direction. Eventually some individuals foraged within 5 m of the falcon, even to 2 m away in some cases. Colonies of ants that picked up a forest-falcon for several days in a row often lost birds, but White-plumeds seemed braver than other species. It seemed that they trusted in their considerable ability to fly rapidly and lightly, whereas larger dominant antbirds were too slow-moving to forage close to a falcon. However, a White-plumed Antbird foraging near a falcon always seemed alert, watching it and fleeing instantly if it took wing.

Maintenance behavior

Mosquitoes cause quick twitches of the head or pecks into the air. Attacking army ants cause pecking at the toes, dancing about on the perch or sudden leaps 5 cm or more into the air, and finally flight. For a subordinate species, the White-plumed Antbird is attacked by ants rather often because, as noted below, it often infiltrates daringly among the dominant birds directly over the ants rather than staying at the outskirts of a raid.

The head is ordinarily scratched over the wing (17 records). During scratching, the crest is strongly sleeked backward. One bird wiped its head on the perch rather than scratching.

Preening birds were seldom observed, because preening sites close to the ants and the observer tend to be preempted by dominant species. Short bouts of preening commonly interrupt periods of waiting for prey over the ants, especially when an attentive nearby dominant antbird makes foraging dangerous. It is possible that much of the preening of White-plumed Antbirds is done in these short bouts, for they have such a difficult time getting food in situations of high interspecific competition that they forage or hunt for places to forage most of the time. They usually seem clean and neat, and must preen sufficiently.

Perches used by preening birds are much like ones used for foraging but tend to be slightly thicker and less inclined (Table 13). Dominant antbirds and many subordinate ones (Willis, 1972a; Fire-Eyes, this report) tend to move high when preening, making concurrent foraging difficult; such high perches are used less often by White-plumeds.

After preening, toestanding and full-side stretches (wing, tail and leg on one side) were noted. Probably other common stretching motions (yawning; half-flexes of wings above the back) occur also. Sitting or resting birds were seldom observed.

Bathing in a small creek, with fluttering and preening afterward, was noted once.

Table 13. Preening perches of White-plumed Antbirds

Height(m)	*No.*	*Angle(°)*	*No.*	*Diam.(cm)*	*No.*
0-0.1	21	0-20	36	0-1	31
0.2	25	40	22	2	34
0.3	13	60	16	3	4
0.4	13	80	3	4	2
0.5	4	100	6	5	4
0.6	2			7	1
0.7	3			10	4
0.8	1				
0.9	3				
1.0	1				
2.0	4				

The bird squats slightly to defecate. Opening the mouth and bowing the head slightly, regurgitating hard insect parts, was occasionally noted.

Selection of habitat undoubtedly helps avoid extreme temperatures; temperatures near the forest floor are very constant in a tropical forest (Allee, 1926, Brinkmann & Góes Ribeiro, 1971). Use of second growth, which becomes very hot at midday, was recorded only for early morning, late afternoon, and on cool, cloudy or rainy days. No bird followed ants into full sunlight or into open areas or remained with them in a zone in which I felt uncomfortably hot. However, chipping and tail-flicking and other signs of nervousness when foraging in capoeira or into the edges of open areas in the early morning indicated that this aspect of habitat selection could have been connected with alarm behavior rather than maintenance. Prey availability may also be less in not areas.

I did not observe sunning behavior. Temperatures of the species are about average for a small bird, hence below those of most of its larger dominant competitors; this is true even though it is an extremely active and fast-moving bird when not waiting immobile for prey. Body temperatures are well above environmental temperatures; maintenance undoubtedly requires such behavioral strategies as ruffling the feathers while resting - especially at night or on cool, rainy days. Immobile foragers often fluffed feathers and retracted the head, tactics that sugest heat conservation (Fig. 22).

Foraging behavior

Drinking water from a leaf on the forest floor was noted once. Probably most water comes from the insect prey.

White-plumed Antbirds, in contrast to most previously studied small and subordinate ant-following birds, seem completely dependent on following army ants. The extreme adaptations this has required extend to all types of its behavior, as noted above and below. Briefly, it survives in a hostile world by being speedy - a prototype for the "Road-runner" of cartoons, or of the "fugitive species" in ecology. It finds ants or active parts of the ant raid faster than larger birds, or it infiltrates among them and speeds away a few centimeters at each attack. Few other birds even try to forage within 5 m of *Micrastur ruficollis*. Speed perhaps helps lower predation levels when traveling between ant swarms, too. It is a dangerous and solitary traveling life, and apparently a short one, but reproductive rates are pushed up by quick divorces that put a female with a new male while her earlier male is still caring for the young one. The symbol of the species could well be the white arrowhead formed by its crest and beard.

I never saw a White-plumed Antbird foraging away from army ants (other than once apparently following white-lipped peccaries at Bartica in Guyana), but occasionally I saw or heard one traveling rapidly through the forest, as if going from one swarm of ants to another. At times I met banded birds at one colony, enroute between swarms, and

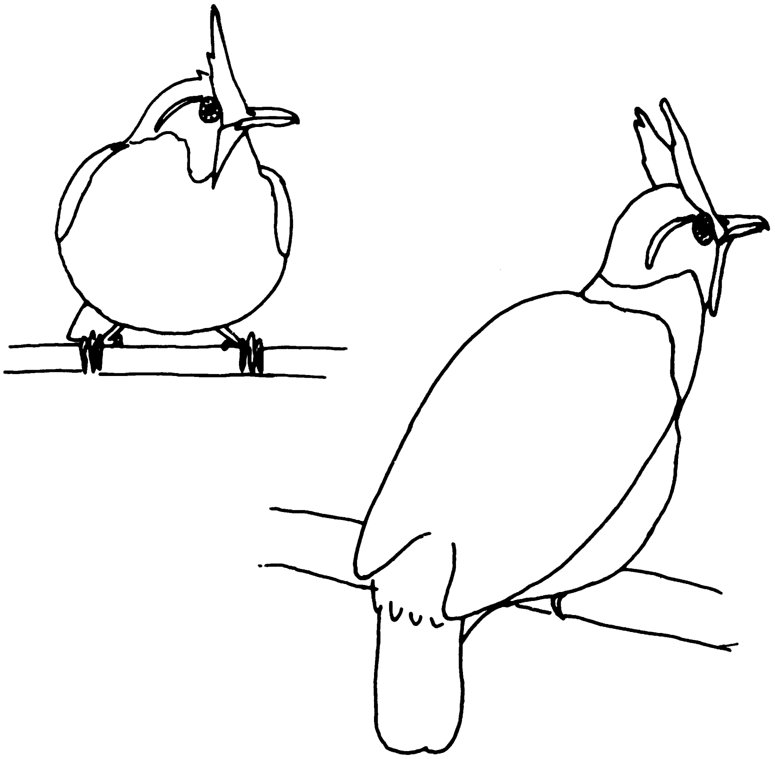

Figure 22. White-plumed Antbirds foraging with feathers fluffed.

at a second swarm. In the evening, I sometimes heard one or more birds zeesinging or singing in the sandy woodlands along creeks, but never managed to see them. Following them was generally impossible; individuals quickly become quiet and darted away in different directions. I never noted them following other species, not even other species of ant-following birds; but they were quick to come to sounds of ant-following species.

They investigate inactive statary ant bivouacs, arriving separately or in pairs (male-female, male-young, or female-young) in rapid passages that often require a mist net to confirm: at one colony that failed to swarm I caught nine separate birds in two hours with a mist net set 10 m from the bivouac. Birds follow ant columns to or from bivouacs, as one can quickly verify with a mist net or by standing along the ant trail. Most are unseen and unheard until they hit the net, and the rest are sudden whiffs of air passing the observer or faint songs well away from him. It is very easy to catch them with mist nets set anywhere near ants, and one soon builds up a long list of banded birds that are never seen again. New birds are constantly appearing, although some individuals may stay around for long periods.

When an ant colony stops raiding or enters a habitat unsuitable for antbirds, such as an open field or the open rows of a forest plantation, White-plumed Antbirds wander only for a few minutes before dispersing to distant colonies. Many birds visited two colonies the same day, and a few visited three; in the course of a few weeks some individuals visited four or five colonies. These individuals must have been at other colonies not known to me on the many interspersed days when I did not locate them. Transfers between colonies were very frequent although tame birds sometimes stayed with a given colony several days. Quite often sever-

Table 14. Characteristics of perches of foraging White-plumed Antbirds

Height(m)	*No.*	*(%)*	*Angle(°)*	*No.*	*%*	*Diam.(cm)*	*No.*	*%*
Ground	9		0-20	410	19	0-1	1146	57
0.1	454	20	40	187	9	2	595	29
0.2	794	35	60	127	6	3	148	7
0.3	522	23	80	184	9	4	43	2
0.4	210	9	100	1197	57	5	29	1
0.5	100	4	120	13		6	21	1
0.6	55	2				7	7	
0.7	34	2				8	9	
0.8	27	1				10	6	
0.9	11					12	2	
1.0	10					15	2	
2.0	23	1				20	14	1
3.0	5					25	5	
4.0	1							
	2255			2118			2027	

al new birds appeared at a colony one day and disappeared the next, as if another colony with which they were associated had temporarily entered an unsuitable habitat or acquired a dangerous hawk follower. White-plumed Antbirds are also very quick to move to other branches of a swarm of ants and to hunt parts of a swarm temporarily unoccupied by large competitors. They use many of the techniques used by Spotted Antbirds in evading large competitors in Panama (Willis, 1972a), e. g., foraging behind logs, near the observer (mostly young birds), behind, ahead or to the side of the other birds, etc. Their use of daring infiltration into the midst of dangerous large competitors is far greater than in Spotted Antbirds or even Fire-Eyes (see under interspecific agonistic behavior).

Most foraging, like preening, takes place near but not on the ground, so that this is not one of the subordinate species that moves up when larger competitors are present. Slight tendencies for high foraging noted by Oniki & Willis (1972) now seem, in retrospect, due to timidity of birds studied for short periods; timid birds tend to forage high. The 385 observations by D. Wechsler (included in table 14), peaking at 0.3 m rather than 0.2 m, also may reflect the definitely greater timidity of his birds. I had to be especially careful with this species, using mainly records of individuals watched for more than 6 months and hence fairly tame. Heights of 279 perches taken before attempts to capture prey tended to be slightly lower than those summarized in Table 14:28% below 0.1 m, 39% between 0.1 and 0.2 m; probably birds close to the ground get more prey. However, some prey was taken at 3 m above the ground (Table 15).

Vertical and horizontal perches are favored (Table 14), as in nearly all ant-following antbirds other than Fire-Eyes. I have noted that preening perches, by contrast, tend to be horizontal even though this species commonly preens while foraging. Angles of the 264 perches taken before attempts to capture prey were much like angles for all foraging perches. Diameters of perches are mostly under 1 cm; the small diameter of perches is about the only difference

Table 15. Heights of food capture for White-plumed Antbirds

Height(m)	*No.*
0-0.1	1690(95%)
0.2	26
0.3	11
0.4	13
0.5	6
0.6	6
0.7	8
0.8	1
0.9	1
1.0	3
2.0	11
3.0	5
Total	1781

Table 16. Foraging sites and methods of White-plumed Antbirds

Site	*Methods*			
	Sallying	Gleaning	Leaftossing	Total
Ground, log	1631	50	5	1686
Trunk	3	2		5
Stem, twig	2	16		18
Leaf	22	1		23
Debris	8	12		20
Air	6	2		8
Not noted	6	12		18
Total	1678	95	5	1778
Percent attacks[a]	10.7	1.1	0	9.8

[a] Percent of records resulting in attack by another species.

between this species and its nearest competitors at Reserva Ducke. As is true for other antbirds (except for *Hylophylax poecilonota),* perches over a few centimeters in diameter are mostly near the horizontal: only 4 of 38 perches of 8 cm or more in diameter were over 45 degrees in slope (none of 23 over 10 cm in diameter were over 45 degrees). Diameters of 262 perches taken before tries at prey were much like diameters of all foraging perches.

On its perch, a White-plumed Antbird waits quietly, cocking or turning its head in a fluff-bodied and short-necked stance (Figs. 17,22). When prey moves, the antbird darts at it instantly and flees with equal speed. Even a preening bird darts instantly for prey. All antbirds capture prey fairly rapidly, but the light and mobile White-plumed is especially rapid. Nearby larger species are often reduced to attacking the fleeing White-plumed as it carries prey away, unless the White-plumed does not try for the prey. Nearly 10% of attempts at prey capture resulted in attacks by other species of birds (Table 16). Very few attempts (0.7%) resulted in attacks by another White-plumed.

By far the commonest foraging method (Table 16) is sallying to the ground and back to a perch. Such sallies tended to be short mainly because larger competitors are often nearby; of 115 records, 43 sallies were within 0.1 m, 38 from 0.1 to 0.2 m, 22 to 0.3 m, and the rest scattered out to only 1 m away. Flying to snap prey off vegetation or out of the air was relatively rare, except when snapping prey off leaves. However, I did see one bird fly just over 4 m upward at 45° to snap an insect from the air; and another flew up 3 m at 45° to snap prey from a tree trunk. Pecking prey from the ground or other surfaces also was infrequent, and pecking prey off leaves especially rare. Pecking was much rarer than sallying for prey, even though pecking is inconspicuous and attracted few attacks (Table 16); probably few prey appear close enough to a bird to peck. At times a bird slides quickly and sneakily down a perch to peck prey on the ground (Fig. 23), then sidesteps up again. Or, it may swing downward across a vertical perch like a pendulum, pecking as it passes the ground. Tossing leaves on the ground (by grasping between the mandibles and flicking the head sideways) was rare, in part because dominant antbirds try to murder a White-plumed that pauses to toss leaves. Deep leaf litter therefore caused failure to capture prey at times. A leaftossing bird sleeks the crest and beard. The rarity of methods other than sallying to the ground is characteristic of dominant ant-following antbirds (Willis, 1973a), not of subordinate ones (e. g. Willis, 1972a), and reflects the extent to which White-plumeds usurp prey of dominant birds by being speedy.

Prey items are much the same as for other ant-following birds (Table 17), and prey are often about the length of the exposed part of the bill (some 14mm; in the field, length of prey is estimated as a multiple of this figure) or greater. This indicates that the

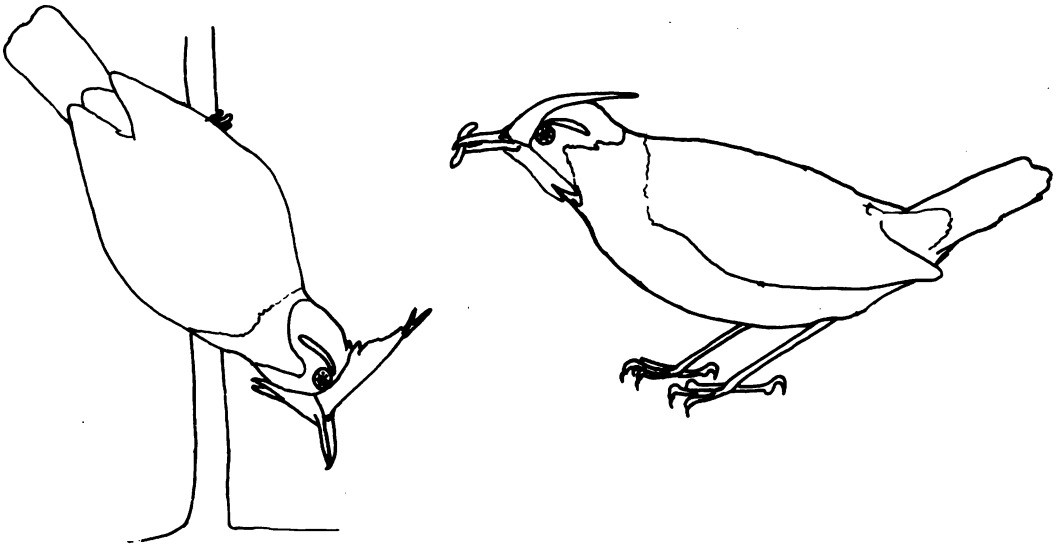

Figure 23. Foraging White-plumed Antbirds. Pecking prey from the ground by yawing inconspicuosly downward, left. Eating prey away from ants, right.

species is not avoiding large prey taken by large competitors, and is indeed poaching in their niches.

Very large items are ignored or even (in one case of a large scorpion) scare off the small bird. Large prey items are usually carried away and dissected on the ground (Fig. 23). At times a bird chews the prey with head down, drops the prey, and picks it up, by rotating (yawing) on a low vertical perch. Dissection with shaking of the prey often, as in larger antbirds, involves chewing and eating one leg at a time, then eating the main body parts; but the White-plumed may avoid attracting attention of large competitors by hurriedly and mightily swallowing a large prey whole. The dissecting bird commonly sleeks the crest back on the crown and the beard back on the throat, probably reducing visibility, and raises the plumes again on returning to foraging.

"Anting" is occasionally used for small prey, apparently ones with chemical defenses. The prey is chewed in the tip of the bill

Table 17. Types and sizes of prey taken by White-plumed Antbirds

Food	*Number of Prey Items of Given Length (mm)*										
	?	0-5	-10	-15	-20	-25	-30	-35	-40	-45	-50
Unidentified		21	11	28	7	4	5		1		
Spider	14		2	15	3	4			2		
Spider egg sac	1			1							
Centipede					2			1		2	
Roach	3		1	13	12	9	6	3			1
Cricket	5		2	3		1			1		
Grasshopper	2			4	2	3	1	1			
Beetle	1			3	1		2				
Caterpillar							1				
Ant larva	29										
Gecko				1		1					
Total	55	21	16	68	27	22	15	5	4	2	1

and dabbed rapidly into feathers of the tail or wings. As in other birds, the shoulders are often exposed, and the tail is closed. The prey may be dropped or eaten. In one case a prey chewed and dropped by one juvenile was grabbed by another, which also dropped it.

At a swarm, there is such a constant flux of White-plumed Antbirds that one can scarcely watch an individual bird for more than a minute unless it is immobile between larger birds. White-plumeds are likely to move *toward* a large and dangerous competitor if it captures a prey or two. Any movement, even a large antbird attacking another large one, attracts a White-plumed. When traveling between foraging perches, White-plumeds commonly move to 0.5-1.0 m up, and may wait until competitors separate slightly before moving lower to forage.

White-plumeds race to slender stems on which ants are ascending with larvae and peck off one larva after another, tossing each ant worker attached, until forced to flee when a larger bird moves in. Piles of dead leaves trapped in the bases of stemless palms furnish nest sites for the birds, and during ant raids attract groups of up to 10 White-plumeds, which capture prey rapidly. Areas around such stemless palms provide few large perches for large woodcreepers and are apparently too open for most large antbirds.

Open undergrowth of the forest, in which most larger and slower birds seem silent and wary or nervous, is excellent for the fast-moving White-plumeds, even when a forest-falcon is present. At Mitu in Colombia, a circle of undergrowth kept open by ants of an ant-plant was occupied during the passage of an ant swarm mainly by White-plumed Antbirds, while larger antbirds stayed in the normally dense undergrowth around the circle.

Competition and agonistic behavior

Interspecific competition. Interspecific competition is the most obvious feature of the lives of White-plumed Antbirds when one watches individuals that are no longer alarmed at his presence. The species has carved out a niche of constant ant following mainly by persistent infiltration into the ranks of larger birds. In foraging, it is quick to use sites away from larger birds, but if no isolated sites are available it sneaks in between the larger birds despite occasional attacks. Prey captures by large birds attract rather than repel it, and repeated attacks by a large bird just cause the White-plumed to move between perches in a circle, often one of less than a meter in diameter!

Speed and constant alertness are required in such a dangerous niche, for large birds claw White-plumeds severely on the ground if they catch them. I did not see any peck one, but clawing alone could seriously hurt White-plumeds. Rapid chirring or screaming and sudden lunges (as in the hand) ordinarily enable a trapped White-plumed to escape quickly.

To a certain extent, large birds eventually stop the futile exercise of chasing White-plumeds near them, but any White-plumed that tries for prey is attacked instantly. Often a White-plumed stays immobile when foraging near or among large species, even when they are capturing prey near it or hopping past less than half a meter away; and it waits for a chance to make a lightning sally for prey close to its perch. The White-plumed then flies instantly for the margins of the swarm, seldom pausing to sping on the ground or chase a prey.

Table 18 lists attacks, displacings, and returns on and by White-plumed Antbirds. Only the slightly smaller Scale-backed Antbird is subordinate, and it usually forages at the periphery of swarms or away from ants. Rufous-throated Antbirds are the main competitors of White-plumeds, attacking them even more than do other White-plumeds. Black-headed Antbirds, hopping antbirds that follow swarms only part of the time at dense forest edges, supplant White-plumeds readily but usually are in denser growth than are White-plumeds. Both Rufous-throats and Black-heads regularly supplant White-plumeds that are not sallying for prey. Two woodcreepers that attack White-plumeds show higher percentages of attacks linked to actual attempts by the antbird for prey. The White-chinned Woodcreeper chases White-

Table 18. Interspecific interactions for White-plumed Antbirds[a]

Other Species	*Supplantings*	*Displacings*	*Returns*
Rufous-throated Antbird	/1885(9.1%)[b]	/79(3.8%)	/29
White-chinned Woodcreeper	/118(20.3%)	/8(25%)	/5
Black-headed Antbird	/90(7.8%)	/5	/1
Black-banded Woodcreeper	/21(14.0%)		/5
Rufous-capped Antthrush	/3		
Plain-brown Woodcreeper	/1	/2	
Red-billed Woodcreeper	/2		
Spot-winged Antbird	/1		
Scale-backed Antbird	4/	1/	

[a] Names follow Meyer de Schauensee (1970). Attacks by White-plumeds above diagonal lines, attacks on White-plumeds below diagonal lines.

[b] Percent of instances caused by tries of White-plumeds for prey.

plumeds commonly, but larger species (Black-banded and Red-billed Woodcreepers) and one that forages high (Plain-brown Woodcreeper) seldom do so.

At Manaus, only White-plumed and Rufous-throated Antbirds and White-chinned Woodcreepers follow ants for nearly all their food; Black-headed and Scale-backed Antbirds, as well as four woodcreepers (Black-banded, Barred, Plain-brown, and Red-billed) follow ants regularly but often forage away from ants; other species seldom follow ants (Oniki and Willis, 1972). White-chins, at 55 g, are uncommon woodcreepers that dominate the center of most swarms in the absence of a large antbird. Rufous-throated Antbirds, at 30 g, take the zone around White-chins much as the related Bicolored Antbirds take the zone around large Ocellated Antbirds in Panama (Willis, 1973a). In both regions, the antbirds move centrally when the large competitor is absent.

In Panama, the small Spotted Antbird occupies a ring peripheral to the two large antbirds, but has to spend half its time away from ants because the outer ring is often unproductive. An Amazonian close relative of the Spotted Antbird (the Spot-backed Antbird, *Hylophylax naevia*) rarely follows ants; it uses only the half of the Spotted Antbird niche away from ants, and even so has to compete with Scale-backed Antbirds there. Since the Scale-Backed Antbird also adds to peripheral competition in the outer ring over ants, and since the Black-headed Antbird periodically moves into the outer ring as well, White-plumeds are forced to survive in less than the half of the Spotted Antbird niche over ants. They have therefore taken to the dangerous interstices left among large ant followers around the centers of swarms.

White-plumed Antbirds are thus in very close contact with the common Rufous-throated Antbirds, but rarely penetrate their ring into the central core favored by White-chinned Woodcreepers or occupied at times by even larger woodcreepers. The frequent attacks by Rufous-throated Antbirds and rare attacks by woodcreepers result primarily from greater contact with Rufous-throats.

From eastern Colombia and Ecuador east to the Rio Negro near Manaus, large Reddish-winged Bare-Eyes *(Phlegopsis erythroptera)* and medium-sized White-faced Antbirds *(Gymnopithys leucaspis)* take the two central zones at ant swarms, while westward rather large Sooty Antbirds *(Myrmeciza fortis)* replace Black-headed Antbirds even deep in forest. In some forests, such as at Umbria in Colombia, White-plumeds compete with these first three plus medium-large Hairy-crested Antbirds *(Rhegmatorhina melanosticta)*. There, my notes record White-plumeds darting between larger antbirds like "fighters among bombers", even "coming back for more" right after supplanting attacks. White-faced Antbirds supplanted them 15 times (displacing them twice); Sooty Antbirds supplanted them 13 times (displacing 3 times); a Reddish-winged Bare-Eye and an Undulated

Antshrike *(Frederickena unduligera)* each supplanted one once. I recorded intraspecific attacks only 5 times in the same period of observation. At Zatzayacu in Ecuador, I recorded single supplantings by White-faced and Sooty Antbirds and by Bare-Eyes, as well as twice by Hairy-crested Antbirds. At Mitu in eastern Colombia, Crested Antbirds *(Rhegmatorhina cristata)* supplanted White-plumeds a few times, as did the Bare-Eyes and White-faced Antbirds.

I did not find White-plumeds at two locations in the plains along rivers in eastern Ecuador, nor at one site in the plains (Yarinacocha) nor one in the foothills (San Alejandro) in Peru. At Limoncocha, Ecuador, the large Black-spotted Bare-Eye occurs with Reddish-winged Bare-Eyes, White-faced and Sooty antbirds, but not Hairy-crested or White-plumed Antbirds (Pearson 1972 and my own observations). Recently, D. and E. Tallman (pers. comm.) have found White-plumeds near Limoncocha in open woodland, which may lack some of the large antbird competitors.

At Putuimi in eastern Ecuador and Yarinacocha in Peru, White-plumeds are replaced by a small antbird of almost the same size, the Lunulated Antbird *(Gymnopithys lunulata)*. This southern species and the related white-chested Antbird (*G. salvini*), with perhaps some assistance from larger southwestern species (Reddish-winged and Black-spotted Bare-Eyes, Hairy-crested Antbirds), may block White-plumeds from extending out into the southern Amazonian floodplains in eastern Peru and thence into southern Brazil. Lunulated and Salvin's Antbirds perhaps have the advantage of being able to forage above larger antbirds at times (Willis 1968a), although not as well adapted as White-plumeds for sneaking among large antbirds.

The complexities of replacements of subordinate species of ant-following birds from eastern Ecuador into eastern Peru deserve more study, for another species of unknown behavior (*Pithys castanea*) also occurs in the region. Distribution seems very patchy, because of differences in habitat or "forbidden combinations" of competitors, reminding one of patchy species combinations on islands near New Guinea (Diamond, 1975). It is curious, for instance, that Black-spotted Bare-Eyes and White-plumed Antbirds seldom occur together (specimens of both are recorded only for Puerto Yessup, in Peru), for this Bare-Eye is related to Reddish-winged Bare-Eyes, which often occur with White-plumeds.

Intraspecific competition. Competition among White-plumed Antbirds is not very evident, for individuals tend to be separated by individuals of larger species. Even when three or four White-plumeds forage near each other, agonistic behavior rarely is evident. All seem to concentrate on foraging, as if they cannot afford to waste time chasing each other when a larger species could arrive at any moment. The birds stay 0.5 m or so apart, but show only faint signs of aggression or rare chases. However, larger foraging groups of White-plumeds often interact antagonistically. Simple chases are fairly common, with very faint whirrs of wings or snapping and puffing noises. At Manaus, we had 750 records of supplantings and 55 of displacings, less than for interactions with Rufous-throated Antbirds. Only 18 supplantings (2.4%) and one displacing were directly connected with chases for prey. Supplantings are often unrewarding, the supplanted bird staying only 0.2-0.5 m away despite occasional attacks. Brief pecks sometimes enforce an attack, but I seldom noted fights.

Sequences of supplantings sometimes involve songs (with beards spread) or chipping as well as snapping or puffing, but none of the calls are loud. Chipping and zipping sequences of multiple supplantings sometimes sound like alarm and scare large antbirds.

Aggressive threat involves a graded display much like the "challenging" display of related antbirds, with faint snarling. The chest and at times neck and belly feathers spread, as do the faintly barred back feathers (Fig. 24). The tail is raised to the line of the body from the normal position just below the body line. Often the spread tail seems somewhat tented, higher in the middle. In one case, in an up-and-down fluttering and snapping fight, the wings were spread on alighting as were the tail and body

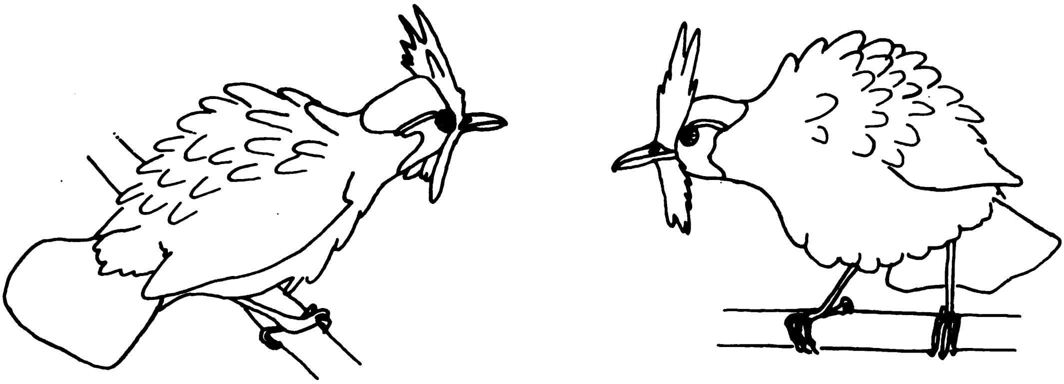

Figure 24. Challenging White-plumed Antbirds.

feathers. At high intensities, the bird rises by extending and splaying the legs. The head commonly is "arched" on the neck, so that the closed bill remains horizontal or points slightly downward instead of upward as would be expected when the bird extends the legs. At times the bill points at the other bird as the neck extends. The crown and head tend to sleek as in other antbirds; but, unlike them, the long crest and beard spread and ruffle forward. One bird in the hand raised and spread the chin plumes at me as it spread its belly feathers and tail widely. One threatening bird hopped toward the other, pivoting 90-120°for each hop, as if to show the spread plumes and body in alternating side views.

It is likely that white head plumes serve as relatively static aggressive signals between individuals, whatever other functions the plumes may have (such as disruptive coloration). The relative immobility of the plumes may help because dominant species habituate to a constant signal, while White-plumeds could still be attentive.

Submissive display is a weak "cringing" as in related antbirds. The White-plumed crouches low (i. e., flexes the legs), ducks the head (i. e., retracts the neck while extending the head on the neck), closes the tail, and flits the wingtips now and then. As in Fire-Eyes and Spotted Antbirds (Willis, 1972a), submission is poorly developed compared to dominant antbirds, and often supplanted birds seem in normal postures. Subordinate birds forage until the instant of attack, or endure pecks or attacks with only minor movements of the body or short flights to nearby perches. A bird adapted to live amid large and dangerous competitors perhaps cannot be effectively attacked by its own species.

Age, sex and location effects on agonistic interactions. Young White-plumed Antbirds are ordinarily low on the intraspecific peck order and are supplanted even by their parents as soon as they start to feed themselves. At times a young bird is supplanted by a younger one, however, or a young bird supplants its parent. As a young bird becomes independent, it may loudpeep constantly among large ant followers, which supplant it back and forth. Older birds are much better at avoiding large species or at usurping places near or away from them and do not loudpeep.

I knew the sex of too few White-plumed Antbirds to detect patterns well. However, the few known females rarely attacked other birds, except for attacks on juveniles and on other known females. I had no certain case of a female supplanting her mate or another adult male. Males that were breeding in the study area often supplanted or challenged other birds, including females, but I did not note any cases of a male attacking his mate.

I did not note any strong spatial pattern for dominance. Three males that bred in the study area were usually the most dominant birds, and their widely overlapping home ranges had different centers. Other mated males entered at times, sometimes with offspring. However, interactions between these males were too few to say if there is a pattern in which the male on his own territory is dominant (as in most related ant-following antbirds). Breeding males were the birds most often involved in zeesinging and wingwaving, but this display may be sexual rather than agonistic. My impression is that adult males have huge and overlapping home ranges but that each tends to center his activity in a separate region in which he is dominant. Females move at times from one male to another (see below), and young birds move about irregularly.

Zeesinging and wingwaving. Occasionally, a breeding male separated from other birds, at 20-50 m from an ant swarm (or in creek valleys in the evenings), performed zeesinging and wingwaving. The "zee" notes continue on and on as the male, in an upright pose, looks about while waving the spread wings back and forth. The crest and beard are sleeked, the tail closed or partly spread, and the rufous rump exposed (Fig. 21, left). Extraneous noises or movements cause the sounds to fade and the wingwaving to slow and close, but often the series resumes after brief interruptions. I do not know if the display is sexual or agonistic. Often it followed intense interactions of rival males or families, but at other times it followed sessions when I was chasing a young bird away from adults in attempts to net it.

Reproductive behavior

Analysis of reproductive activity in White-plumed Antbirds is made difficult by the great mobility of each pair between ant colonies and by the frequently independent movements of male and female at (occasionally between) colonies of ants. Both are to be expected from the low-status foraging niche, which seldom allows enough room for male and female to forage together. A step toward the almost complete independence of foraging of similarly low-ranking male and female Plain-brown Woodcreepers (Willis, 1972b) is a tendency for female White-plumeds to start new nests with new males, leaving the old males to care for single young. Courtship and pair formation, however, are rather similar to that in other antbirds, including courtship feeding, mutual grooming and considerable interaction between members of a pair at least until nesting is completed.

Courtship feeding. As in related antbirds, males feed females. A few locally resident males, generally ones that had nests during the period of my study, were the only banded birds seen to feed females successfully. Young males were not seen to successfully feed adult females, though young males did investigate nest sites and tried to feed fledglings or females at times.

On capturing prey, a male wandered with prey in tip of the beak some distance from the swarm, giving songs or tweeting or serpentine-tweeting notes, until he located the female or she flew up. If no female appeared, the male ate his prey. Feedings were rapid, with trilling notes from one or both birds. No special movements, except arching the head to expose the rufous collar, were noted for the male; but the female sometimes gaped and half-crouched, fluttered the wingtips, and sleeked the crest and beard to receive food. Often she extended her head, closed her tail, and leaned away from the male to eat. He occasionally flicked the tail and nipped at her side or head, but usually flew off. At times the tweeting female flew up and flitted the tips of her wings next to her mate or even almost pushed him bodily off his perch. One such female flew up to her mate and trilled, but he ate the food he had just captured. Usually she foraged as well, but at times a female waited and preened in cover near the swarm with an indolence more often noted for females of dominant species. Probably copulations follow feedings at times, as in related species.

Occasionally males without a mate try or even succeed in feeding dependent grown young of other parents.

Mutual grooming. At times a pair sit or preen together, usually several meters from the ants. Trilling or tweeting notes greet the arrival of a mate. At times one or the other swells the rufous collar and arches the head as the mate arrives and sidles up with flitting

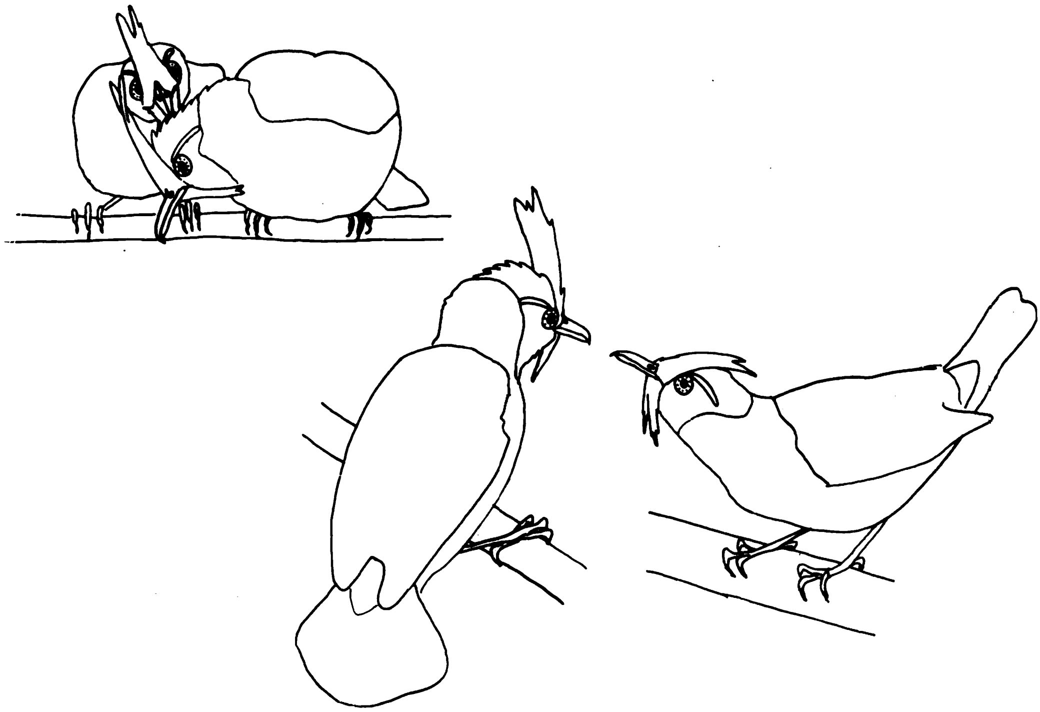

Figure 25. Mutual grooming (above) and invitation to grooming (below) in mated White-plumed Antbirds.

wing tips (Fig. 25). The arriving bird may hop away and then back near the mate, flitting again. At times there is mutual grooming, one nipping the lowered crown of the other as the latter arches and swells the neck. Faint tweeting notes mark the brief exchanges of nibbling. When the female leaves, the male often looks about and starts to preen. It seems possible that the rufous collar is connected with mutual grooming exchanges, for I saw no other display in which the collar was as strongly spread. Mutual grooming and courtship rather than juvenal patterns of feeding were noted for young "females" (birds of short crests and ones that accepted food) only after they gained rufous collars and most of their white head plumes.

Pair relations. Divorces seemed very common in White-plumed Antbirds, so that I had much trouble establishing who was mated to whom. In one case where two young left a nest, male and female each cared for one young, and the pair seemed to stay together after independence of the young. However, the male often took his young bird to a different ant colony from the one used by the female and her young bird. In the few cases where only one young survived, the male always cared for it after it left the nest. The females in these cases disappeared or began to accept food from other males; in one case the female quickly nested with her new mate and often stayed with him as he cared for the single young. Apparently the female thus may gain a new nest rapidly. In another case where nest(s) were unsuccessful, the female disappeared, and the male gained the above female from his neighbor. These preliminary observations suggest that females quickly change mates, even when the old mate is still alive, in contrast to other antbirds in which constancy of mates is usual. The pairing of young females as soon as they acquired adult head plumage suggests that young females start nesting early, probably at about 6-8 months of age.

While mated, pairs often travel together between swarms but occasionally appear separately. Songs and tweeting notes keep pairs more or less together enroute. At swarms, the pair wander together if there is little competition from larger species, apart if there is much competition. When there are many White-plumeds and not many large birds, the pair wander together or apart. Courtship feeding and mutual grooming or sitting or preening together occur occasionally. I noted no attacking between members of a pair. When the male is separated from the female, he sometimes zeesings, but ordinary songs and tweeting are much more common. A female changing mates occasionally receives food from both males alternately, although her first mate is likely to be feeding a young bird and seldom feeds her.

Nesting behavior. Only two young "males" (birds with long crests that tried to feed young but never accepted food) were seen to investigate possible nest sites as they got their first head plumes. In each case, the young male sat atop a pile of dead leaves where petioles of a stemless palm came from the forest floor, spread (raised) his crest and raised his head (Fig. 17), looked about, picked up a tiny twig, turned, stood, sat again, and sleeked his crest again, nibbled at a nearby strand, etc. One pushed his breast into the leaves a few times, so that he created a small depression.

The only previously reported nest (Willis, 1972c) was a neat cup in such a mass of leaves caught around the petioles of a low palm. At this nest, the pair came near the two spotted eggs with tweeting notes but did not sit.

Male and female disappear alternately during incubation and brooding, suggesting that both incubate and care for nestlings. The pattern of incubation is not clear, however, for the birds moved between colonies too much for me to know whether the presence of a female implied that her mate was on the nest and vice versa. It is likely that, as in most antbirds, the female is on the nest at night, and the male takes the first incubation period in the morning. Incubation and nestling periods were not determined but probably are about 15 days and 12 days respectively, as in most antbirds.

Care of fledglings and growth of young. Small young out of the nest are very difficult to detect, for they stay in treefalls and other dense tangles up to 50 m from the swarm unless density of antbirds there is very low. At times, one or both adults disappear while giving tweeting notes and songs, but it is difficult to see them carrying food or to distinguish the movements from normal carrying of food off to the margin of a swarm for dissection. The young do have an exceptionally loud single-noted song, or "loudpeed," when deserted by parents for some time. All young that I discovered at this time had tails one-third to one-half the adult length and flew fairly well. One, seemingly deserted by its parent (I never saw it or the mother again), peeped over and over every 12 seconds or so (1-41 seconds) 100 m from a colony of ants that had stopped swarming. It preened, sat with reddish rump fluffed up, champed the bill, and jerked the head up with each loud *pseeeeeey*. When chased, it circled short distances through the undergrowth and was easily captured in a mist net. At this time, the father was with another fledgling at another ant colony. Probably such young have been out of the nest less than a week and are 15 or 20 days out of the egg or about a month old (since egg laying).

Two weeks later, at an estimated age of 1.5 months, the tail is adult length; the head is still gray and the gape angles pale. In noncompetitive situations, each fledgling forages actively near its parent. The young bird flutters the wings and bows at the parent, raising the closed tail so as to show it and the red rump (Fig. 26). The head may be bobbed up and down. The young gapes at the parent now and then. By 2 months of age, or one month out of the nest, the young bird (Fig. 17) is loudpeeping desperately, double to quintuple peeps, as it tries ineptly to forage among hostile large birds and is harassed unmercifully. In the hand, one sees a few concealed white feathers on the head and a few rufous ones on the nape. The parent is likely to wander away from the young and feed it very irregularly despite its fluttering, gaping, and squeaking enthusiasm when fed.

The young bird receives more pecks than food from its parent in the next two weeks, although the parent allows it to forage

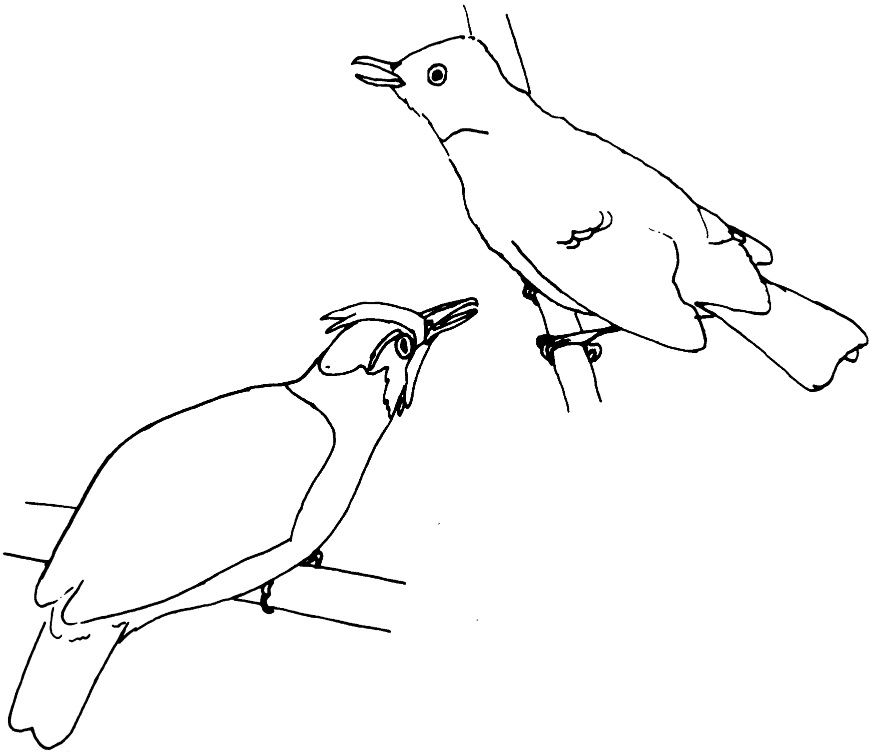

Figure 26. Adult White-plumed Antbird without food tweeting (left) as young loudpeeps as if before a feeding (right).

beside it and still gives tweeting notes and songs to lead it (loudpeeping, 1-2 notes each) from one swarm to another. By 3 months of age the young bird is rather independent and is stopping the series of desperate loudpeeps that mark its transition to independent foraging. Short white feathers on the forecrown of the independent young bird are visible in the field by this age. The nape is patchy red and gray by 3.5 months, and the parent supplants or ignores the young as if it were an unrelated bird. In one case, however, a young bird supplanted its parent a few times at this age. In the next month the white forehead and beard plumes grow rapidly as do white postciliary feathers and the rufous collar. However, the head plumes are still short and mixed with dusky juvenal feathers at 4.5 months of age. By 5.5 months, only a little dusky remains amid the head plumes, which are still slightly shorter than adult length (in young males, the plumes are about the length usual for adult females). By 6 months of age, the young seems adult except for one or a few dusky feathers amid the white head plumes. Presumed young females are being fed by adult males by 7 months of age. At eight months of age or earlier, presumed young males have head plumes as long as the best of adult males (Fig. 17) and check nest sites or try to feed young or females. The tips of tertial feathers are still rusty, however, and occasionally one finds a brown feather in the plumes of the head.

Molt commences at about 4.5 months of age with the innermost primary (number 1) on each side, reaches numbers 3 about a month later, numbers 6 at about 7.5 months of age, and presumably ends about 10 months of age.

The amount of white on the head is variable between two and five months of age; younger birds usually lack white, and older ones resemble adults.

Nesting seasons. Table 19 gives the number of nests that received eggs during

Table 19. Nestings of White-plumed Antbirds in different months

Year	*Month and Number of Nestings*[a]											
	J	F	M	A	M	J	J	A	S	O	N	D
1972						1						1[s]
1973	1[m]		2	4	2	2	3	2	1		2	2,1[m]
1974		2	3			1						
D[b]		2	5	4	2	3	3	2	1		2	2
G[c]	7	8	9	5	6	3	4	5	3	6	5	8
Total	8	10	14	9	8	7	7	7	4	6	7	12

[a] As judged from young birds out of the nest. [b] 1973-4, Reserva Ducke records only. [c] 55 young specimens from museums, plus 15 young at Mitu, Umbria, Yaapi, Bartica, and Nappi, in various years. [m] Manacapuru. [s] Serra do Navio.

different months of my studies. The table is derived fom estimated ages of banded young, using information in the preceding section. A few unbanded young are included when I could be certain they were not banded later or repeated later. A slight peak of recorded nests in March and April (subtotal) is largely due to the fact that I worked July and August in both 1973 and 1974, and pick up most young at about 3-4 months of age as they begin to wander away from the home areas of their parents. A decrease in nests in September-January is possibly significant, as this is the dry to early rainy season, and is the main breeding period of the competing larger White-chinned Woodcreepers and Rufous-throated Antbirds. However, I suspect that more data will demonstrate that as a species, the White-plumed Antbird nests throughout the year, as is suggested by data from 55 specimens of young birds from other regions and observations of 15 young out of the nest at various places other than Reserva Ducke (Table 19).

Nesting success and repeat nestings. Little information is available on nest success, though nest failures were occasionally recorded by watching pairs at ant swarms (as in Willis, 1973b). In this species, it is difficult to be certain that one of a pair is incubating when only one is present at a swarm, for pairs sometimes forage at separate ant colonies. Feeding the female is a good sign of non-nesting, as the male never feeds the female when he is helping take care of eggs or nestlings. Occasionally he feeds her when feeding fledglings, however. I undoubtedly missed some nests that failed. Even so, nest predation could not have been very high. Oniki (1979) has indicated that nest predation in these equatorial forests seems less than in some others.

Individual birds nest more than once a year. Male MRYG cared for a young bird out of the nest from late December to late February (his female and the other young disappeared); then he nested immediately with a new female, and had one young out of the nest by April 13. As he cared for the young until mid-June, his female moved to male WGGM, whose mate had disappeared after some unsuccessful nesting attempts. Their young was out of the nest in early July, at which time male MRYG was trying to feed young females. Both males and their females were in molt during some of the nesting attempts, but molt seemed slow or arrested during the attempts. These and other fragments of information suggest that males and females nest more or less continuously, except when caring for young out of the nest or when temporarily without a mate because of high divorce and disappearance rates. Females must nest repeatedly after reaching 8 months of age, for there always seemed a surplus of males without mates, while no known adult female was without a mate. However, the sex of many birds was unknown, so it is possible that some were unmated females or nonbreeding females.

DISPERSAL AND SPATIAL BEHAVIOR

Social behavior is relatively poorly developed in White-plumed Antbirds, except

Table 20. Numbers of White-plumed Antbirds following ant swarms

Month	*Number of Swarms with Given Number of Individuals*														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	17
Sept., 1972		1	1	2	3	2	1								
July, 1973	3	2	6	6		1									
August	7	8	15	10	11	1	3	5	1						
September	21	7	19	10	12	4	2	1	1						
October	12	3	16	7	6	7	4	1		2					
November	22	9	9	13	8	4	2	2	1		1				
December	16	15	16	9	4	2	1			1					
January, 1974	26	10	16	11	3	3	1	5							
February	9	7	19	4	6	5	1								
March	12	2	12	20	3	1									
April	21	8	13	3	8	4		2	1	1	2				
May	12	8	7	8	11	2	3	3	3	2	1				
June	9	8	11	9	3	3	1	3	3	2	2	1		1	
July	7	3	7	6	10	5	3	3	1	3	1			3	1
August	4	2	3	2	1	6	2	3	1	1	1	5	3		
Total[a]	171	82	148	102	75	46	20	23'	11	12	8	6	5	5	1

[a] September 1973 to August 1974 only.

for pair and adult-young interactions. Individuals, pairs, and families do gather readily at swarms of army ants where I often recorded up to 7 individuals and once recorded 17 (Table 20). There is relatively little fighting, and individuals sometimes forage 0.5 m apart with only occasional pecks or supplantings. However, individuals or pairs and families usually wander separately at and between swarms. I did note individuals arriving at swarms nearly synchronously at times but suspect that arrivals coincided accidentally. Social behavior is seemingly parasitic rather than mutualistic, birds exploiting each other in gathering at concentrations of food rather than forming clans or other groups. It is possible that they avoid solitary visits to swarms for reasons of protection against predators or to saturate dominant competitors so much that the competitors become habituated, but these possibilites would be difficult to prove. Data in Table 20 do not indicate saturation techniques, for two birds is the most common number present at swarms.

The movement of birds among colonies of ants is extreme and irregular. A given colony often fluctuates from one or two birds to 10 birds and back to one or two in a few days. At times most of the birds are at one colony one day, at another colony a few hundred meters away the next day. Both habitat and behavior of the ants (failure to swarm, raids into above-ground *Camponotus* nests and consequent failures to continue raiding on the ground, etc.) force the birds to move at times. Large numbers of competitors sometimes seem to attract birds but at other times (as when 25 or more Rufous-throated Antbirds follow a single ant colony) seem to repel them. When ants enter semiopen zones, the White-plumeds stay inside cover, never following into open "cerrado" secondary scrub-deserts or into yards of houses. White-plumeds follow commonly to the very edge of the forest, even in zones where there is much sprouting vegetation due to partial clearing. They enter dense second growth but tend to abandon colonies therein when the sun is strong and hot at midday. Edges of clearings or treefall zones in the forest are used readily, as long as there is shade. In the tall, dark undisturbed forest the birds seem slightly less common than at disturbed forest margins but do not decrease as much as do Rufous-throated Antbirds. However, the record of 17 White-plumeds at one swarm and several records of 10-13 individuals come from near forest borders.

The fluxes of individuals are particularly strong among independent young birds, which wandered the full length of my study area (3 km) or more at times. Even adult, nesting birds wandered much of the length of my study area (2-3 km) at times. Maps of representative individuals of these two categories do not show strong localization of individuals (Figs. 27-30), except that the adult "resident" birds seem slightly localized. Because I rarely found a given individual more than half of the days of a given month, the birds could also have been wandering well off my study area. However, I was not able to confirm such movements when I checked colonies 1-3 km off the study area within Reserva Ducke on a few occasions. Occasional appearances of banded birds from these distant colonies at colonies within the study areas suggest that an individual adult probably wanders across an area 3-5 km in diameter and that it probably stays in a 2 km area most of the time. Possibly adult males tend to dominate others in the centers of non-overlapping "territories", but evidence is scanty. With this kind of wandering possible, it is not surprising that many banded birds were not seen again, and that I had difficulty taming birds because they tended to desert quickly for other colonies.

Population sizes are difficult to estimate because of movements of individuals. Despite large numbers of birds at some ant swarms, total numbers are low; about 1.6 adult males, 1.2 adult females, 1.0 young under six months old, and 1.4 wandering older young or birds of uncertain status per km^2, or 1.1g per hectare, in the 2.8 km^2 of forest on the study area at Reserva Ducke. When occasional use of 40.5 ha of forest plantations and of 54.2 ha of second-growth is counted, 5 birds per km^2 or just under one gram per hectare seems about the maximum likely density for the part of the 3.7 km^2 of area used.

Mortality rates are similarly difficult to estimate. Several birds banded in September, 1972, were still present in August, 1974, but most birds disappeared rapidly. Few birds

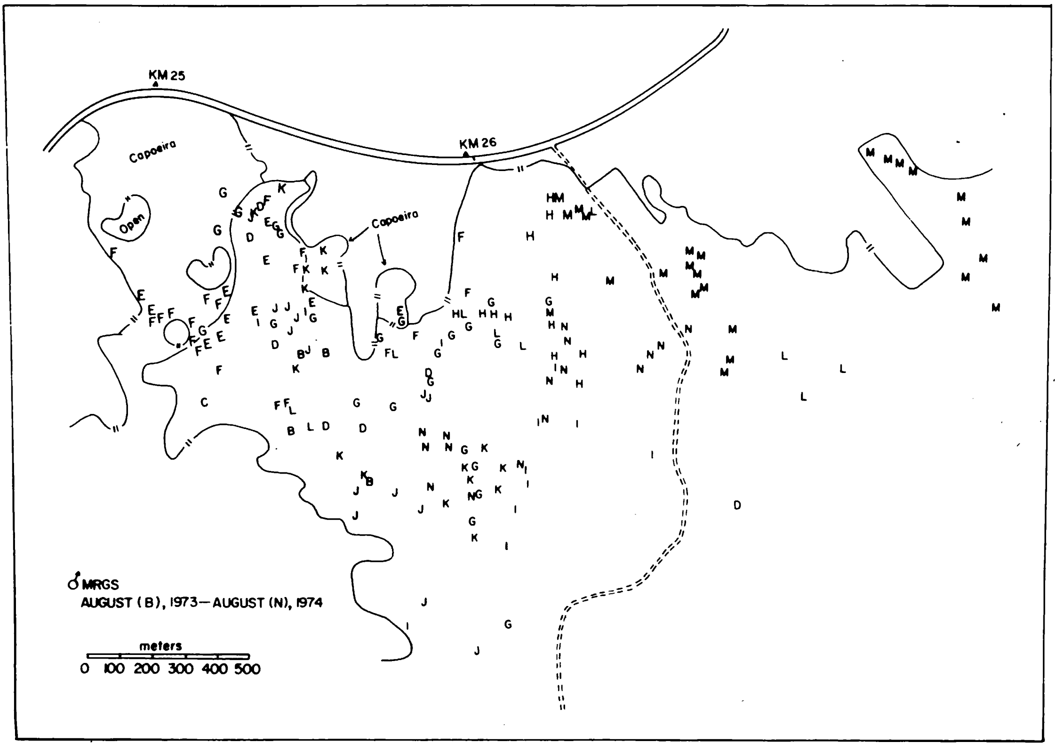

Figure 27. Locations for male White-plumed Antbird MRGS, the northwesternmost of males in the study area.

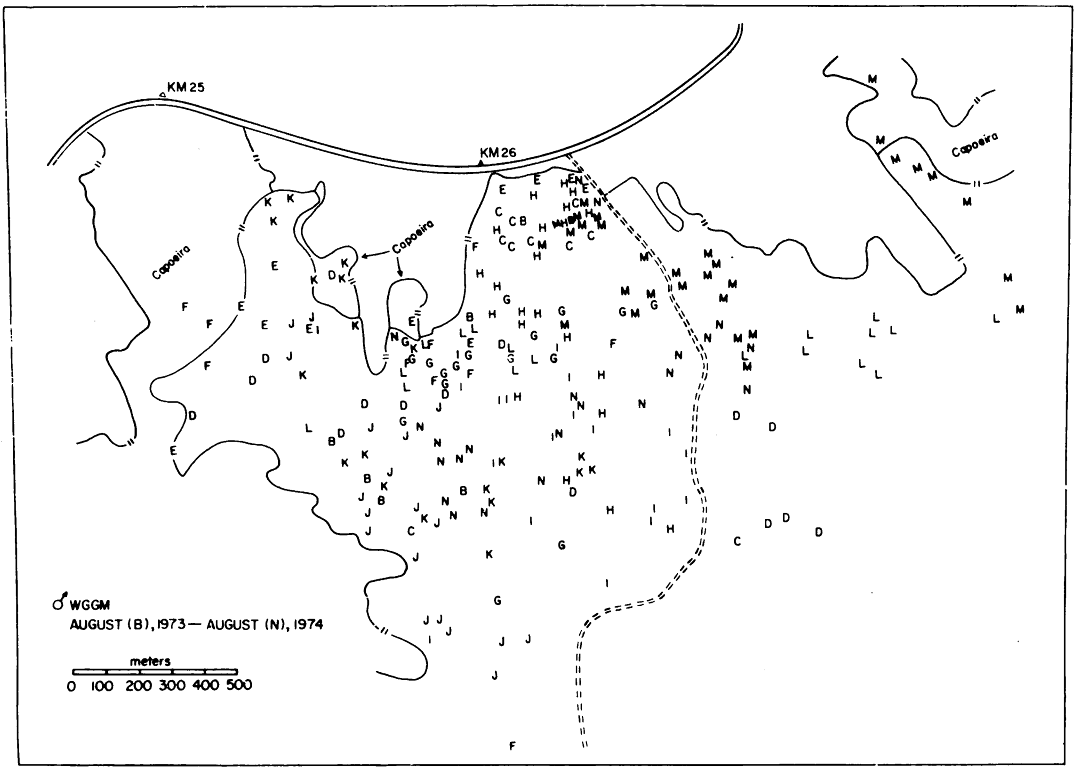

Figure 28. Locations for male White-plumed Antbird WGGM, who centered his area near the center of the area mapped.

banded in 1973-1974 were still present in July, 1976. I suspect that the species has a fairly high mortality rate because of its vagile life, but confirming that a bird is dead and not just outside the study area is difficult when pairs and populations exhibit little stability. A study of populations in *Pithys albifrons* will probably require several researchers working jointly for several years, unless new radio or other techniques are used. The fact that there is a high proportion of young birds and of birds with rusty margins to the wing coverts in specimen collections suggest high mortality rates; otherwise, fully adult plumages would be more common among specimens.

DISCUSSION

Much of the behavior of White-backed Fire-Eyes and of White-plumed Antbirds seems related to their literally and figuratively marginal niches in the aggressive societies of ant-following birds. However, they have rather different ways of exploiting their subordinate positions, and differ in some respects both from each other and from similarly subordinate Spotted Antbirds in Panama (Willis, 1972a).

Similarities in Social Behavior. Tendencies to be nonsocial, apparently because subordinate birds often must forage at small scattered sites and cannot afford to attract attention of dominant species by joining or calling their kin, are the most trenchant similarities among the subordinate antbirds. Groups in these species are mostly of unrelated and antagonistic individuals. Although pair bonds are never as short as in the similarly subordinate Plain-brown Woodcreepers (Willis, 1972b), male and female antbirds of a pair commonly wander separately around a swarm of ants rather than foraging together as do pairs of dominant antbirds

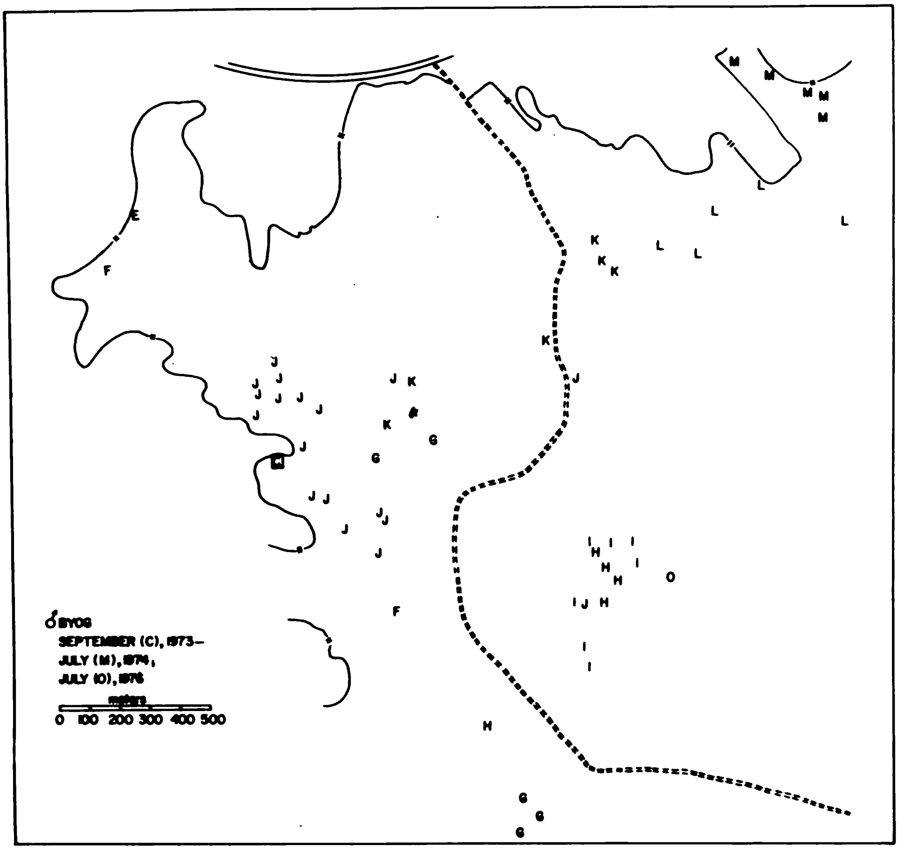

Figure 29. Locations for male White-plumed Antbird BYOG, who nested near the lower right of the area mapped.

(Willis, 1973a, 1979). Male and female White-plumed Antbirds of a pair sometimes forage at separate colonies of ants, and they "divorce" readily. Young of the three subordinate species do not stay with adults to form clans but are deserted as soon as they are foraging fairly well on their own. Nepotism, in a sense, works only for dominants.

Deemphasis of submissive behavior also seems correlated with subordinate status in the three species. The exaggerated submissive behavior or "etiquette" necessary for subordinate individuals of dominant species of antbirds to stay near their conspecifics would be disadvantageous for individuals of nonsocial subordinate species, which could attract dominant competitors every time they displayed to conspecifics.

Differences in care of young. **In several subdominant and subordinate species of** antbirds (Willis, 1967, 1972a), the young stay with their parents and are fed up to 50 or 60 days after leaving the nest, probably because the varied techniques of a subordinate species often may be more difficult to learn than are the stereotyped feeding techniques of a dominant antbird. (Black-spotted Bare-Eye and Ocellated Antbird young are obtaining most of their own food by 30 days out of the nest.) However, the White-plumed Antbird is a subordinate species with a stereotyped feeding technique, and its young become independent about as rapidly as do young of dominant antbirds. Fire-Eyes are intermediate in duration of association with young, which require 30-50 days out of nest to gain independence. Their bouncing techniques are not complicated, but they show a diversity of foraging motions that must take time to perfect or mature.

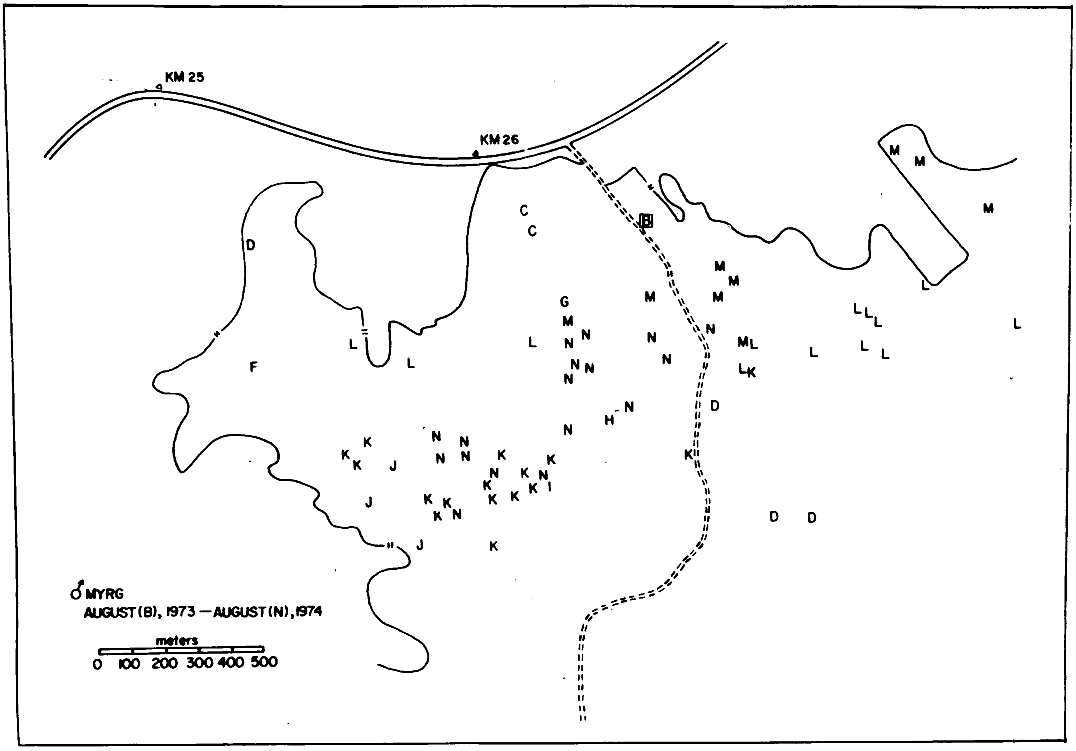

Figure 30. Locations for unmated male White-plumed Antbird MYRG, a presumed first-year male.

Another possible correlation is with foraging near the center of antswarms, where fleeing arthropods are most numerous. Dominant species and White-plumed Antbirds work centrally, in the zone of high prey density, and thus young catch food rapidly without much hunting if competitors are not too numerous. Young White-plumeds find it very difficult to stay centrally, and their persistent loudpeeping may disturb larger birds or attract the parent to give more food. Subordinate species like Fire-Eyes work peripherally where arthropods have had more time to hide in a variety of places that young birds may have to learn or mature to exploit.

Similarities and Differences in Alarm Behavior. Possibly as a result of reduction in most pair and family associations and consequent deemphasis of any alarm calls due to kin-selected behaviors, the three subordinate antbirds do not often keen and freeze at distant danger. Also, their low status often keeps them at the periphery of swarms, where freezing or keening is more likely to be dangerous than for centrally foraging families of dominant antbirds (the last keen and freeze regularly).

All three subordinate antbirds remain conspicuously active at hawk-alarm or panicking types of alarm behavior, with sharp calls. These calls seem easily locatable to predators, and the conspicuous activity must also draw attention to the bird. Perhaps the sudden and irregular actions startle, confuse, or mislead the predator, or give the bird time to forage by scaring away dominant birds. The calls and activity seem unlikely to warn related birds, and dominant birds that do have relatives nearby are less likely to panic than are these birds.

The short chipping calls of Spotted and White-plumed Antbirds, contrasting with longer calls in more dominant species, may be due to greater aerial danger to subordinates of repeated calls in the fairly open understories where they live. Fire-Eyes of dense undergrowth have long and complex alarm notes (chip-boos, double-boos, etc.) However, southern species of Fire-Eyes lack the complex calls yet live in even more cluttered undergrowth of subtropical or vine-crowded woodlands (Willis, in prep.). Perhaps very dense undergrowth encourages mammals that might attack antbirds with long calls. It may be that short notes also allow escape from attacks of dominant birds, because only Fire-Eyes are accomplished at hopping, which makes it difficult for a dominant bird to trap them. Still, the long alarm notes of northern Fire-Eyes must have some advantage, perhaps related to effective scaring of dominant larger antbirds (larger antbirds are lacking where southern species of Fire-Eyes live) or to effective distraction of northern predators (more diverse than southern predators; but little is known about causes of mortality for southern or northern Fire-Eyes).

Fire-Eyes mob and chirr (rattle) at mammals less than do White-plumeds or Spotted Antbirds, perhaps because mammals are more dangerous in cluttered undergrowth where Fire-Eyes live; and Fire-Eye hopping is likely to be less effective for escape from mammals than is the rapid flight of White-plumeds and Spotteds. White-plumeds perhaps mob more than do Spotteds because the former have to go to a distant colony rather than merely forage away from ants if the disturbing mammal stays. Also, White-plumeds fly more rapidly and are perhaps safer from mammal attacks.

Differences in Territorial Behavior. Fairly strong territoriality in Spotted Antbirds, moderate territoriality in Fire-Eyes, and virtual absence of territories in White-plumeds is probably related to an increase in ant-following frequency from the first species to the last; to follow ants persistently when subordinate, it becomes necessary to wander widely. Territories probably help prevent trespassing individuals from working areas first, thus reducing food supplies in unknown patterns, when the first two species forage away from ants. Over ants, the food supplies are reduced in a known area only, and there is little disadvantage if a trespasser stays, as long as it forages away from the small area needed by the territory owner. Also, the trespasser is more likely to be persistent and difficult to eject when birds follow ants.

Territoriality, in turn, requires aggressive behaviors: loud songs from the territory, well-developed challenging displays and calls, intolerance extending to frequent fights, and multiple supplantings. Spotted Antbirds and Fire-Eyes show these characteristics; they are muted in White-plumeds, which might attract larger birds to their infiltrated sites. Fire-Eyes are more aggressive than Spotteds, for Fire-Eye home ranges overlap more, and there are more individuals per ant swarm than in Spotteds. Fire-Eyes are also more persistent at staying near a dominant bird of their species and use more hopping escape patterns than do Spotteds. Probably Fire-Eyes cannot forage away from ants as well as can Spotteds and hence need to stay near swarms even when subordinate intraspecifically.

Differences in Pair Constancy. The high divorce rate in White-plumeds, compared to moderate rates in Fire-Eyes and relative marital constancy in Spotteds, probably depends on the relative lack of territoriality in White-plumeds. They wander so widely that a female scarcely gains by staying with the same male and learning his territory; she is in other areas most of the time. She is free to move to a new male for the relatively slight advantage of nesting a bit sooner with him, for she need not stay on the area of the old male. Fire-Eyes divorced quickly when their home areas were cut down.

Similarites in Courtship. To some extent, the three subordinate antbirds have more courtship activity than do domineering species; Spotted and White-plumed Antbirds as well as Fire-Eyes have some mutual grooming between mates; Fire-Eyes have a draping display as if to show a nest site or to bow before a female; and White-plumeds have a strange wingwaving-zeesinging display that perhaps is connected with courtship or male assertiveness when separated from mate or family. All, like dominant antbirds, have courtship feeding, but feeding is rather rare if many antbirds compete at a swarm. I suspect that there is not enough food for subordinate species and that they turn to other behavior pattens in courtship instead of feeding females. Lack of constant association between mates in the subordinate species may also lead to development of special displays to overcome aggression or to avoid mistaken identification bred by lack of association. It is known that short pair bonds are often associated with complex courtship in other groups of birds, such as hummingbirds and grouse. Lack of frequent contact apparently leads to more social ritual in many birds.

Differences in Sexual Dimorphism. Both male and female antbirds incubate and care for young, so that cryptic plumage for nesting is unlikely to be the reason for sexual dimorphism. Perhaps dimorphism depends on the female having wide spaces to forage over ants if she does adopt a dull plumage. With much space about of low foraging value, the male would have to move long distances to supplant her, gain little, and hence be unlikely to attack if he sees by her plumage that she is a female and not a male competing with him for territory. In birds near the swarm center, attacks for food reasons could eliminate the dull-plumaged female; she might need to mimic bright plumage of the male to retain her place. Most of the strongly sexually dimorphic and followers (*Hylophylax naevioides, Pyriglena* species, *Myrmeciza fortis* and *M. immaculata, Percnostola rufifrons, Gymnocichla nudiceps, Gymnopithys lunulata* and *G. salvini*) wander around the periphery of swarms whether dominant or not. (*M. fortis* and *M. immaculata are the only ones fairly high on the peck order*). White-plumed and most dominant antbirds are sexually monomorphic and crowd in near the centers of ant swarms. Only in Reddish-winged Bare-Eyes, sexually dimorphic but dominant antbirds needing careful study, is central location at swarms linked with dimorphism.

Another factor in sexual dimorphism may be the increased aggressive behavior in Fire-Eyes, Spotteds, and most subordinate antbirds other than White-plumeds at swarms. In such conditions, the bright-plumaged female may be attacked constantly and not have the ability to defend herself. Her bluff would be called too often.

Perhaps lesser dimorphism (females have black heads or heads and bodies) in certain subspecies of Fire-Eyes is linked with less room for individuals to forage peripherally or with lesser aggressiveness of males. Females of the northern Andean subspecies *castanoptera* have black heads and bodies; only their mantles are brown. It seems that they use brown female plumage only when they turn to flee. Montane ants forage slowly because it is cool, prey do not flee far, and birds have to concentrate near swarm centers. Few large antbirds occur in the mountains, so that social ties and kin selection may be more frequent among the Fire-Eyes due to higher dominance status. (However, southern species of Fire-Eyes lack large competitors yet are very dimorphic). Black-headed females of the subspecies *similis* between the Tapajós and Xingu Rivers presumably confront both Black-spotted Bare-Eyes and Bare-eyed Antbirds (*Rhegmatorhina gymnops*) at many swarms, hence are sandwiched well out at the edges of swarms without much space. *P. leuconota picea* of the central Peruvian Andes is like *similis* in plumage, but I do not know its situation other than that it is montane.

Differences in Mortalities and Nesting Seasons. Apparently adult mortality rates are high in White-plumed Antbirds (predators probably catch them as they move about) and in Fire-Eyes (predators are probably better able to approach birds in the cluttered undergrowth where the species lives). The mortality rate is low for Spotted Antbirds (birds stay on their territories, where they can learn hiding places; and there may be low predator success in open undergrowth (see Willis, 1974). Nesting success rates are low in Spotteds (about 10%), medium in Fire-Eyes (about 20%), and higher by an undetermined amount in White-plumeds. Spotted Antbirds have short nesting seasons, while Fire-Eyes and White-plumeds have long nesting seasons. Otherwise, reproductive characteristics vary little in these antbirds; all nest the first year, lay two eggs per clutch, take about the same time to rear young, and nest repeatedly to replace lost clutches or to rear additional broods throughout the nesting season. Spotted Antbirds, because of their short nesting season, are less "r-selected" than the other two species. The others may be r-selected for long nesting seasons because of high adult mortalities, giving advantages to those which reproduce often. Young Spotted Antbirds face an environment full of adults, and would have little chance to survive in competition with them. Thus, reproductive energy is perhaps directed to competitive ability of adults or some other channel. Long nesting seasons are not an attribute of the subordinate species where its population dynamics do not favor high reproductive rates. Likewise, dominant species sometimes have long nesting seasons: high adult and young mortality seems to explain repeated nesting in Ocellated Antbirds (Willis, 1973a).

Differences in Preening. White-plumeds preen while waiting among larger competitors, but Spotteds and Fire-Eyes preen in secluded sites. Probably White-plumeds cannot waste foraging time or give up central locations once achieved, and hence do not move peripherally to preen. Short flights for prey, and rapid movement peripherally with prey, probably are necessary for White-plumeds to avoid attacks by larger birds; peripheral movement to eat is thus not a disadvantage, and some White-plumeds preened after such moves.

Differences in Foraging Behavior. As is the case for Lunulated and Salvin's Antbirds (Willis, 1968a), Fire-Eyes and Spotteds regularly move above large antbirds to forage. Perhaps White-plumeds do not do so because there is relatively little foliage and hence food at these levels at Manaus, and few perches except for the thick trunks used by woodcreepers. Wetter forests have more foliage at these levels at Belém, in western Colombia (Willis, 1967), and from Ecuador and Peru east to the Madeira (Willis, 1968a). Lunulated and Salvin's Antbirds may take over from White-plumeds in the last region because greater diversity of foliage above the ground favors them rather than low-foraging White-plumeds.

Feeding behaviors differ in other respects among Spotteds, White-plumeds, and Fire-Eyes. All sally to the ground near the swarm centers when no dominant antbirds are present but behave differently if dominant antbirds arrive. Spotteds wander peripherally or above swarms, or forage away from ants. White-plumeds fly rapidly and infiltrate among large antbirds. Fire-Eyes hop peripherally, hence require horizontal perches, and therefore favor woodland or edge habitats rather than vertically-oriented forest interior sites. Probably hopping uses energy more slowly than flying, and hence allows high densities or large size on a given food supply; Fire-Eyes are certainly larger and commoner than the fast-flying but energetically expensive White-plumeds.

Analyses of data in Tables 3 and 16 of this paper and in similar tables of other papers (Willis, 1967, 1972a, 1973a, 1979) show that dominant and subdominant antbirds are rather similar in foraging locations (Table 21) and methods (Table 22), while subordinate antbirds vary more in these respects. White-plumeds are rather like dominant antbirds in foraging locations and methods. By contrast, Spotteds forage extensively above the ground by sallying, while Fire-Eyes forage moderately often above the ground and use more gleaning than usual on the ground.

Differences in Geographical Ranges. Despite sufficient foraging differences between subordinate antbirds to qualify them for the label of "competitive exclusion" were they to occur together, they are not sympatric anywhere. White-plumeds extend south along the lower slopes of the Andes into Peru, but are replaced in the nearby lowlands by Lunulated Antbirds (Willis, 1968a). Just higher on the Andean slopes in cluttered subtropical woodlands, Fire-Eyes extend north into Colombia. *Hylophylax naevia,* a close relative of Spotted Antbirds but one that does not follow ants very often, occurs sympatrically with various subordinate ant followers over most of Amazonia. Local competitive exclusion due to partial niche overlap could explain the allpatric ranges, or habitat preferences already noted could do so.

None of these subordinate species occurs in forests in the great region between the Madeira and Xingu Rivers in Brazil, although *H. naevia* occurs there. Fire-Eyes ex-

Table 21. Sites of attempts for prey in ant-follwing antbirds[a]

Species	*No.*	*Attempts at Given Location (%)*						
		Ground	Trunk	Limb	Foliage	Debris	Air	?
Dominant								
Black-spotted Bare-Eye	2238	94.0	0.9	0.8	2.3	1.3	0.8	—
Ocellated Antbird	3895	94.8	0.9	1.6	1.8	—	0.9	—
Subdominant								
Bicolored Antbird	8537	90.6	1.7	4.1	2.3	0.5	0.8	—
Subordinate								
Spotted Antbird	1602	68.7	5.4	10.4	11.8	b	2.6	1.2
White-backed Fire-Eye	3504	80.2	2.4	3.9	8.9	1.4	0.7	2.4
White-plumed Antbird	1778	94.8	0.3	1.0	1.3	1.1	0.4	1.0

[a]Records over swarms of *Eciton burchelli* or *E. rapax*. [b]Included in "Foliage"

tend into this region in sandy or otherwise low-stature woodlands. I found them in low woodlands near Santarém, for instance; back in the main forest they were replaced by subdominant *Rhegmatorhina gymnops* (Willis, 1969). Far to the south on the upper Paraguay River, Fire-Eyes were in low woodlands on sandy soil while *R. hoffmannsi* replaced them in taller woodlands (Willis, 1976a). Absence of a subordinate antbird in forests of the region may therefore be a result of competition with the subdominant *Rhegmatorhina,* or of insufficiency of horizontal perches that favors vertically clinging *Rhegmatorhina* in tall woodlands. Since Fire-Eyes occur in even taller and more vertically oriented forests near Belém in the absence of *Rhegmatorhina,* but in reduced numbers compared to less vertical habitats near Belém, both factors may play a part. Probably Salvin's or White-plumed Antbirds could live with *Rhegmatorhina* species were they to reach the region between the Madeira and Xingu, since they live together in other regions. Niches at times are unfilled in the sense that few species may split foraging opportunities differently in one region than do more species in an adjacent one.

Differences in Subspeciation. In the genus *Pyriglena,* there are well differentiated races but poorly differentiated species. Fire-Eyes are similar to many other antbirds in their morphology and behavior (Chestnut-backed Antbirds, for instance; Willis & Oniki, 1972). The many candidates for related genera include *Rhopornis, Myrmeciza,* and *Percnostola.* Spotted Antbirds have poorly differentiated races but are represented by two morphologically similar and behaviorally different species east of the Andes (*H. naevia* is very similar, but is much less se-

Table 22. Gleaning motions, as percentages of food attempts[a]

Species	*% of Attempts Represented by Gleaning*		
Dominant	**Total**	**Above Ground**	**On Ground**
Black-spotted Bare-Eye	7.2	44.4	4.8
Ocellated Antbird	8.7	59.4	5.7
Subdominant			
Bicolored Antbird	8.4	45.3	4.3
Subordinate			
Spotted Antbird	10.9	23.4	5.0
White-backed Fire-Eye	21.3	57.1	12.5
White-plumed Antbird	5.3	48.9	3.0

[a]Most tries other than gleaning were sallying. Only records at swarms of *Eciton burchelli* and *E. rapax* are included.

xually dimorphic and rarely follows ants; *H. punctulata* is morphologically like *naevia* but sallies for prey in foliage of the open understories of seasonally flooded riverside forests). Links of these three "spotted *Hylophylax*" with other genera are not strong. Scale-backed Antbirds *(Hylophylax poecilonota)* are currently placed with them but seem closer in morphology and behavior to the genus *Hypocnemioides.* White-plumed Antbirds have moderately differentiated races and are behaviorally and morphologically very distinct from other antbirds. The less unusual White-masked Antbird **(*Pithys castanea*) of northeastern Peru** may link them to the genus *Rhegmatorhina,* but field studies are needed.

It is sometimes assumed that actively subspeciating groups are in active evolution toward species, but we should not assume that one always leads to the other. Rapid evolution will produce an array of different species and genera, while subspecies may in**dients, the spotted *Hylophylax* occupy forests that are slightly more seasonal (due to** have evolved away from their nearest relatives less than have the spotted *Hylophylax* or the species of *Pithys.* Since the three groups are all subordinate at ant swarms, we are dealing for the moment not with a subordinate-dominant axis of evolutionary rates but with some other. What could lead to different evolutionary rates in the three groups?

Habitat differences seem a possible reason for different rates of evolution. When one considers habitats to be gradients between tropical rain forests and barren ground, *Pithys* occupies habitats near the extremely favorable (for vegetation) ends of the gradients, **the spotted *Hylophylax* occupy forests that are slightly more seasonal (due to** flooding or, northward, to seasonal rainfall), and *Pyriglena* center in seasonal or montane vine-tangled woodlands of even lesser stature.

If we accept, with Haffer (1969) and others, that there have been climatic fluctuations on a wide scale, we see that habitats at the rain-forest end of the gradient have been unstable on a long time scale. In cool and dry epochs, the most extremely developed rain forests are pinched together from north and south. They may disappear, being replaced by more seasonal forests suitable for spotted *Hylophylax* but not for *Pithys;* or they may persist for long periods as isolated "refugia".

In either case, a species within these forests is subjected to strong evolutionary pressures. If the habitat disappears, it must adjust to living in a more seasonal type of forest. If only "refugia" remain, it is likely to develop different forms that are subject to new evolutionary pressures as species disappear (isolated habitats quickly lose species; Willis, 1974). As warmer and more humid conditions return, the nonseasonal forest spreads or reappears near the climatic equator, subjecting forms within it to encroaching vicariants as refugia reunite in the first case or to rapid selection of nearby species to occupy the "new" habitat in the second case. In neither case is a species likely to return to its former state, even though the forest has done so; evolution is unlikely to produce the same form twice. Evolution of very distinctive forms occurs, and subspecies tend to be replaced by different species or even genera.

Meanwhile, the Fire-Eyes of intermediate habitats have been subjected to lesser pressures. An intermediate or polar habitat is not lost when climates become dry or wet, but just moves closer to or farther from the equator. (Locally, of course, it may be trapped or lost due to east-west barriers, as the European forest was trapped against the Alps in glacial times and lost many species). The bird living in such a habitat can move with it. Moreover, if there are climatic cycles in an environment with locally humid and dry sites (or cold plus wet sites, etc.), the intermediate habitat of that area will be isolated in the local dry site at or near the peak of rainfall and in the local humid site during or near the low-rainfall epoch; it is isolated twice as frequently as are the nonintermediate habitats of that environment, but each period of isolation is shorter. Doubled frequency and halved wave length of habitat patchiness, too short for reproductive isolation but frequent enough for subspeciation, could help explain the high number of subspecies in Fire-Eyes, and also their relatively weak speciation. One might expect extensive subspeciation and infrequent speciation to be characteristic of intermediate habitats. Polar or other open habitats have birds able to move about and show neither subspeciation nor speciation.

Any relatively slow evolution of species of intermediate habitats should eventually lead to replacement of these species by superior competitors arising up the habitat gradient. This means that more species should move down the habitat gradient or out of the rapidly evolving guilds in tropical rain forest than return to it. Net movement will be slowed or even blocked by good competitors already present in peripheral habitats, but even a slow outward flow from the forest will over geological time completely fill all lower habitats and exclude previous forms. Environmental disasters, such as dry or cold epochs or recent human activities in the tropics, can remove the forest and hence its production of forms for a time; but this only shifts the zone of major production to the next habitat down the gradient. The most recently evolved forms will be central or forest genera and families, or groups derived from them and spreading into open areas; primitive forms will be peripheral or open-area birds.

Haffer (1975) has found that Amazonian forms have repeatedly moved around the northern end of the Andes into Central America, eliminating earlier related stocks. There is no evidence of any movement of competing forms in the reverse direction. A similar process has been called "taxon flow" (Wilson, 1961; the original "taxon cycle" seems a misnomer) when it occurs on islands. Species moving from a species-rich mainland are superior competitors when they reach species-poor islands, and force local species to move to the centers of islands and thence to extinction. Taxon flow onto islands has one curious aspect that has slowed its detection on the mainland: it is usually wandering-prone species of open habitats that cross to islands, hence it seems that open-area species replace the species present on the island whether these latter are forest species or not. Above, we have seen that open-area species of the mainland derive their competitive pressure from the forest on the mainland. Forest forms of the mainland are therefore replacing any forms on islands via an intermediate passage through open areas. Taxon flow onto islands is basically the same process as taxon flow on the mainland: net movement of newly evolved forms from any habitat with a fairly high number of species to any with low numbers.

Haffer's results could have arisen in part from simple spread of Amazonian vegetation. This is not just moving the taxon flow from the bird (carnivore) level down to the plant (lucivore) level, if recent neotropical climates are warming or becoming more humid. One could expect cases that mimic taxon flow whenever climates change. The only good evidences of taxon flow are those movements occurring without or in the opposite direction to climatic change, unless we can find no cases of "return to Eden" even during climatic deterioration. At the moment, I know of no evidence suggesting net invasion of Amazonian forests by nonforest species, and suspect that net flow outward is the rule. It is true that flow outward may produce considerable evolutionary change, as in the forest woodpeckers that became ground-living *Colaptes* (Short, 1971), but the process is driven from the forest.

In these contexts, I consider Fire-Eyes to be primitive or moderately modified former Amazonian birds that cannot compete well with crowded present-day ant-following guilds there. Their hopping techniques are not what restricts them to second growth and woodlands, for at Belém they occur in forests, while many of their relatives are still hopping in Amazonian forests away from ants. I doubt that a southern ancestor of the genus became an ant follower and then spread northward against the competitive gradient. Indeed, there is one bit of evidence that suggests that southern Fire-Eyes are inferior even to northern ones. In eastern Pernambuco and Alagoas, *Pyriglena leuconota* is the species present *(P. l. pernambucensis),* even though isolated today from similar nominate *leuconota* in the Belém region by 1000 km of dry habitats. Continuous forests to the south of Alagoas are occupied first by *P. atra* and then by *P. leucoptera,* which either were unable to spread northward into Pernambuco or have been replaced there by *P. leuconota* in the last wet epoch. The former suggestion is very improbable, the latter very likely. If the latter is true, taxon flow has again been outward from the Amazonian forest.

The spotted *Hylophylax* are also likely to be moderately primitive forms, ones that do not compete well with crowded Amazonian ant-following guilds. Only west of the Andes has one form, *H. naevioides*, found ant-following viable in the relatively uncrowded guilds there.

White-plumed Antbirds and two species studied earlier (Willis, 1968a) are subordinate species that compete directly with Amazonian ant-following guilds. They seem unusual species, without close relatives, and are likely to be fast-evolving new forms.

Adversity and Diversity. Despite or because of differences in the extent to which they have evolved away from their nearest relatives in other genera, the subordinate ant followers are diverse when one compares them with each other (Table 23). Is it possible that the niche of a subordinate ant follower encourages diversity more than does the niche of a peripheral or a dominant ant follower?

Peripheral to the subordinate ant followers, there is a diverse but unspecialized array of "amateur" ant followers (Willis & Oniki, 1978). Some are dominant, such as large motmots (Momotidae), but only small subordinate birds like Scale-backed Antbirds are persistent at ant following. The amateur ant followers are mostly specialized for other ways of life, and hence compete inefficiently with the subordinate and dominant professional species. Few amateurs interact agonistically with any professional ant follower. It seems unlikely that the ant-following situation exerts any evolutionary pressure of consequence on the amateur species.

They are almost excluded from ant following, so that their diversity is mainly due to other factors. In a sense, they face too much adversity in food supplies and hence do not evolve within the system.

Central to the subordinate ant followers at a swarm are the dominant antbirds, woodcreepers, etc. (Willis & Oniki, 1978). These birds are similar in their foraging niches (Tables 21 and 22) and in other aspects of behavior. It seems that there is only one best way to exploit the ants, and that birds as diverse

Table 23. Similarities and differences among subordinate antbirds

Similarities (7)	
Low male-female sociality	Frequent chipping and panicking
Extra courtship displays	Little submissive etiquette
Little nepotism	Form competitive assemblages[a]
Little keening alarm	
Differences (23)	
Number of vocalizations	Use of high foraging
Period of fledgling care	Percent time with ants
Length of chipping alarm	Peripheral vs. central foraging
Amount of chirring alarm	Hopping vs. flying
Territoriality	Vertical vs. horizontal perches
Amount of aggressive display	Variability in capture locations
Marital constancy	Use of hovering above ground
Nest season length	Use of gleaning on ground
Sexual dimorphism	Forest vs. woodland preferences
Adult mortalities	Subspeciaton
Nest mortalities	Morphological specialization
Preening over ants	

[a]These form even in dominant antbirds.

as large antbirds and woodcreepers converge on this one pattern. Even the subordinate ant followers converge on this pattern in foraging when dominant ones are absent. Dominant birds interact aggressively with other species. Lack of adversity in food supplies, however, seems to lead to lack of diversification despite high competition.

Historically, the process of diversification in ant-following birds seems likely to start with a new food niche, that of following ants. An amateur bird moves in and evolves as it does so. Being the only bird other than peripheral species, it converges on the dominant pattern of exploiting ants and stops evolving. Meanwhile, another amateur species moves in if food supplies are sufficient and stable enough. It evolves to live over ants and to coexist with the first species. As species are added, diversification is more and more necessary; and the number of species eventually reaches saturation. The original dominant species may be ousted by a faster-evolving species at any time. One thus has a kind of taxon flow, in which amateur birds move centrally over ants as if onto an island, and the dominant species eventually is replaced. To distinguish this local type of taxon flow from that between habitats, the former can be called "niche flow".

The major suggestion of niche flow is that one expects evolution not at the top or bottom of the hierarchy but in the middle. Members of the middle class evolve in ant-following birds, not kings nor peasants. Since competition is unlikely to be stronger at midlevels than above or below, this raises doubts that it causes divergent evolution. (One must exclude static or agonistic responses to competition, such as individuals that have repertoires for competitive and non-competitive situations - Willis, 1966 - and the tendency of White-plumed Antbirds to go on infiltrating despite suffering literally billions of attacks yearly). The greatest food adversity over ants is faced by the amateur, which may be subordinate and always is inefficient. The greatest agonistic competition is faced by the dominant bird, which faces its own species over the swarm center plus the many subordinate and amateur birds moving in peripherally.

Extrinsic competition primarily limits opportunities, and hence reduces or eliminates certain or all genotypes. Basically therefore, it is an eliminatory or stabilizing or converging force. By itself, it can lead to competitive exclusion but not to character displacement. Genotypes that happen to have less extrinsic competition are more successful only if they are not blocked by some other extrinsic competition or other lack of resource. In the absence of new resources, competition only creates agonism and reduces numbers. The assumption that a bird looks at a new competitor and then develops new mutations or gene frequencies to outdo it is a Lamarckian extension from individual to genetic reactions. The bird changes because part of its niche is gone, and will increase only if lucky mutations arise in or near the part of the niche remaining. The only kind of competition that can lead to real niche divergence is "intrinsic", i.e., greater growth and reproduction and dispersal. The cause of character displacement is thus not competition, but change of opportunity. If the habitat changes character displacement may or may not occur just as it may or may not occur when a congener moves in. The latter is merely a special case of the former, and the former seems more important in most cases examined critically (Grant, 1975).

Subordinate ant followers are at least as adapted as are dominant or amateur ones to face the problems of life over their parts of the ant swarms, and all could show diversity despite seeming adversity. Shifting of niche may be difficult for the dominant species because it has to center on the one best way of exploiting ants or be unable to maintain the large size and agonistic expenditures that keep it dominant. Shifting of niche is difficult for the amateur because it is too inefficient to compete over ants. The subordinates are not so limited, and hence can be diverse.

The reason for rapid evolution in diverse avifaunas is almost certainly not competition, but the greater number of niche faces or opportunities in such avifaunas. Competition merely reduces diversity or evolution, and can cause the most saturated guilds to stagnate. This raises the theoretical possibility that the center of taxon flow is not the exact center of the tropical forest or its guilds, but the ring of its many peripheries. Also, tropical forest avifaunas may be less diverse than they should be were competition not present. Neither infinitely increasing diversity nor extreme competition are likely to be keys to diversification, creativity, or progress.

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