The Behavior of Ocellated Antbirds

EDWIN O. WILLIS

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ABSTRACT

Willis, Edwin O. The Behavior of Ocellated Antbirds. *Smithsonian Contributions to Zoology,* number 144, 57 pages, 25 figures, 1973.—A ten-year study of color-banded Ocellated Antbirds (*Phaenostictus mcleannani*) on Barro Colorado Island, Panama, showed that they persistently follow army ants for arthropods flushed by the ants. Dominant over the smaller antbirds that follow ants, they take the best zone low over the center of an ant swarm and drop to the ground for prey. They rest and preen for long periods of maintenance behavior each day, probably because as dominant birds they get food easily. Alarm behavior is similar to that of other antbirds. Agonistic behavior contrasts with other antbirds in having a silent challenging display and an unusually wide spectrum of submissive calls and postures. Courtship is mainly courtship feeding and singing; monogamous mates stay together for years.

The nest is probably sunk in the ground between tree buttresses. Males incubate in the morning and late afternoon, females in the early afternoon and at night. Males and females feed nestlings and fledglings. Pairs renest repeatedly during the rainy season, April to December, but nest predation is high. Young are feeding themselves a month after appearing at swarms with their parents, but then irregularly stay with their parents up to several months (females) or years (males). Loose patrilineal clans form, in which gene transfer between clans is mainly by movement of young females. Daughters-in-law are tolerated. Clan members sometimes forage together, but use much submissive display. They close ranks or "bunch" in disputes with other pairs or clans. The social system is somewhat like that of chimpanzee groups and perhaps like that of early man—two other dominant animals dependent on local and varying sources of food.

The clan system permits complete overlap of home ranges of pairs. The parental pair in an area tends to dominate trespassing pairs and their own offspring. This social system permits great local concentration over good ant swarms. It is facilitated by tolerance for related birds, silent (and thus less disturbing) challenging, and by a wide variety of submissive displays. The Ocellated Antbirds on Barro Colorado concentrated at ant swarms on escarpment zones near the center of the island. Even with these concentrations, however, the species declined to near extirpation between 1960 and 1971.

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Introduction

Ocellated Antbirds (*Phaenostictus mcleannani*, Formicariidae) are the largest (about 50 g) and least common of the three main species of antbirds that persistently follow army ants and capture arthropods flushed by the ants in the undergrowth of humid tropical forests from Honduras to Ecuador (Johnson, 1954; Howell, 1957; Slud, 1960, 1964). Earlier (Willis, 1967, 1972a) I reported on the medium-sized (30 g) Bicolored Antbird (*Gymnopithys bicolor*) and small (17.5 g) Spotted Antbird (*Hylophylax naevioides*). The social organizations of these two species allow them to follow ants all or part of the time even though large species of antbirds dominate smaller ones. This report examines how the social and other behavior of the domineering but specialized Ocellated Antbirds allows them to follow army ants.

Ocellated Antbirds are of special interest to the student of behavior because mated pairs flock over ants, even during the breeding season. Most birds, even ones that flock during the nonbreeding season, separate as pairs on isolated territories when nesting. A few birds, such as Mexican Jays (Brown, 1963), form group territories and nest cooperatively, while a fair number of species, such as gulls (Tinbergen, 1953), nest communally on small territories. Bicolored Antbird pairs form groups over army ants even in the nesting season but are still territorial; the pair on its own territory dominates trespassers (Willis, 1967). Brown (pers. comm.) has theorized that this kind of "loose territoriality" is a stage in the evolution of communal nesting. The study of Ocellated Antbirds now shows a step beyond the stage in Bicolored Antbirds—a stage of separate nesting but formation of altruistic loose families or "clans"—and suggests that group territoriality could also evolve from clan organization. The clans of Ocellated Antbirds resemble in organization the loose clans of chimpanzees (Lawick-Goodall, 1968). Such clans are in some ways more social than the more tightly organized groups of jays and baboons or the aggregations of gulls and cedar waxwings; for instance, clan animals have larger vocal repertoires and greater emphasis on individual recognition of many individuals. The independent evolution of loose clans in animals as different as chimpanzees and Ocellated Antbirds deserves study to see if ecological or behavioral causes are similar, particularly since humans may have developed language and social behavior in a chimpanzee-like system rather than as tightly grouped animals like baboons or gorillas.

I have attempted herein to completely describe the behavior of Ocellated Antbirds. Such "ethograms" or "life histories" normally are boring to a reader in some places and interesting in others, for few readers interested in preening are interested in social behavior and vice versa. I ask patience of the reader, or that he or she skip over sections of little interest. The text first gives a "picture" of the bird from the visual and vocal standpoints; if I had information on odors or other things the bird could use in behavior I would have included them. Second, I describe simple changes in the static picture—locomotion, simple movements, etc. Third, I

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look at complex sequences of movements. These complex sequences are divided into six sections, which should cover all possible behaviors: foraging behavior to the small and positive; maintenance behavior as a reaction to things that are small and negative; antipredator behavior to the large and negative; agonistic behavior to things medium-sized and negative; reproductive behavior to the medium-sized and positive; and spatial behavior to the large and positive. When an activity could be placed in two or more sections, it is described in the section of main interest and mentioned briefly in the others. Social behavior and communication can occur in all six sections. I think that the sixfold way is more desirable than division into social and nonsocial behavior, for behavior must be related to environment rather than studied in isolation as one would do if he merely looked at interactions between animals or lack thereof. The contexts as well as the structures of the animals can, I hope, explain such things as the independent evolution of clan systems in antbirds and chimpanzees.

Common and scientific names of birds here are from Meyer de Schauensee (1970). The common name of the Ocellated Antbird was often "Ocellated Antthrush" until Meyer de Schauensee's earlier book (1966:294). Anatomical evidence (Ames, 1971) suggests that "antthrushes" of the genus *Formicarius* form a rather distinct group; the Ocellated Antbird is not a terrestrial walker like them but a clinging, hopping bird of the low undergrowth, more like the Bicolored Antbird.

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STUDY AREAS.—The main area for field work was the lowland forest of Barro Colorado Island in the Panama Canal Zone. I have described this forest, dates of visits, and methods of study elsewhere (Willis, 1967, 1972b). Here I will note only that birds are mist-netted and banded with individual combinations of color bands for later recognition through binoculars. I have found Ocellated Antbirds at six other localities in Panama (Cerro Campana 900 m, Madden Forest Reserve, Pipeline Road, Rio Agua Salud, Bohio Peninsula, Rio Medio) and at five in Colombia (Tucurá, Boca del Rio Verde, Caño Remolina, Filo de Abibe, and El Tigre). A total of some 40 months of studies on Barro Colorado, 1960 to 1971, contrasts with a total of less than a month of observations at other areas.

ARMY ANTS.—The Ocellated Antbird never, so far as I know, forages more than casually away from swarms of army ants. *Eciton burchelli* and *Labidus praedator,* the only two species that form wide swarms in tropical forests and clearings from Mexico to Argentina, flush large numbers of arthropods. A few other species flush small numbers of arthropods. Ocellated Antbirds follow *Eciton burchelli* almost exclusively, but sometimes follow other species of ants near colonies of *burchelli.*

The behavior of *Eciton burchelli* is described by Rettenmeyer (1963) and Schneirla (1957). A swarm raid emerges from a bivouac, or interlocked mass of ants around the queen and larvae, every morning during a "nomadic" phase of about two weeks. The raid moves outward on the ground all day, and often the whole bivouac moves that night to a new site located by the raiding ants. After two weeks of nomadic raiding the ant larvae pupate and the colony settles for three weeks of the "statary" phase, usually inside a hollow tree. The raids radiate from the statary bivouac like spokes from a wheel, except that on some days the ants fail to raid. Birds often shift to nomadic colonies as soon as the ants fail to swarm, but may return to the statary colony occasionally. The ant pupae and new eggs hatch, and the ants begin another nomadic phase. The five-week cycles continue all year long, dry season and wet season. Because of the greater abundance of organisms in the leaf litter (Willis, MS) in the rainy season (April-December) the ant colonies increase in size during that time. A few colonies then split into small colonies in the dry season, but there is a decrease in average colony size from the splitting. Also, some

colonies are lost because of decreases in numbers in the dry season. On Barro Colorado Island there are about three colonies of *Eciton burchelli* per square kilometer throughout the year (Willis, 1967:7); but the ants wander without regard for territorial boundaries, so that there may be several to none within a given square kilometer of forest.

The Ocellated Antbirds

Ocellated Antbirds are strikingly colored, long-tailed antbirds. Specimens have been painted in color in poses that look like submissive behavior (see later) for Howell (1957: opposite p. 73) and Meyer de Schauensee (1964: Pl. XI). A color photograph of a live bird is in Dunning (1970). Dunning's photograph shows a pallid-faced bird in alarm behavior, captive in a photographic box.

A few species in other antbird genera also have bare, blue faces; but the closest relatives of Ocellated Antbirds are currently considered to be red-faced "bare-eyes," Amazonian antbirds of the genus *Phlegopsis*. It is not certain that the bare-eyes are closely related to Ocellated Antbirds, for their similar ant-following habits may have led to convergence. The Pale-faced Antbird, *Skutchia borbae,* of central Brazil is a white-faced ant follower that may link bare-eyes, Ocellated Antbirds, and the small White-plumed Antbirds, *Pithys albifrons* (Willis, 1968a). Short-tailed medium-sized antbirds of this and several other genera, especially *Rhegmatorhina* (Willis, 1969) and *Gymnopithys* (Willis, 1968b), also seem to bridge the gap between *Phaenostictus* and *Pithys* but may be convergent genera. All of these are ant-following antbirds, and all (as do a few other antbirds) consistently "flick" (Willis, 1967:39) the tail upward and lower it slowly when excited.

The six genera just mentioned might be combined under *Pithys,* the oldest name, were it not that they are almost as diverse morphologically as any birds in the Formicariidae. However, the present taxonomy expresses reasonably well that several rather distinctive forms and groups of forms occur, and that the single species of *Phaenostictus* is distinctive.

There are several subspecies of Ocellated Antbirds. Wetmore (1972) considers that gray-crowned nominate *P. m. mcleannani* range from near the Canal Zone east on both slopes of Panama into northern Colombia, as far as the central Sinú and Cauca drainages, then grade southward on the Pacific slope into dark *P. m. pacificus* from the central Atrato drainage into northwestern Ecuador. Dark-crowned *P. m. saturatus* range from Coclé in Panama along the Caribbean slope through eastern Costa Rica and Nicaragua to the forests of southeastern Honduras (Monroe, 1968). This form ranges somewhat onto the Pacific slope in central Panama and in the region of the Cordillera de Guanacaste in northern Costa Rica. All of the forms stay in humid lowland or foothill forests, up to as high as 1300 m on Cerro Tacarcuna in eastern Panama.

In accordance with Bergmann's Rule, but contrary to Allen's Rule and Schoener (1971), Ocellated Antbirds become slightly smaller in wing and bill toward the equator (Table 1). Females are generally slightly smaller than males, but the differences in length are not reliable for sexing birds in the field. Females, however, usually weigh 44–50 g, males 50–58 g, based on a few weights of specimens and of live birds on Barro Colorado Island. In a few cases, I used weights as a method of sexing birds but only as an auxiliary to the method of observing mated pairs, in which the male consistently feeds the female. Five Barro Colorado weights ranged from 44 to 57.8 g. James R. Karr (pers.

TABLE 1.—*Culmen and wing lengths of Ocellated Antbirds*

Place	Males			Females		
	no.	culmen	wing	no.	culmen	wing
Honduras-Nicaragua	4–4	24.2 (23.6/24.7)	91.2 (85/95)	2–1	23.5 (23.4/23.6)	87 (–)
Costa Rica	30–30	24.4 (22.9/25.7)	92.4 (86/97)	17–17	24.1 (22.5/25.9)	89.2 (85/94)
Panama	39–35	24.4 (22.5/25.7)	91.3 (88/95)	32–32	23.8 (21.9/25.2)	87.5 (84/93)
North Colombia	26–29	23.8 (22.1/25.4)	89.5 (85/95)	18–19	23.2 (21.7/24.6)	86.4 (82/90)
S. Colombia-Ecuador	8–6	23.6 (22.8/24.7)	86.8 (85/90)	9–5	22.6 (22.1/23.6)	83.0 (81/87)

comm.) weighed six birds seven times at the Limbo Hunt Camp, in the Panama Canal Zone, and found a range of 46.9–57.3 g (average, 51.4 g).

Young birds in juvenal plumage molt slowly into adult plumage in the first few months of life (see later); they can be recognized as young until the pale gape angles and the last juvenal feathers are gone. Instead of the pearly gray or brown crowns of adults, the young have mottled crowns of blackish feathers with whitish tips. The forecrown is sometimes bare in very young birds. The mottled feathers disappear last at the rear of the crown. The young have pale gape angles and dusky faces, not the bright blue faces of adults; the base of the lower mandible is whitish rather than the whole bill being black as in adults. Young almost lack the rusty nape and breast so prominent in the adult, although both young and old have black throat or bib feathers. Instead of the black-centered rusty belly feathers of adults, the young have buff or orange-centered blackish feathers. This is the reverse of the pattern of the adult ocellation. The back feathers are black as in adults, but with buff or rusty rather than whitish-brown edges. The greater wing coverts are rather white-tipped in young birds, forming an indistinct wing bar. Black and other colors are duller than in adults, partly because the juvenal feathers have fewer barbs. Most of the color differences from adults can be explained on the basis that juvenal colors should differ from adult colors in characters that are important in adult agonistic behavior (see later).

Molt

Ocellated Antbirds are among the many species, including several antbirds (Snow and Snow, 1964; Oniki, 1971), that molt when they are nesting. There is a complete postjuvenal molt, including wing and tail feathers, in the first four or five months of life; one must be careful to exclude these birds when determining molting seasons. Some 201 dated seemingly adult specimens from museums in the eastern United States show molting ratios (number in wing molt/number not in wing molt) for the months from January to December, respectively, of 5/19, 3/28, 5/30, 4/30, 8/9, 3/4, 4/3, 7/7, 12/3, 5/0, 7/1, 3/1. Thus, although some birds are in wing molt in every month of the year, few are in wing molt from January to April. This is the dry season in Central America, the source of most of the specimens. Most birds are in molt in September to December, which in much of Central America is the last and rainiest part of the wet season.

Many of the May birds in molt come from eastern Panama and northwestern Colombia, a region with a short dry season; however, the few birds from the constantly rainy western part of Colombia south into Ecuador seem to have the September-October molting season of Central American birds, rather than the April-May molting season that is characteristic of most birds of other species south of the climatic equator. Perhaps any tendencies of the few southern birds to an austral molt season are swamped out genetically because the main population of Ocellated Antbirds lives north of the climatic equator, where the boreal molt season is more advantageous. It may also be that, despite climatic differences, the food supply in the litter in western Ecuador peaks at about the same time as the June peak in Panama (Willis, MS); if so, nesting and the following molt (Snow and Snow, 1964) might be arranged so as to divide the available food peak in both areas.

On Barro Colorado Island, the few data indicate wing molt in every month checked; the molting ratios for the months of January to December are 2/3, 0, 0, 0, 1/0, 5/2, 11/1, 11/5, 2/0 1/0, 0, 0. Two birds were recaptured during a single molt; one had #7 from the end of each wing in molt on August 2, and #1 and #3 on each wing in molt on August 8. Another had #3 on one wing, #4 on the other in molt on July 17. On August 2, #5 and #2 were in molt on those wings. Irregularities in molt sequence are probably common, as the Snows (1964:11) noted for another antbird, the Barred Antshrike.

Voice

Calls of Ocellated Antbirds are much like those of Bicolored Antbirds (Willis, 1967:13–16). Ocellated Antbirds, however, apparently lack the aggressive calls of snarling, bugling, and hissing, as well as the submissive call of whimpering. They add, however, a wide variety of intergrading more-or-less submissive calls here described as chittering, whining, screaming, and squawking. In Ocellateds but not Bicolors there is also a special call, "carol-

ing," when the male feeds the female. I recognize 16 named calls for Ocellated Antbirds, compared to 14 for Bicolored Antbirds and 12 for Spotted Antbirds (Willis, 1972a). All three species of antbirds have two additional subtypes of calls, plus various minor modifications and combinations of calls. The number of separate calls are like those or somewhat greater than those for many passerines that have been studied, except for the antisocial Plain-brown Woodcreepers (Willis, 1972b) and the group-territorial Mexican Jays (Brown, 1963), both of which have 5 or so named calls. The increased number of calls from the subordinate Spotted Antbird to the subdominant Bicolor to the dominant Ocellated probably reflects the increasing degree of social interaction from Spotted to Ocellateds. Group territoriality in jays apparently leads not to increases in the number of calls but to decreases. However, one of the less social jays (Hardy, 1971) has only 3 named calls.

CHIRRING.—A loud buzzy descending *cheeeee'yuk* (Figure 1H) is the normal reaction to large terrestrial animals, and thus it is the call usually reported for Ocellated Antbirds (Eisenmann, 1952:36; Slud, 1964:222). The bill is often raised slightly for the note, and the tail may be flicked. A deep version (Figure 1D) is also used by large aggressive males being held in the hand or being badgered by a subordinate bird. The sound is often muffled, especially if chipping is being given too. The audiospectrographic chirrs show decreases from about 4000 to 2000 Hz; there are about 50–60 frequency modulations per second, fewer than the 80 or so per second in chirrs of Bicolored Antbirds. The end of every Ocellated chirr is a burst of white noise, centered about 2000 Hz; this noise is so weak that it shows only on the audiospectrograph for the bird held in the hand. (The "grunts" of another distant bird, Figure 1H, also lack the introductory white noise seen in grunts from a closer bird in Figure 1G).

KEENING.—A faint, whistled *teeeeeee,* very like the *keeeeeee* whistle of Bicolored Antbirds but higher in pitch, is the reaction to such distant and uncertain danger as a passing large bird or an alarm call of another species. At times *teeeeeee, teeeee!* or even three notes are used.

CHIPPING.—Sharp, rather irregular *chip-ip* or *chip-ip-ip* calls are given as a bird flees to cover, is chased by another bird, or sees a hawk fly past. The chipping of an alarmed bird waiting in a safe place becomes a muffled *chut-ut* and sometimes seems to intergrade with muffled chirring, which is also given persistently at such times. The chipping bird often jerks its tail upward violently with each set of notes. Each chip of the trio in Figure 1K is 0.03 second long, and the first goes from 300 to 4500, 1000, and 3000 Hz as a complete sharp-cornered sine wave or Z-wave. Much noise, some of it probably not an artifact, obscures the pattern.

GRUNTING.—Scratchy, short *chaic* grunts, sometimes *chaic-chaic* double-grunts, greet small competitors like Bicolored Antbirds whenever they move near a foraging Ocellated. Four times per second was the maximum rate; usually the grunts are irregularly spaced, almost syncopated, and come at one to three per second. The tail rises slightly with each grunt, and the throat is slightly ruffled. Grunts (Figure 1G) show an introductory burst of white noise about 2000 Hz and up to 0.06 second long, plus a terminal descending chirp (with many overtones) about 0.02 second long. Peak-to-peak, the grunts are 0.22 second or more apart. The pattern of the grunt is more or less the reverse of that of the chirr (in which the first part is musical and the last part is noise).

SONGS.—Both sexes give three types of songs, though the female's songs tend to be less loud and at a higher pitch than those of the male. The striking and far-carrying but seldom-heard "loud-song" is a piercingly loud but thin series (Figure 1A-B) that, like a loud-song of Bicolored Antbirds, rises in pitch and then drops back to rough terminal notes that begin to resemble chirrs: a short one is *Eeeee, eeee, eeeh-eeh-hee-hee-hee-hee-hi-chee, cheeer, cheeer'k, cheeeer'k, cheeer'k*! The graphed loud-song shows three parts: (1) seven *eeee* notes, each slightly under 0.2 second long, the whole part taking 1.5 seconds and rising from about 3000 Hz at the start to 3500 Hz at the end; (2) sixteen rapid *eeih* or *ee* notes, accelerating from 0.17 to 0.07 seconds peak-to-peak (at numbers 11 and 12) and then decelerating, over a span of 1.6 seconds, with the highest pitch of the song 4200 Hz; (3) a terminal flourish of five long *eeeeeyip* notes, declining from 3200 to 2900 Hz as they go from about 0.2 to 0.4 and then 0.35 seconds. Since the terminal five-note flourish lasts 1.8 seconds, the graphed song (an

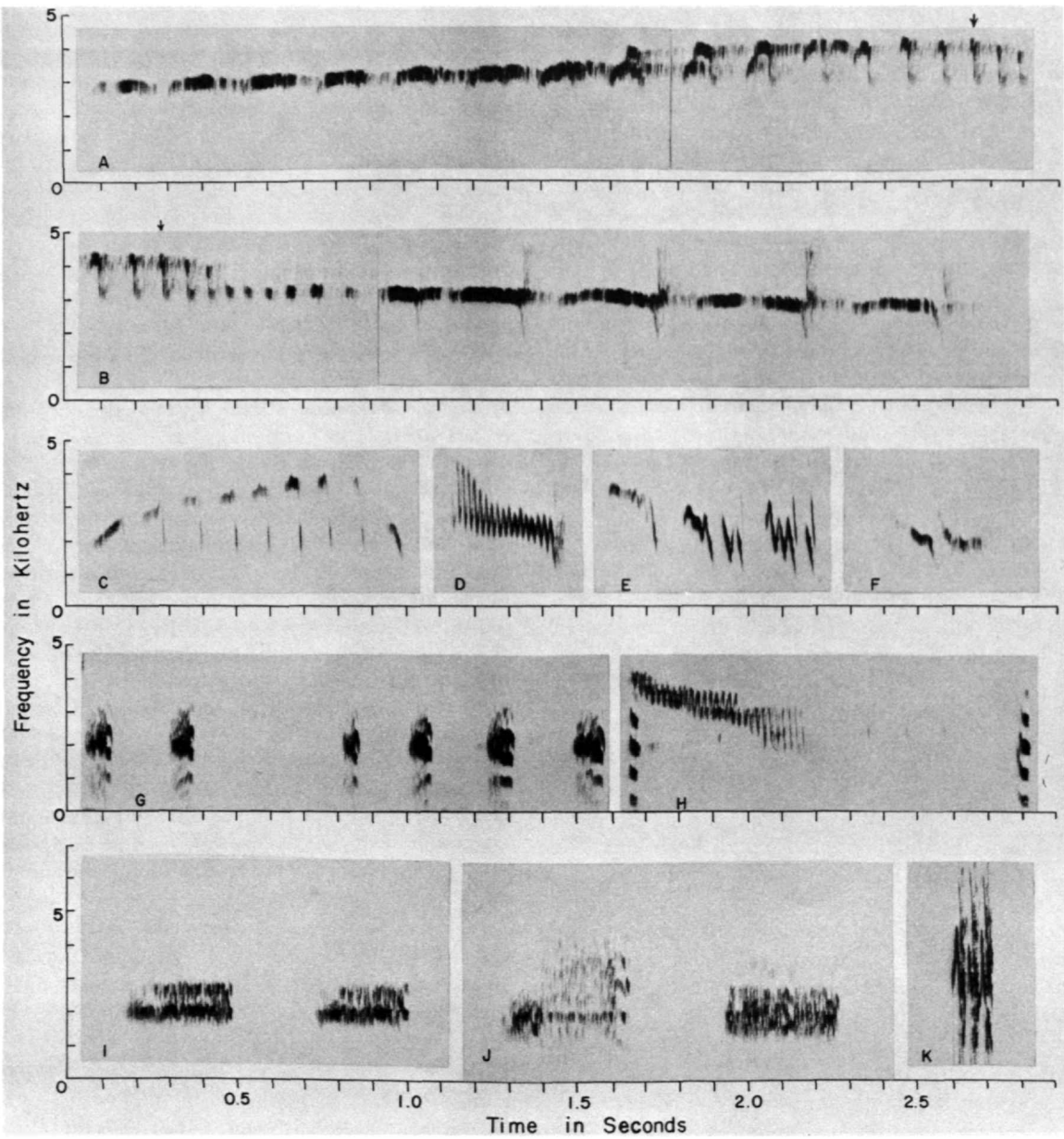

FIGURE 1.—Audiospectrographs of calls of Ocellated Antbirds, from Barro Colorado Island: A, B, loud-song, arrows mark note no. 15 in the song; C, faint-song; D, chirr of male held in the hand; E, strained chirr and two chips from a subordinate bird; F, truncated chirr and whine of a subordinate bird; G, grunts, showing normal spacing; H, chirr, with two grunts, from distant birds; I, whining; J, scream and a whine; K, triple chip.

unusually long one from a bird excited by a recorded playback) is 4.9 seconds in length. Even a bird excited by a tape recorder rarely loud-sings more than 7 or 8 times per minute. The loud-song is given when mates are separated, when rivals are separated, or when a bird leaves a swarm of army ants. The bird changes position little to sing: the tail quivers slightly, and the throat pulses as the bill stays open.

The far more common "faint-song" is used often when a single bird or group of birds is about to travel, so commonly so that I called it the "go-song" for many years. It is a faint series of 3 to 10 or so whistles, rising in pitch and then dropping at the end. There are usually many notes in the ascending first part of the song, one or a few in the descending last part. Each note is accented by a slight downward movement of the tail. *Whee-kee-ki-chew* is what I called a "3–1" faint-song, 3 notes upscale and 1 down. Eisenmann (1952:36) noted a "6–0" song, probably actually a "5–1" song; faint-songs often follow chirring at a human intruder. The longer faint-songs (such as "7–3" and "10–4" songs) tend to be louder, and the loudest and longest add introductory and terminal *eeeeee* notes and become loud-songs. The graphed faint-song (Figure 1c) is a "7–2" song, about 0.9 second long, and rises from 2000 Hz at the start of the first note and about 1500 Hz in the clicks at the end of all other notes to about 4000 Hz at the center of the seventh note. The ninth note is a heavy *chew,* which drops from 2400 to 1500 Hz. The first note is about 0.09 second long, the eighth only 0.04 second, but peak-to-peak intervals are about 0.11 second throughout; thus, spaces between notes are longer at the end of the song. The faint-song seems like the central section of the loud-song.

"Serpentine-songs," as in Bicolored Antbirds, are musical series in which calls rather like faint-songs are connected by low-pitched chirping notes: *ee, hee, hee, hi, hew, hew-hew-hew-hew-hew,* over and over. Possibly "caroling," described later, is a truncated serpentine-song, for serpentine-songs are phrases that attract a mate or young to a site or to be fed.

WHIRRING AND SNAPPING.—The only sound by a dominant bird besides an occasional chirr is likely to be a surprisingly loud whirr of the wings and multiple snapping of the bill as it supplants a subordinate of its own or a smaller species. I have not detected hissing by dominant Ocellateds, although both Spotted and Bicolored Antbirds use that sound in their snapping attacks.

CHITTERING.—Stuttering *i-i-i-i* or *a-a-a-a-a* chatter is one of the complex set of calls of subordinate Ocellated Antbirds being crowded out by silent dominant ones. At times the chittering becomes like a faint-song, as a "chittering faint-song," and may be related to it.

WHINING.—Starting as grunts that become more and more strained and scratchy, *aaah* (Figure 1i) sounds verge into whining *kraihh* whines as a subordinate bird bounces about and tries to avoid being ousted from a swarm. The two graphed whines are 0.3 and 0.25 seconds long, and are bands of noise between 1800 and 2800 Hz. Both whines end in harmonic chirps much the way grunts do.

SCREAMING.—Whines grade into variable piercing squeals, *eeeieeh*! and the like (Figure 1j). The first note graphed is a whining scream, the second one a whine. The scream is a burst of white noise from 500 to 4500 Hz, with a main whistle about 2000 Hz; it ends in a harmonic chirp much like the harmonic chirp at the end of a grunt, but a chirp that tends toward the frequency modulation of a chirr. It is possible that these harmonic chirps are actually verging on low-intensity chirrs, for subordinate birds use strained chirrs and chips as part of their whining and screaming at times. For instance, Figure 1e graphs a strained *cheeyk chitik chitik,* a chirr followed by two double-chips, and Figure 1f gives a *chee-aik,* a truncated chirr and truncated whine. Sounds similar to screaming are sometimes given by birds in the hand.

SQUAWKING.—A bird that is chittering, whining, and screaming may give a sudden CHWAIHK! squawk when supplanted.

PEEPING.—As in other antbirds, young separated from their parents or begging for food sometimes peep. The main kind of peeping later grades into singing and is a rising *pee-pee-pee-pee-pee-pee.* Often each note quavers, *pee'e,* as a "quavering peeping."

SQUEAKING.—Young squeak *waiaih* when fed, and resume peeping after feedings.

CAROLING.—The male or female feeding a young bird, or male feeding a female, usually gives at the moment of feeding a distinct but not con-

spicuous series of 1–15 whistled notes, the first few at a higher pitch than the last few: *chee chee chew chew!* or the like. Caroling often sounds irregular, as if two birds are calling, but it is definitely given by the feeding bird and not the fed one when a male feeds a male or a young bird. If the feeding bird holds back with the food, however, the other may give a faint caroling, often *chee chee chee* notes that do not descend in pitch. (These notes may be "chirping.")

GROWLING.—When a well-fed female antbird refuses the food and caroling of her mate, she growls a brief *chah-ah-ah-ah* series. The series is somewhat like one kind of chittering.

CHIRPS.—Faint *cheur* chirps go back and forth between mated Ocellated Antbirds at times. There seem to be many such faint sounds, but they are inaudible at a distance and hard to tell from the chirps of other antbird species with them. When the female Ocellated sees her mate with food, the chirps are usually *chee* or *chee-chee* and grade into caroling notes.

Postures and Movements

Figures 2D, J illustrate basic or "standard" postures (Willis, 1967:16) for the Ocellated Antbird. The long tail is rather down and the head nestled far back, giving a humble or puffed look compared to the posture in Bicolored Antbirds. Perhaps Ocellateds bring the large head and bill over the center of gravity by retracting them "humbly."

Like Bicolored and Spotted Antbirds, Ocellateds cling easily to slender vertical perches (Figures

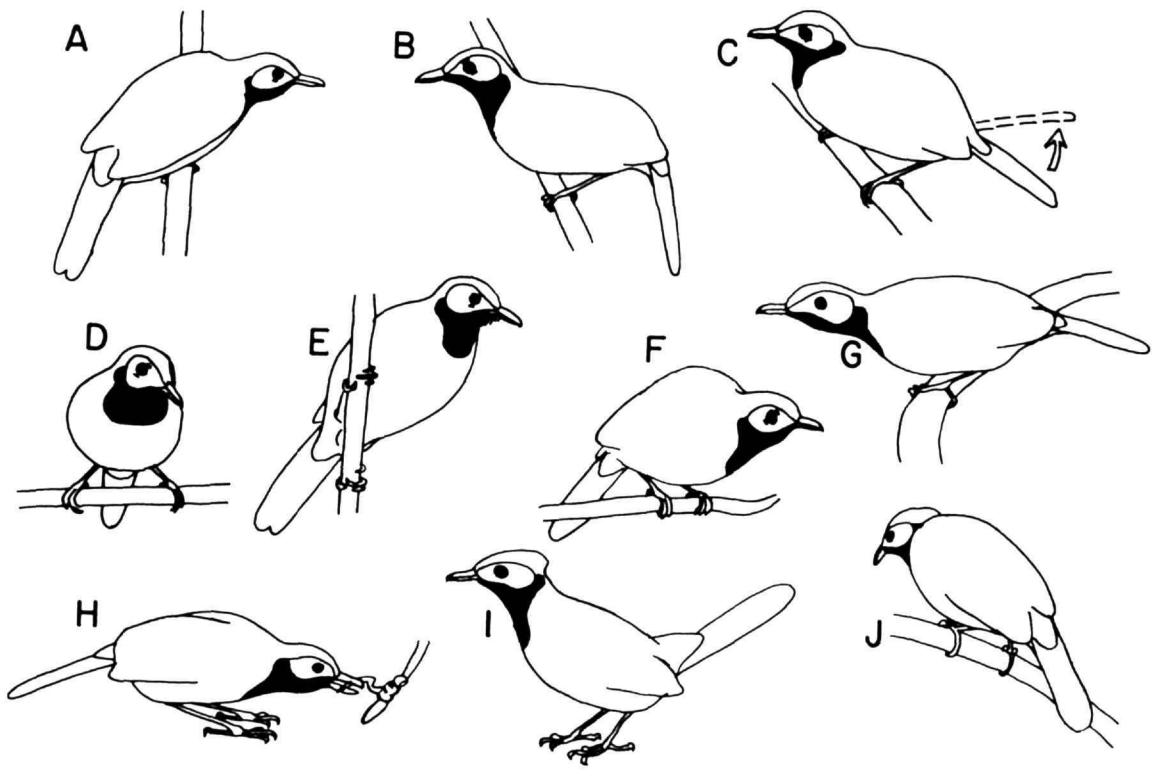

FIGURE 2.—Foraging Ocellated Antbirds, from field sketches: A, subordinate bird keeps low and watches dominant ones while foraging; B, the body often forms a parallelogram in side view; C, slightly alarmed bird flicks or jerks the tail upward now and then; D, normal or standard posture; E, alert dominant bird forages busily; F, very "humble" posture of female waiting for me to lead her to ants; G, swinging on a liana; H, dissecting prey on the ground; I, hopping on the ground after prey ran under leaves; J, standard posture from the rear.

TABLE 2.—*Perches used by foraging Ocellated Antbirds* (foraging over swarms of army ants, Barro Colorado Island, 1 October 1960 to 30 September 1961, only)

Height of perch			*Angle of perch*			*Diameter of perch*		
height in meters	*no. records*	*percent*	*angle in degrees*	*no. records*	*percent*	*diameter in cm*	*no. records*	*percent*
0.1	292	11.6	20	560	25.6	1	218	21.0
0.2	708	28.2	40	314	14.4	2	451	43.6
0.3	750	29.8	60	272	12.5	3	212	20.5
0.4	400	15.9	80	137	6.3	4	84	8.1
0.5	194	7.7	100	892	40.8	5	36	3.5
0.6	62	2.5	120	8	0.4	6	10	1.0
0.7	28	1.1				7	2	0.2
0.8	32	1.3				8	5	0.5
0.9	6	0.2				10	2	0.2
1.0	5	0.2				15	9	0.9
2.0	27	1.1				25	1	0.1
3.0	4	0.2				log	1	0.1
4.0	4	0.2				buttress	3	0.3
5.0	0	0.0						
6.0	1	0.0						
Total	2513			2183			1034	

2A, E; Table 2). In all three species, toes III and IV of the lower foot stay together in locknut fashion; presumably this prevents rotation of the foot on slippery surfaces, such as wet saplings. The toes spread in three directions, which probably aids stability. The ability to cling permits all these antbirds to stay perched near the ground over army ants even in the dark undergrowth of tropical forests, where nearly all perches are vertical light-seeking trunks. When on a horizontal perch, an Ocellated stands rather far back and must flutter a little to get the feet over the perch in moving forward; however, the toes can dangle and need not be tightly clasped.

Ocellateds do not cling well to thick trunks and normally use perches 1–2 cm in diameter (Table 2). I have seen birds slip and flutter when trying to perch on buttresses only 6 cm in diameter. As has been suggested for Spotted Antbirds (Willis, 1972a), using slender perches probably allows clear views of predators and prey as well as being more suitable for the claws and feet of these birds. Also,

TABLE 3.—*Records of foraging techniques of Ocellated Antbirds* (5 October 1960 to 4 October 1961, over swarms of army ants, Barro Colorado Island, only; figures in parentheses are records from 5 October 1961 to 2 September 1970)

Place of capture	*Motion for capture*				
	sally	*lunge*	*toss leaves*	*?*	*total*
ground, rock, root	3393 (1517)	210 (56)	63 (8)	12	3678 (1581)
log	5	4 (1)			9 (1)
fallen debris	1	4			5
trunk, buttress	23 (6)	12 (2)			35 (8)
liana, stem	24 (4)	36 (11)			60 (15)
limb	3	1 (1)			4 (1)
twig, petiole	1	11 (4)			12 (4)
leaves	22 (3)	35 (5)			57 (8)
air	9	26 (3)			35 (3)
?	0 (9)	0 (1)			0 (10)
Total	3481 (1539)	339 (84)	63 (8)	12	3895 (1631)

army ants rarely climb or attack up slender stems. However, stems under 1 cm in diameter bend with the weight of the heavy Ocellateds and tend to be avoided more than such stems are avoided by smaller birds.

The claws, toes, and legs of Ocellated Antbirds are very thick and strong. The curved claws easily break human skin when one holds a bird. This is the largest bird I know that regularly clings across rather than along a vertical surface. Allometric increases in leg size with larger body size perhaps would make a larger clinging bird almost a monstrosity. Ocellated Antbirds cling less often than do Bicolored Antbirds (Table 2, angle of perch), suggesting that the former are slightly too large to cling easily.

Like Bicolored and Spotted Antbirds, Ocellated Antbirds pitch or swing around vertical or other perches quickly and easily. Reversing direction on a perch involves little more than footwork and a slight upflirt of the tail.

An Ocellated hops and bounds between perches close together and flutters short distances too. The bird about to fly often faint-sings, then points the body in the direction of flight (Figure 3A). Flight is rather slow, fluttery, and direct; on longer flights the bird glides briefly now and then (Figure 3B). About the only time a bird misses a beat is when it passes between saplings close together. The long tail seems to beat up and down or to drag slightly and comes down for alighting (Figure 3C). Perhaps it is used for braking this heavy bird, especially in sallying for prey (see later); but it also flicks conspicuously during alarm and thus may have communicatory functions as well. The wings often spread widely on alighting, but flight usually starts with a jump rather than with wide spreading of the wings. Consequently, the first part of flight may be an arc or the descending segment of one. Flight is not fast or maneuverable, so that pugnacious Buff-throated Woodcreepers (*Xiphorhynchus guttatus*) sometimes chase Ocellateds in the air, even though the large antbirds easily supplant these woodcreepers on perches. An Ocellated Antbird maneuvers in and out of tangled undergrowth well enough and sometimes flies 20 to 30 m, but ordinarily it stops on a perch, peers ahead, and flies 10 to 20 m at the most to a suitable new perch as it travels.

Wandering

Ocellated Antbirds seen or heard away from ants are almost always traveling to or from ant swarms or are searching for them. Mostly Ocellateds keep low in forest undergrowth, usually about 1–2 m up, faint-sing to each other or loud-sing periodically and travel rapidly from one perch to the next. If they see a human, they chirr. They seldom cross open areas, but I have seen them cross an open stream (Rio Agua Salud) 10 m across; these birds moved up to 3–6 m above the ground and flutter-glided across like chachalacas (*Ortalis* spp.). I have seen Ocellateds follow ants out of the forest into grass and brush at the edge of a back yard (Cerro Campana), but I have never seen them enter the laboratory clearing on Barro Colorado.

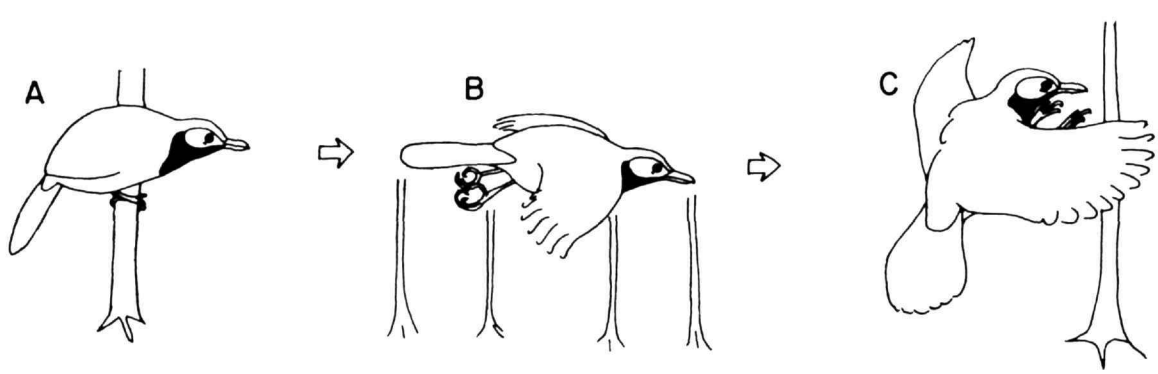

FIGURE 3.—Ocellated Antbird traveling: A, the bird points and lowers the front of the body; B, an occasional brief glide interrupts the flight; C, the bird alights with feet high, wings and tail spread.

Ocellateds do not join the wandering mixed flocks of antwrens (Johnson, 1954; Willis, 1972a) but sometimes accompany or are followed by ant-following birds, especially Bicolored Antbirds. On days when a colony of ants is not swarming one often sees groups of Bicolored and Ocellated Antbirds wandering low through the undergrowth, as a front or in leapfrog fashion. At times other ant-following birds, such as Barred and Plain-brown Woodcreepers *(Dendrocolaptes certhia, Dendrocincla fuliginosa)* and Gray-headed Tanagers *(Eucometis penicillata),* wander at 5–10 m above the two antbirds. Infrequently Spotted Antbirds join the motley traveling group. At times an Ocellated Antbird goes to or follows a Spotted Antbird, which is another species that commonly follows ants. Once a single song from a Spotted Antbird was enough to bring in an Ocellated.

To find a new bivouac of the "nomadic" colony of army ants in the early morning, Ocellated and other antbirds commonly search along the path of the raid of the previous day; sometimes they miss the new bivouac. Then they wander widely, join any bird that sings, and look around it. A female and her young female got so used to me at a colony that one morning they veered off to me (Figure 2F) and thus missed the ant bivouac they soon would have hit. Ocellated Antbirds wander along the ant trails and toward songs of other Ocellateds if the ants "fold" their swarm late in the day. Playing tape-recorded songs of Bicolored Antbirds near such folded swarms brought Ocellateds in on five occasions; playing Ocellated songs quickly brings in Ocellateds.

Johnson (1954:47) theorized that chirrs of Ocellated and other antbirds attract other birds to ants. Since chirring is normally only a response to the observer or ground predators, it is rare for undisturbed antbirds to chirr. I observed Ocellateds arriving at swarms on several occasions, and few chirred more than a few times at me before starting to forage silently. More often, the arriving bird was silent or faint-sang. Chirring does not seem to be used as an attractant or clue, although it could accidentally be a clue.

Ocellated Antbirds that cannot find an active nomadic raid of the army ant *Eciton burchelli* sometimes visit the tree where a statary colony they previously followed is hiding. They circle the base of the tree and follow any line of ants to the distant swarm. Once the above-mentioned female and her young female encountered a line of ants; the adult turned correctly toward the ant swarm (which, as any ant-follower should know, is in the direction from which the ants carry food!), but the young bird turned toward the ant bivouac.

If there is no line of ants or swarm, Ocellateds sometimes wander about or wait in cover nearby, preening and faint-singing, for up to several hours at a time. At other times they move off and check another statary colony. They sometimes move from one colony of ants to another during the course of a day or move back and forth between colonies every day or two, even colonies a kilometer apart. Probably each bird knows of the general whereabouts of a few other colonies even when it is primarily following only one nomadic colony.

Foraging

When waiting for food over army ants (Figures 2, 4), the Ocellated Antbird looks about with quick movements at its low perch, turning its head 30 or so degrees each time and occasionally cocking the head. Usually it is hunched with head retracted and tail down. If no prey appears, or if ants attack up its perch, the bird hops or flutters a short distance. Usually birds face the rear of the swarm of ants from just behind the foremost ants, and a bird that moves ahead to keep over the ants must turn around each time it stops to forage. Often, before moving, the bird faint-sings a few times.

Dominant or lone birds often move low, at normal foraging heights. A subordinate bird may move up to a meter or two off the ground to look around before traveling or dropping to a new site. Birds

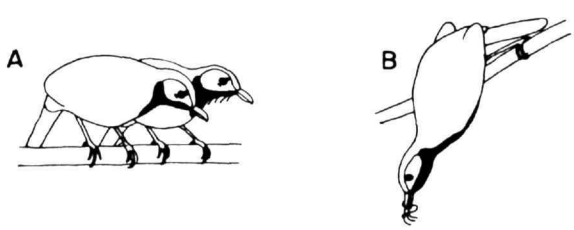

FIGURE 4.—Ocellated Antbirds foraging: A, mated pairs often forage together, though one bird or both often ruff the throat; B, a peck at the ground.

disturbed by a human or ground predator often move to 1–2 m up, too.

Since a swarm front of *Eciton burchelli* moves about 15 m per hour (Willis, 1967:6), the birds have to move occasionally to keep over the active part of the swarm. At times a bird moves laterally on the swarm front, right or left, to a more active part of the front. If the ants stop activity on this front the bird begins to faint-sing, wander, and check other small groups of ants. Finally it moves, faint-singing, back toward the ant bivouac or in the direction the ants are retreating. Often it finds the ants flowing to the attack on some other branch raid, but if the ants are just returning to the bivouac the bird wanders back and forth along the ant trail, around the raid and bivouac at the two ends of the ant trial, and then leaves faint-singing or loud-singing for another ant colony.

At times a foraging Ocellated clings so low over the ants that its tail or lower wing touches the leaf litter, but more often the bird is about 0.2–0.3 m above the advancing hordes (Table 2). Ocellateds sometimes stand on lianas or roots, but seldom stand long on the ground itself. Logs are seldom used, but a bird may hop under a log as the ants pass.

Ocellateds usually dart down to catch food just flushed by the ants, then bound back up to a perch so fast that the army ants have little chance to counterattack (Table 3). The bird about to chase prey holds the head up alertly, then lowers it and points the bill rapidly as if at an erratically moving prey, and leaps. The tail goes up briefly as a brake as the bird hits the ground and often is spread as the bird grabs the prey and returns to the perch. A brief jerk of the tail follows a successful swallow, and the bird turns to look for more prey. Over 75 percent of such sallies to the ground are within 0.5 m of the perch, less than 1 percent over 2 m (Table 4); distances are almost exactly like those for Bicolored Antbirds (Willis, 1967:30).

Sometimes an Ocellated, tail up, hops, bounds, and spins nimbly among the ants if prey escapes the first peck in a sally to the ground. The longer hops are twice the length of the body. Ocellateds are not really terrestrial and do not walk on the ground the way Black-faced Antthrushes do; but Ocellateds hop on the ground more readily than do Bicolored Antbirds. Ones that are hopping keep the tail somewhat raised; standing birds have tails down (Figures 2, 4).

TABLE 4.—*Heights of attempts at prey for Ocellated Antbirds* (Barro Colorado Island, over swarms of army ants; records within parentheses=5 October 1961 to 2 September 1970; records outside=5 October 1960 to 4 October 1961)

Height in meters	*Numbers of records*	*Percent*
0.1	3645 (1583)	97.84 (98.2)
0.2	18 (5)	0.48
0.3	15 (3)	0.40
0.4	6 (3)	0.16
0.5	8 (2)	0.21
0.6	3 (1)	0.08
0.7	2 (8)	0.05
0.8	5 (2)	0.13
0.9	5 (0)	0.13
1.0	1 (0)	0.03
2	10 (4)	0.27
3	6 (1)	0.16
4	2 (0)	0.05
Total	3726 (1612)	

At times an Ocellated tosses dead leaves by swiping at them with the bill or pecking them and tossing them. Occasionally the bird stamps the feet as it twists about, shoving leaves out of the way with its body. Less often, the antbird sallies clumsily and flutteringly to snap prey out of the air or off above the ground. Prey on or above the ground is likely to be pecked off (Figure 4B) after the bird hops to a nearby stable perch. Occasionally an Ocellated flies to vegetation 3 or 4 m up, cranes the head at moving prey, and gets it or not before returning near the ground. Once a female peered up with one eye and then the other, hopped upward, and suddenly did a sally to the ground and got a grasshopper that had dropped past her from 2 m up. In wetter forests than on Barro Colorado Island, such as at El Tigre (Colombia) and the Rio Medio (Panama Canal Zone), dense vegetation grows up the trunks of trees and is sometimes used by Ocellated Antbirds; I have seen them wander briefly up to 8 m above the ground in epiphytes and vines on slanting tree trunks. Most prey, however, comes from the ground (Table 5).

Once a young female Ocellated, resting, stole booty from an army ant. Thievery is more common in subordinate antbirds, especially Bicolored Antbirds (Willis, 1967:30).

TABLE 5.—*Distances of sallying to the ground for Ocellated Antbirds* (foraging over swarms of army ants, Barro Colorado Island, 4 October 1960 to 2 September 1970)

Distance	*No. of records*	*Percent*
0.1	184	16.9
0.2	235	21.6
0.3	158	14.5
0.4	120	11.0
0.5	122	11.2
0.6	52	4.8
0.7	29	2.7
0.8	61	5.6
0.9	8	0.7
1.0	25	2.3
2	85	7.8
3	4	0.4
4	3	0.3
5	1	0.1
6	1	0.1
Total	1088	100.0

The stereotypy of foraging is not matched by sterotypy of prey (Table 6). Prey from scorpions and spiders to roaches and katydids are snapped up eagerly. Millipedes and sowbugs, however, are common in the leaf litter, but are not taken often. Caterpillars and other items that seldom occur in the leaf litter are also rare in Ocellated diets. The commonest items were orthopterans (sensu lato) and spiders. Only large items could be identified in the field; many beetles probably are among the unidentified small insects.

Birds foraging away from competitors and uninterruptedly at good sites over the ants darted for food at intervals of 3 to 258 seconds (average = 38.5; median = 24). This is about the same rate as in Spotted and Bicolored Antbirds foraging uninterruptedly.

Prey is mostly the length of the exposed bill ("1 B" or exposed bill length = 18.2 mm) or less; but some larger items are taken, much as in Bicolored Antbirds. Tiny items are swallowed so rapidly that they can seldom be identified. Prey items over 10 mm in length sometimes require chewing, shaking, and gulping. The bird often holds its bill up and chews such an item conspicuously. Large items may be dissected, much as in Bicolored Antbirds (Willis, 1967:31); the prey is carried away from ants, each leg is shaken until the body falls

TABLE 6.—*Food items taken by Ocellated Antbirds* (see explanation in Table 4)

Kind of prey	*Length in mm*												
	?	*0–5*	*10*	*15*	*20*	*25*	*30*	*35*	*40*	*45*	*50*	*55*	*Total*
sowbugs	9												9
scorpion	1					2	1	1	2		2	(1)	9 (1)
whip scorpion	(1)				1						(1)		1 (2)
spider	10 (18)		7	9 (4)	40 (18)	6 (6)	5 (2)				(1)		77 (49)
millipede	1												1
centipede	1				(2)					1	1	(1)	3 (3)
stick insect											1		1
roach	4 (4)	1	3	14 (10)	33 (10)	3 (1)	5 (1)		2			2	67 (26)
cricket	(1)			1	7 (11)	2 (6)	(2)			(1)			10 (21)
grasshopper	4		3	8	29 (4)	4 (2)	5			(1)			53 (7)
katydid					1	(2)			3				4 (2)
caterpillar							1		1				2
ants	(4)		(1)		(1)								(6)
hymenopteran	1		1										2
lizard					(1)				2			1	3 (1)
insect	14	1	1	1					1				18
arthropod	2				1 (1)								3 (1)
leaf	2												
?	5 (6)	89 (6)	76 (12)	23 (5)	41 (26)	(2)	4 (2)		1 (1)	2			241 (60)
Total	52 (34)	91 (6)	91 (13)	56 (19)	153 (74)	17 (19)	21 (7)	1	12 (1)	3 (2)	4 (2)	3 (2)	504 (179)

off, then the head and thorax are chewed off, and the abdomen is eaten last. The dissecting bird holds its head low and hunches the body (Figure 2H). It jerks its tail up briefly now and then. The legs are splayed, the rear toes pointing inward (reverse pigeon-toed).

After dissecting prey or chewing juicy prey, Ocellated Antbirds often wipe the bill repeatedly in the usual fashion, base to tip on alternate sides with quick strokes. At times a foraging bird gapes repeatedly and regurgitates a few exoskeletons of prey, but a slight raising of the tail to drop white excreta is much more common.

Ocellated Antbirds sometimes drink water from the "drip-tips" of leaves but seldom drink at other times. Their prey are so juicy that they probably need little free water.

During medium or heavy rains Ocellateds faint-sing or loud-sing and move to cover. Light rains, which do not interfere with ant foraging much, do not stop Ocellated foraging either.

Foraging Competition and Grunting

Ocellated Antbirds dominate most other ant-following birds and as a result occupy the central and best foraging zones over antswarms. Smaller birds and some larger ones are "supplanted" (driven from their perches) with loud snapping of the bill and a whirr of wings on an arrowlike attack. As a consequence, many competitors move away as soon as the antbird approaches ("displacings"). Some must watch until the antbird leaves, then move in and forage where it was ("returns"). Supplantings, displacings, and returns are listed in Table 7.

Bicolored Antbirds, abundant competitors over the ants, draw most of the attacks of Ocellated Antbirds. Even pointing the bill at a Bicolor and jerking the tail a few times will sometimes send Bicolors away. The Bicolors persistently infiltrate the ranks of Ocellated Antbirds, even though the latter grunt and try to keep the central and best zone free of these competitors, thus relegating them to the outer

Table 7.—*Antagonistic foraging interactions of Ocellated Antbirds* (5 October 1960 to 21 January 1971, Barro Colorado Island, birds foraging over swarms of army ants)

Species A	*Antagonistic interactions (losses/wins by species A to Ocellated Antbirds)*			
	supplantings	*displacings*	*returns*	*fighting*
Intraspecific				
Ocellated Antbird	1033	459	11	9
Interspecific				
Bicolored Antbird	2360/3	465	35	–
Gray-headed Tanager	186/1	49/1	8	–
Plain-brown Woodcreeper	76	40	10	–
Spotted Antbird	64	65	4	–
Buff-throated Woodcreeper	11/3	5	–	–
Slaty Antshrike	5/3	–	–	–
Swainson's Thrush	7	5	–	–
Chestnut-backed Antbird	7	–	–	–
Wood Thrush	3	–	–	–
White-whiskered Puffbird	1/1	–	–	–
Kentucky Warbler	1	2	–	–
Canada Warbler	1	–	–	–
Thrush species	1	–	–	–
Anolis frenatus (lizard)	1	–	–	–
Gray-cheeked Thrush	–	1	–	–
Broad-billed Motmot	/2	–	–	–
Black-striped Woodcreeper	/3	–	–	–
Rufous Motmot	/6	/3	–	–
Squirrel Cuckoo	/8	/17	2	–
Barred Woodcreeper	/13	/5	–	–

concentric "zone" around the ants. When a subordinate Ocellated Antbird is getting little food, it usually heads for the nearest Bicolored Antbird and supplants it, especially if the Bicolor tries for food one or two times. Probably this is an efficient technique, for the Bicolor is likely to be in the best place that is not occupied by dominant Ocellateds. Twice a very subordinate female Ocellated, badgered by other Ocellateds, was supplanted from behind by a Bicolor; and once a very irate Bicolor chasing other Bicolors managed to supplant an Ocellated. This Bicolor tried again, but the Ocellated just ignored his lunge the second time. Bicolors are much smaller than Ocellated Antbirds (30–36 v. 45–55 g) but differ less in bill length (culmen of 113 east-Panamanian Bicolors, $\bar{x} =$ 20.8 mm; culmen of 71 Panamanian Ocellateds, $\bar{x} = 24.1$ mm). Thus, Bicolors probably take many arthropods that are of interest to Ocellateds.

Gray-headed Tanagers and Plain-brown Woodcreepers persistently move down to the ants but are chased up by the grunting or attacks of Ocellated Antbirds (Willis, 1966, comments on the woodcreepers). An Ocellated pounced on and pecked one young Tanager that foraged low; it then foraged high. Once an Ocellated beat a Tanager to prey because the Tanager started from 4 m up, the Ocellated from 0.3 m up. Spotted Antbirds evade the Ocellated Antbirds in many ways—by going high or peripherally, behind bushes, etc.; they seldom are attacked because they wander in the concentric zone outside the Bicolor zone rather than in the zone next to Ocellated Antbirds (Willis, 1972a). Many other species are attacked if they come near the Ocellateds, but most species do not come close.

In dense cover there is less fighting and less grunting at competitors. Perhaps there are more prey in such situations, but the main reason more birds can be peacefully accommodated is that they can stay somewhat out of sight of each other.

Repeated grunting keeps many possible competitors away from Ocellateds. An Ocellated starts or speeds up its grunting as a small competitor appears or approaches, or even if a distant small bird catches an insect. When the small bird moves off or behind cover, the grunting stops as if switched off. Once the rapid grunts at a Bicolored Antbird became a rattling *cha-a-a-i-in-in-imp-imp-imp* series, rather like chittering or growling. The Ocellated may grunt even if preening, but it is usually foraging busily when it grunts.

Grunting is never given at larger birds, even nearby Barred Woodcreepers or White-whiskered Puffbirds (*Malacoptila panamensis*). (Once an Ocellated spread its throat feathers and extended its head toward a Puffbird, which ignored it.) Even grunting at other Ocellateds is very rare; I recorded only two cases in which dominant males grunted at subordinate females, and one case in which a female grunted at her grown son as he wandered past. Other sounds, noted under "agonistic behavior," are used when Ocellateds forage together and no small species are present. However, I specifically recorded grunting at approaching Bicolored Antbirds on Barro Colorado Island 381 times, at Spotted Antbirds 44, at Gray-headed Tanagers 22, at Plain-brown Woodcreepers 20, at Chestnut-backed Antbirds (*Myrmeciza exsul*) 7, Slaty Antshrikes (*Thamnophilus punctatus*) 3, Buff-throated Woodcreeper 1, and Golden-collared Manakin (*Manacus vitellinus*) 1. I noted grunting at combinations of small competitors and in situations where other Ocellateds were present with small competitors on many other occasions. I recorded grunting at Bicolors also at the Madden Forest Reserve, Limbo Hunt Camp, Rio Agua Salud, Rio Medio, Cerro Campana, and El Tigre, and at Spotteds at the Limbo Hunt Camp.

Grunting even displaces scolding chirrs at the observer at times; an Ocellated disturbed by me and seeing a Bicolored Antbird move in over the ants often stopped mobbing and started frantic foraging and grunting, by a kind of "social facilitation"; however, I once noted that grunts stopped as a snake (*Pseustes poecilonota*, a nest robber) glided past and resumed after it was gone.

A few species dominate Ocellated Antbirds. A pair of Slaty Antshrikes supplanted an Ocellated Antbird three times near their young, and Buff-throated Woodcreepers sometimes harass the slower-flying antbird, but usually the antbird dominates these two species. An aggressive Black-striped Woodcreeper (*Xiphorhynchus lachrymosus*) chased three Ocellateds one day, but these woodcreepers usually forage high above ants. When motmots fly down to capture prey, they scare out Ocellateds; the Rufous Motmot (*Baryphthengus ruficapillus*) sometimes hogs a horizontal perch low over the cen-

ter of a swarm for several minutes, but gives the ants up to the circling antbirds when the ants move away from the horizontal perch. Ocellateds sometimes have their crests raised when working near motmots. Squirrel Cuckoos (*Piaya cayana*) are more agile than motmots and can flutter down and scare out antbirds in chases for prey or just take a perch from them. Cuckoos are like motmots, however, in preferring horizontal perches, which seldom are available near the ground.

The only effective competitor of Ocellated Antbirds on Barro Colorado was the Barred Woodcreeper. This large woodcreeper usually ignores the antbirds, which circle it rather boldly. They tend to avoid the open places and large trunks it favors, so there is little overlap; however, it supplants them vigorously at times.

Presumably the big ant-following Rufous-vented Ground Cuckoo (*Neomorphus geoffroyi*), once present on Barro Colorado Island, dominates Ocellated Antbirds. Black-crowned Antpittas (*Pittasoma michleri*) and Rufous-crowned Antpittas (*Pittasoma rufopileatum*) do so, the former at the Limbo Hunt Club (Panama) and the latter at El Tigre (Colombia). Black-chested Jays (*Cyanocorax affinis*) scared one Ocellated down from 8 m up at El Tigre.

Off Barro Colorado Island, I recorded Ocellated Antbirds supplanting Bare-crowned Antbirds (*Gymnocichla nudiceps*) at Tucurá and Caño Remolina in Colombia, Immaculate Antbirds (*Myrmeciza immaculata*) at El Tigre, Ruddy Woodcreepers (*Dendrocincla homochroa*) at Cerro Campana (Panama), and Red-throated Ant Tanagers (*Habia fuscicauda*) on the Bohio Peninsula (Panama). The general rule in all these supplantings, as on Barro Colorado, is that large birds supplant small ones.

Maintenance Behavior

As befits relatively dominant members of a community, Ocellated Antbirds spend their extra leisure time preening or resting in cover near but seldom over the ants. Females fed by their mates, and females low on the intraspecific peck order, often rest and preen for long periods. Preening perches are generally under clumps of the palm *Oenocarpus panamensis*, in dense treefalls or vine tangles, or in similarly safe places. The perches are usually horizontal (Table 8). Resting probably saves energy and reduces danger from predators; preening probably guards against small things that might harm a bird, such as cold and rain and parasites.

Preening, Stretching, Resting

Preening has not been analyzed in detail but is generally similar to that of Bicolored Antbirds (Willis, 1967:35–36). In two bouts of preening, about five minutes apart, a male Ocellated started with the upper and under surfaces of the wing, followed by the scapulars and around the wing base, then the upper breast, then the flanks and the edges of the abdominal apterium. Finally, he preened around the tail after scratching the head and preening the upper back. Feathers, particularly of the tail, are preened from base to tip. Ocellated Antbirds scratched over the wing (30 times), seldom under the wing (7 times).

After bouts of preening, or when a bird stops foraging and is about to move to cover for preening, common stretching motions are toe-standing, right and left stretches, and double-wing or "half" flexes.

The resting bird (Figure 5A) sits with head retracted, tail somewhat down, and body feathers fluffed. At times one extends its toes briefly or lets them dangle. Females being fed by their mates spend most of the day preening and resting, and

Table 8.—*Perches of preening and resting birds* (PB=preening birds; FR=females resting, waiting for mates to feed them)

Height in meters			*Angles in degrees*			*Diameter in centimeters*		
height	*records*		*Angle*	*records*		*diameter*	*records*	
	PB	FR		PB	FR		PB	FR
0.1	3	4	20°	67	39	1	10	5
0.2	15	8	40°	40	12	2	58	26
0.3	24	8	60°	12	2	3	25	7
0.4	34	8	80°	3	1	4	9	3
0.5	25	8	100°	2	1	5	6	9
0.6	9	8				6	–	1
0.7	14	3				7	–	2
0.8	7	7				15	1	–
0.9	6	2						
1.0	5	4						
2	20	5						
Total	162	65		124	55		109	53

at such times use horizontal perches about 2 cm in diameter and 0.4 m up, just as do preening birds (Table 8).

Mutual grooming has not been observed, except perhaps for one young female that seemed to pick spider webs off her mother's head. Since young often nibble or gape at parents, this perhaps was not actual grooming.

Bathing

Ocellated Antbirds occasionally bathe in small creeks, once in a pool of water atop a shelf fungus. Baths may be at any hour of the day, for I have recorded them from 7:55 A.M. to 6:15 P.M. At times several Ocellateds bathe, sometimes with Bicolored Antbirds. The Ocellated hops down toward the water, looks at it and around, stands in the water, quickly dips the breast, and throws water over the neck and head by fluttering the wings in a spray of water. Except for these brief fluttering dips, the head remains up and the bird keeps a wary lookout. The tail may be partly spread and rest on or in the water. The back is sometimes fluffed to show the grayish bases of the interscapular feathers. Then the bird hops or flies to nearby perches, shakes the rear end vigorously, and preens the tail and other feathers from base to tip. At times the bird hops in and out of the water, alternating bouts of bathing with brief alert periods or sessions of preening. Then it retires to cover to preen energetically.

Anting

Occasionally Ocellated Antbirds capture a small prey, hold it in the tip of the bill, chew it (Figure 5B), and brush it through the primaries or undertail coverts in typical "anting" (Whitaker, 1957). In 24 instances of anting, 10 items were finally eaten and 2 thrown away. In the other 12 cases, I did not see what happened to the prey. Possibly anting is a foraging behavior, brushing off distasteful secretions of prey on wings and under the tail, as I have suggested for other ant-following species (Willis, 1967:32–33). At times Bicolored and Ocellated Antbirds anted actively near each other with similar items, apparently ants or other social insects flushed by the army ants. In Bicolored Antbirds, most anting is by subordinate and presumably hungry birds; but in Ocellated Antbirds 8 cases of anting were by subordinates, 1 by a dominant bird, and 13 by birds that were not competing with other Ocellated Antbirds (most were competing with Bicolored Antbirds).

Anting may also soothe skin irritated by molt, as Potter (1970) suggests, for in 1961 all my records were from July to November, the main months of molting in this species. In later years I have had several records for May and June, months in which molting is uncommon; but I have no records for a few visits in January and February, months in which there is little molt.

Male Ocellated Antbirds anted on 18 occasions, females on 6. Probably the tendency of females to rest while males feed them leads to this disparity of observed numbers.

Reactions to Army Ants and Other Insects

Ocellated Antbirds are dominant to most other birds and thus can usurp the perches low over army ants. As a result, they are exposed to the attacks of army ants more often than are other species that follow ants. Ants often turn back on

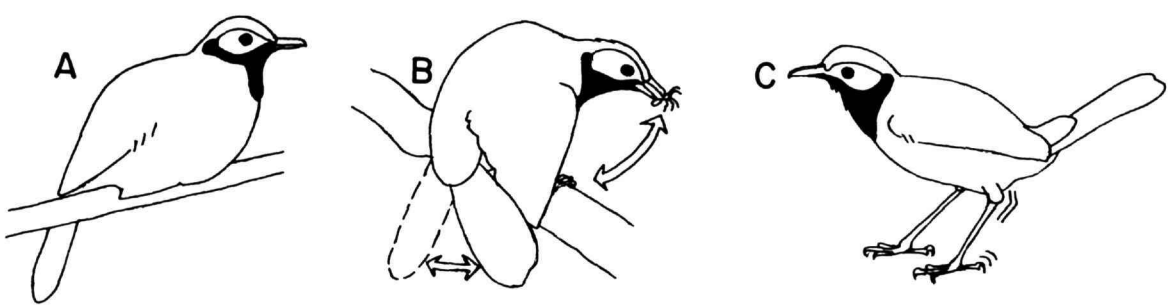

FIGURE 5.—Maintenance behavior: A, resting; B, anting; C, bird on the ground jiggles the leg at attacking army ants.

encountering the foot of a bird, unless ants in the main body of the swarm push them up. Occasionally, however, ants bite or sting the antbird. Typical reactions of Ocellated Antbirds to attacking ants include stamping or quivering (Figure 5c) the foot that ants are attacking, pecking at the offending ants and tossing them into the air, jiggling or jittering back and forth from one foot to the other, dancing about as if on hot coals (mostly when getting prey on the ground), and finally fleeing to a new perch if the ants persist. The body is usually high on the legs, which are extended. The tail sometimes jerks or flicks upward a few times as ants attack. At times the Ocellated champs the bill (mandibulates) before hopping off. At one ant bite, a bird jumped 0.3 m in the air like a Blue-black Grassquit (*Volatinia jacarina*). Ant attacks probably discourage use of the ground and other broad perches, such as logs and fallen limbs.

At times an Ocellated Antbird loses all or part of its prey to the ants. One female Ocellated watched the ants pour over a dropped leg of a grasshopper and champed a few times. Others chirred faintly on similar occasions.

Mosquitoes flying by occasionally elicit a peck.

Antipredator Behavior

Ocellated Antbirds are probably prey as well as predators, for there was a rather high disappearance rate on Barro Colorado Island in 1960–1970 (Willis, MS). I never saw any hawks or other predators attack Ocellateds, but they become alarmed very easily. As in Bicolored Antbirds, the three major kinds of alarm displays other than reactions to insects are freezing with keening, panicking with chipping, and mobbing with chirring. Screaming (as in the hand), flight to cover, and tameness and investigating are less common reactions to predators.

FREEZING

At distant danger, such as a large bird flying past or a bird giving an alarm call, Ocellated Antbirds often freeze (Figure 6A, E) and keen briefly. The head extends (as in Willis, 1967:17, "extending" means opening the angle between the part cited and the main part of the body, and "flexing" means closing the angle between the part cited and the main part of the body) as the bird ducks or

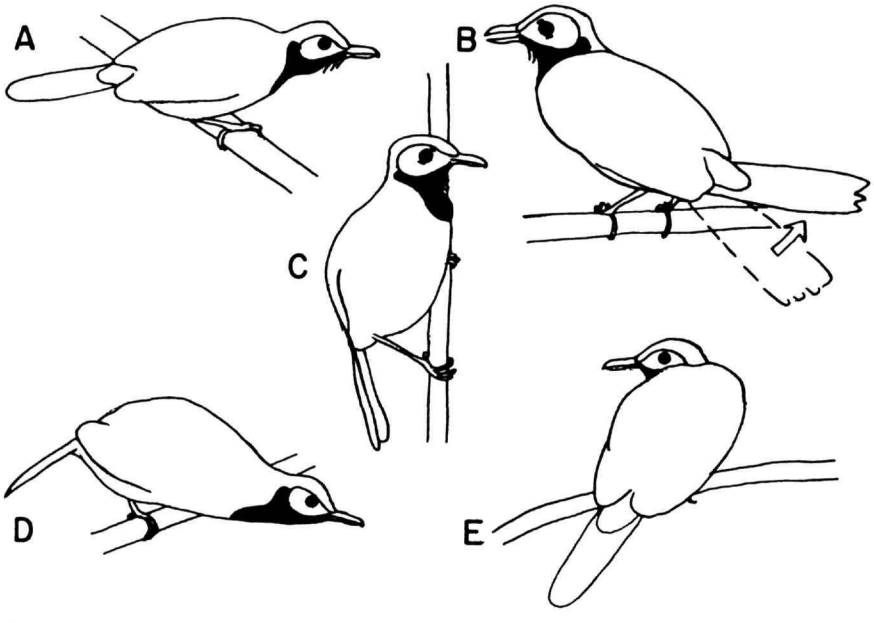

FIGURE 6.—Antipredator behavior: A, freezing at keening from another bird; B, chirring and tail-jerking at distant thunder; C, alert watching; D, investigating me (at El Tigre); E, a freezing pose kept for 12 minutes.

inclines the front part of the body downward. Probably the femora are flexed to produce the lowering of the front of the body, for the bird often crouches. The tail remains closed and is not flicked. The body is sleeked. Birds may freeze, as at the stroke of a wand, then resume foraging as if suddenly released from a spell. Ongoing grunts at competitors also halt during the freezing and resume suddenly at its end.

Freezing, or keening and freezing, were 15 times reactions to alarm calls (Plain-brown Woodcreeper, 5; keening Bicolored Antbirds, 3; Barred Woodcreeper, 3; Collared Aracaris, *Pteroglossus torquatus,* 1; Black-striped Woodcreepers, 1; chipping Ocellated Antbirds, 1; Slate-colored Seedeater, *Sporophila schistacea,* 1) and 6 times reactions to large birds (Double-toothed Kite, *Harpagus bidentatus,* 2; Crested Owl, *Lophostrix cristata,* 1; Tiny Hawk, *Accipiter superciliosus,* 1 at Limbo Hunt Camp; Barred Forest-Falcon, *Micrastur ruficollis,* 1 at Boca del Rio Verde; *Ramphastos* toucans, 1). Keening by other Ocellateds also caused freezing. Once one froze as a helicopter passed over, and another ducked as a Squirrel Cuckoo flew over.

Panicking

At close danger, Ocellated Antbirds chip and flee for low tangles or other cover, where they flick their long tails actively and chip sharply. They crouch low on their legs. The display is often social, with several birds chipping and flicking in irregular alternation. At times there is a long period of hysteria, with paroxysms or outbursts of chipping and tail-jerking. If danger is not so pressing, the antbirds chip and flick irregularly during foraging. They move quickly, darting for prey as if being attacked, and turn the head sharply as they look about alertly. As the panic abates, the chipping becomes muffled "chut-ut" sounds and often grades into muffled chirring. The flicking continues and gradually dies out, with many short bouts later.

The flicking of the tail is somewhat different from that of Bicolored Antbirds, which flick the spread tail upward and then lower it gently for the next flick. Ocellated Antbirds spread the tail less often, and lower it quickly after each sudden upward jerk. Moreover, the tail often goes above the line of the body in its upward movement, rather than stopping at the line of the body as in Bicolored Antbirds. During active flicking, the Ocellated tail is in a downward or resting position between flicks, while the Bicolored tail is always moving and seldom is in the up (resting) position. The tail seems to serve as a signal of excitability or alarm in both species. Possibly the long tail of Ocellated Antbirds compensates somewhat in display conspicuousness for the fact that it does not spread widely. However, the long tail may be more necessary for balance in flight or for spreading in aggressive displays, as described below. It may also be needed as a brake for the large body in sallying to the ground, as described earlier.

The alarm calls of Plain-brown Woodcreepers and Spotted Antbirds often (5+ records each) cause chipping, panicking, flight, or intention movements of flight, such as reversing on the perch or jerking the tail, in Ocellated Antbirds. Alarm calls of several other birds sometimes cause panicking, such as Black-breasted Puffbirds, *Notharchus pectoralis,* 1; Buff-throated Woodcreeper, 1; Slaty Antshrike, 1; Black-throated Trogon, *Trogon rufus,* 1; and Bicolored Antbird, 1. Wings overhead, 2; and flying large birds often cause panic (Wood Owl, *Ciccaba virgata,* 1; Semiplumbeous Hawk, *Leucopternis semiplumbea,* 1; White Hawk, *Leucopternis albicollis,* 1; Double-toothed Kite, 1; Hook-billed Kite, *Chondrohierax uncinatus,* 1; toucan, 1; Collared Aracari, 1; Chuck-will's Widow, *Caprimulgus carolinensis,* 1; Rufous Motmot, 3; Barred Forest-Falcon, 1 at Boca del Rio Verde). An agouti (*Dasyprocta punctata*) dashing through a swarm caused panic once; but usually slow-moving agoutis are ignored or only force the bird to fly up to 1 or 2 m above the ground briefly. My waving a hat and (twice) standing near young birds caused panic in tame Ocellateds; and humans often cause muffled chipping.

Mobbing

The usual reaction to large ground animals, especially humans, is mobbing with chirring. Probably both activities normally disturb and drive away predatory mammals, which could not catch prey well if some small bird were giving the alarm and fluttering nearby. Chirring calls, as I have noted elsewhere (Willis, 1967), probably mimic the growls of carnivores and drive away nonpredatory but in-

terfering mammals. Chirring calls and muffled intermediates between chirring and chipping calls often alternate, for mobbing often grades into panicking or vice versa. If moderately tame birds are mixing panicking with mobbing, however, an observer can quickly turn their chipping and muffled chirring to pure chirring and mobbing by walking toward the birds a few steps. Birds usually chirr when they first see an observer, then gradually begin muffled noises. Finally they either warily return to foraging or start faint-songs, loud-sing, and leave the swarm.

In mobbing, the bird jerks the spread tail upward frequently (Figure 6B). At times each flick of the tail coincides with a chirr, the *cheee* part on the upstroke and the terminal *yuk* part on the downstroke. The bare and bright blue face is often turned toward the observer, but it is restricted in area by the fact that the crown feathers are slightly spread, thus covering the bare area almost down to the eye. The throat feathers are also ruffled but tend to spread down from the bare face and thus expose more of it below the eye. Often the mobbing bird swings around and around a vertical perch, seemingly showing off the blue face and dark eye as a possibly frightening "eyespot" design (Willis, 1969:378). By contrast to sleek-bodied freezing and panicking birds, mobbing birds are either inflated or fluffed out. Probably the ocellated pattern is displayed by this fluffing.

Mobbing is usually a social activity, necessarily so in many cases because these birds are so social. Once the chirrs of a bird in the net brought up two distant others to chirr at me. When local Ocellateds were tame and had stopped chirring at me, the persistent chirrs of a distrustful newcomer were often enough to start the tame birds chirring. It thus is often mobbing in the strict sense, that of mob attack.

Often a bird terminating mobbing, or a moderately tame one that is jerking the tail a little but is not excited enough to chirr, does "toe-looking" (Figure 7). The bill points down at the feet, and one face and then the other is turned to the observer as if the bird were a human bashfully looking at his feet but keeping an eye on another human at the same time. This may also display the "eyespot" design of the face, possibly in a somewhat threatening way. Once a female toe-looked as her

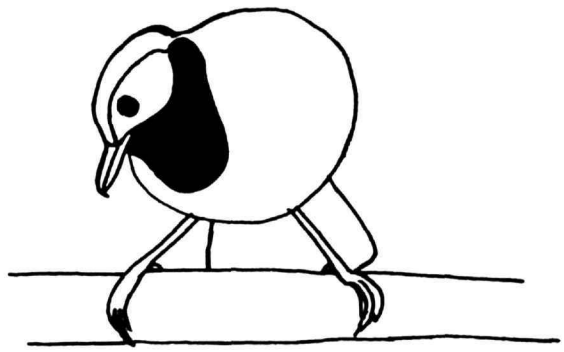

FIGURE 7.—Toe-looking.

mate chased an intruder, suggesting that toe-looking may be thwarted attack. Once a female chirred and toe-looked when her grown young female preened near me. At times a tame bird grunts at the approaching observer, as if he were a little antbird. Champing the bill, tail-flicking, and other displacement activities often accompany toe-looking or grunting. One tame female near me champed her beak as three people photographed noisily at some distance from us.

Many chirring reactions were to mammals: 7 times to passing humans, even when the birds were ignoring me; 7 to tayras (*Eira barbara*); 5 to coatimundis (*Nasua narica*), especially ones dashing through; 4 to white-faced monkeys (*Cebus capucinus*), especially ones on the ground or ones grunting at me; 2 to squirrels (*Sciurus granatensis*); 2 to collared peccaries (*Tayassu tajacu*); 1 to a squawking, running agouti; 1 to a passing four-eyed opossum (*Philander opossum*). As noted later, even tame antbirds chirred if I stood near their young or held them in the hand, and chirring was the normal reaction of antbirds to me unless they were tame. Snakes gliding by twice caused chirrs; once it was the nest-robbing snake *Pseustes poecilonota*. Sitting hawks also elicit chirrs, plus at times chipping: Ornate Hawk-Eagles, *Spizaetus ornatus*, 2; White Hawk, 1; Gray-headed Kite, *Leptodon cayanensis*, 1; Common Black Hawk, *Buteogallus anthracinus*, 1, in the Madden Forest Reserve. A Squirrel Cuckoo gliding in once caused chirrs; as noted earlier, this cuckoo often supplants and thus competes with Ocellated Antbirds. Alarm calls of other small birds, especially the buzzing ones of reactions to sitting predators, caused chirrs several times: chipping and chirring of Bicolored and

Spotted Antbirds, the chirrs of other Ocellated Antbirds, the *ah'rrrrrr* and *cah-cah* of Slaty Antshrikes, the stieking of Plain-brown Woodcreepers, 6, the *wh'kurr* of growling alarm of a Barred Woodcreeper, the *peer-peer-peer-peer!* alarm of a Buff-throated Woodcreeper.

Other uses of chirrs seemed to express mild alarm or irritation: at the start of thunder or rains (Figure 6B); when an insect that had run under leaves could not be found even by tossing the leaves; when a juicy part of an insect dropped into ants; before a clumsy sally up at an insect from an exposed perch 2 m above the ground; at the crash of a falling log. One female chirred when her mate supplanted their daughter.

Reactions When Captured

Ocellated Antbirds kick and chip when captured in mist nets. Often they chip or chirr when the first panicky attempts to escape fail. In the hand, tame birds are likely to give a few vehement chirrs. Naive birds, unaccustomed to humans, are more likely to squeal violently or to attempt a kick-fluttering escape now and then than to chirr and ruff their throats at one. Their faces become pallid rather than the bright blue of chirring birds. Many birds chirr or chip as they flee upon release. Often birds peck at one's finger, holding and twisting it in the hooked tip of the bill with painful effects.

Flight, Tameness, and Curiosity

Silent flight to cover or intention movements of flight, such as turning away from a passing big bird, are common. Usually panicking or freezing movements accompany the flight. The loud alarm calls of Plain-brown Woodcreepers and other birds sometimes provoke simple flight to cover. Simple flight often involves hiding behind tree trunks or low cover, out of the sight of the observer. Such birds become alarmed if they see the observer or his eye through a hole in the vegetation, but otherwise they can be watched through such holes.

Ocellated Antbirds on Barro Colorado Island are less tame to humans than are Bicolored Antbirds, and hence far less tame than Spotted Antbirds. The larger the bird in this series, the less tame it is initially. Ocellated Antbirds join in the general mobbing and chirring of all three species when one first approaches a swarm of ants. The Ocellated Antbirds commonly move up to 1 or 2 m above the ground, stare and toe-look at one, and finally flee for low cover with chipping notes. From cover, there is a pandemonium of muffled chirrs, chips, and faint-songs. One sees long black tails jerking vigorously in the dark cover. Then faint-songs begin, and finally loud-songs as the Ocellateds desert for another swarm of ants or hide for long periods in distant cover.

Over the course of a few hours, if birds stay near the ants and one is careful to stay well behind the ants, the Ocellated Antbirds gradually become less agitated. They sneak in to the ants whenever they can do so behind low cover. They flush with chirrs if one approaches, but then return if one retreats a little. Eventually they only faint-sing and move a little if one tries to see them in the low cover. Finally they stay, looking about warily and foraging cautiously (Figure 6C). Over the course of a few days, some birds habituate to one or become fairly tame. They never approach one's feet the way tame Bicolored Antbirds do, but they do forage and carry on their other activities fairly normally. They are especially likely to become bold if tame Bicolored and other antbirds lead the way. However, an Ocellated Antbird often avoids the end of a swarm near the observer even after one has known the bird for several years. Birds that one meets again after an absence of several months chirr, but soon become fairly tame. It takes persistent watching of individuals to get close enough for filming (3–5 m), however, and even in tame birds natural behavior patterns are fully expressed only when one is 10 m or more away.

Crippled birds are unusually wary and hide in cover or panic even when the observer is no stranger to them. One male with a broken wing chirred and hopped to 7 or 8 m up a liana as I passed.

In some areas, Ocellated Antbirds are tamer than the ones on Barro Colorado Island. On the Rio Agua Salud and Navy Pipeline Road, not far from Barro Colorado Island, they seem much tamer. Perhaps this is because hunting of mammals in these areas has removed most mammalian predators, so that the birds are less threatened by mammals than they are in a game reserve like Barro Colorado. Possibly the low palms and other undergrowth in less mature forests protect them better too. In one

forest with dense undergrowth, that of El Tigre in Colombia, Ocellateds did tail-flicking much less than they did on Barro Colorado.

In the mature forests on Barro Colorado, there are large areas of very open undergrowth in which Ocellated Antbirds are very shy, periodically jerking their tails and looking about alertly as they forage. Instead of mobbing, they usually flee one's approach. When tame birds work such open undergrowth, they are very quiet, alert, and quick to flee for cover. They get little prey in such areas, for they are too busy looking around rather than down at the ants. Most of their foraging comes in areas near or in cover. Large groups of birds are more active in foraging in open undergrowth, probably because an individual can afford to leave some of its alertness to the many other eyes of the group and concentrate more on foraging.

Common mammals, such as agoutis and peccaries, usually disturb Ocellateds very little. The birds fly up to 0.8 m or so above the ground and drop back down after the mammal passes.

In no locality are Ocellated Antbirds very curious. Even young birds seldom approach the observer to look him over the way young Bicolored Antbirds do. A few birds peer at one during breaks in chirring (Figure 6D), at least in places with plenty of cover. Perhaps the dominance of Ocellated Antbirds makes it possible for them to find food without investigating every nook and cranny, so that they are not investigative in general. Usually they do not have to forage near the observer, the way subordinate and young Bicolored Antbirds must do when Ocellated or dominant Bicolored Antbirds take the other areas of ant swarms.

Agonistic Behavior

Agonistic behavior, as in earlier papers (Willis, 1967, 1972a), will here be considered competitive reactions to animals of more or less the same size as the behaving animal. Those kinds of attack and escape that have to do with attacking prey or escaping from predators or parasites are discussed above. The agonistic behavior of Ocellated Antbirds includes submissive display, flight, aggressive displays, attack, and fighting. Interspecific agonistic behavior, mostly simple attack and fleeing, has been discussed under Foraging Competition.

Submissive Displays

Ocellated Antbirds, the dominant birds over swarms of ants, have more submissive displays and perform them far more often than they do aggressive ones. They have more submissive behavior than does the subdominant Bicolored Antbird (Willis, 1967:45–48) and far more than does the subordinate Spotted Antbird (Willis, 1972a). As is usually the case in antbirds, the submissive behavior is displayed mainly to dominant members of the species rather than to other species.

Although the Ocellated Antbird has many submissive displays, they intergrade and do not form distinctive clusters or what Morris (1957) has called displays of "typical intensity." For purposes of description, the spectrum of submissive displays may be divided into five groups: cringing, wing-waving, pleading, bunching, and nibbling.

Subordinate Ocellated Antbirds quickly take a humble pose when dominant ones come near. These birds always look somewhat humble, because of their habit of foraging with low tails and retracted heads, but the cringing subordinate lowers its head and tail still more. When the dominant bird alights above it, the cringing bird sometimes seems to drape itself like a wet rag (Figure 8D). The angle between head and neck is extended, keeping the head almost level even when it is lowered, nearly to the ground. At times the bird bobs the head, emphasizing the low pose. Usually the whole head seems sleeked and snakelike, but at times the throat feathers are ruffled. Throat spreading is often associated with bill wiping or with successful retreat from a dominant, suggesting that it may be aggressive behavior conflictingly present in the submissive display.

The bare blue face is pallid, and the area is restricted by crown and throat feathers, which close like an iris diaphragm around it. Plate XI in Meyer de Schauensee (1964) shows this effect. (The pallid face and closed facial area in this painting actually result from using specimens as models, but the pose illustrated is accidentally rather close to cringing.[1] The head faces ahead rather rigidly, but the eyes

[1] The bird pictured in Howell (1957) is naturally blue in the face but has an unusually closed facial area; perhaps the artist, Don Eckelberry, saw a mobbing or alarmed bird but used specimens for the final picture.

diverge and move actively, and the body moves from side to side so that the frozen head can still look about.

The body often seems fluffed, but a fleeing bird often sleeks. The bird seems to shrink in place, for it crouches or clings close to the perch; however, the toes are loose rather than clamped. The lowered tail seems to jiggle slightly at times; usually the cause is "chittering," a faint rattling sound that is used mainly during cringing. The bird seems to freeze or be inhibited about foraging; the dominant bird is likely to supplant it if it goes for prey. Often the chittering leads to chittering faint-songs as the subordinate bird bounds or flutters away from its opponent. Often the bird goes downward in moving away from the opponent, even to the extent of hopping away along the ground. If the dominant bird follows, the cringing bird slinks about with chitters and snakelike motions.

If the bird had been grunting at another species before cringing, it stops abruptly as it begins to cringe. Even a dominant Ocellated moving nearby may cause the subordinate to stop grunting. However, a cringing bird pressed but not attacked by another sometimes prolongs the grunting; the notes become long and scratchy "whines" mixed with chittering noises. Often the whining bird begins "wing-waving." The tips of the wings flick out more and more often, until the bird is fluttering spastically (Figure 8B). The wings are sometimes waved very widely, often in jerky alternation with disjointed upward flicks of the closed tail (Figure 8G). The head may be snaked forward and back and often is jerked back as the tail jerks up, so the bird seems spastic or compressed by the closing of an invisible box. The whining noises extend at times into squealing ones, mixed with chittering and with chittering faint-songs. Wing-waving and whining are typical displays when young birds or adult females are crowded by aggressively displaying other adults. The wing-waving bird may face toward or away from the dominant opponent, or even hop toward it with gaping (Figure 8B).

Often the wing-waving grades into or alternates with an even more assertive display, "pleading." The wing-waving or other bird hops up to the silent aggressor and, tongue up, gapes or even screams in its ear (Figure 8H). The gaping pleader holds the rear of the head low, for the head is hyperextended on the neck. It gapes almost as if to swallow the head of the aggressor, which may send it fluttering away with a swift peck or, nonplused by the vigor of the screaming and pleading, hop away for the moment. At times birds gape at each other in brief quarrels over a single food item. The pleading bird may continue to chitter, whine, squeal, wing-wave, and tail-jerk. The body is fluffed, the tail somewhat spread, but down (even on the ground). The bird may even push the dominant bird about bodily.

"Bunching" is a social kind of submissive behavior. The birds of a family crowd close together, the subordinate members of the group following like shadows and alighting within a few centimeters of the dominant male each time he alights (Figures 8E, F and 9). At other times the male goes to the female as the menacing other birds approach. I often felt afflicted by double, triple, or even quadruple vision, for the birds of each group sometimes alight in a row on a vertical or other perch and display at the opposing group like monkeys of the "see no evil, hear no evil, speak no evil" type. F. Gary Stiles and I have seen Groove-billed Anis (*Crotophaga sulcirostris*) in western Mexico give even more effective aggressive team displays, the shoulder-to-shoulder birds of two different groups rushing back and forth at each other on the ground like opposing teams in football; and DeVore and Hall (1965) report that male baboons (*Papio anubis*) group effectively to meet a dominance challenge; but the bunching of Ocellated Antbirds contrasts with these in being mostly restricted to subordinate pairs or families.

Occasionally a bunched pair or family does manage to supplant the dominant opponent; once I saw two birds of a family alight to either side of the opposing male and squeeze him out like a seed from a grape. Moreover, the upper or dominant bird of a team may be challenging weakly (Figure 8E), or all birds may do so. Usually the weakest members of a family crowd close to the dominant one of their family as if inciting him not to retreat from the dominant bird of the other family.

Often a pair or family crowds close together to forage during intervals in the dispute (Figure 9A). They may gape or nibble at each other, especially the female and young birds (Figure 9B). At times both opposing groups bunch at each other, for the female of a family is small and likely to be ousted

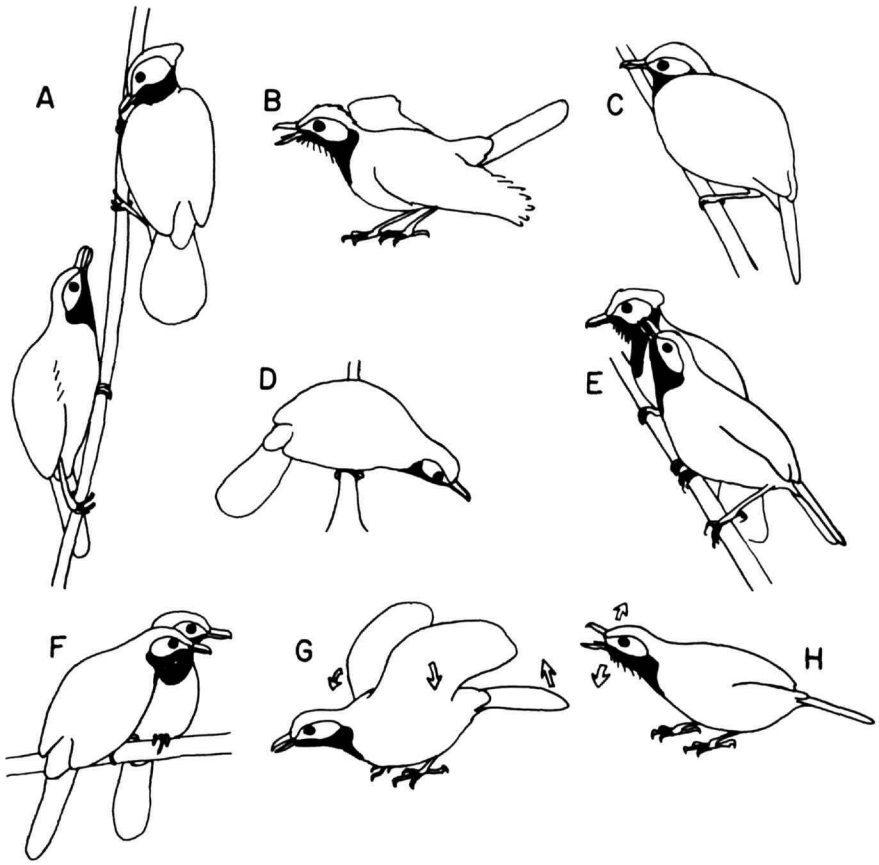

FIGURE 8.—Submissive behavior: A, subordinate bird, below, pleads with challenging dominant one, above; B, screaming and wing-waving bird pleads as it pesters a dominant bird; C, subordinate bird rests at the periphery of a swarm until dominant birds leave; D, cringing bird takes very low pose; E, female (in front) bunches with her weakly challenging mate (note ruffling of crown as a submissive movement) and nibbles at him; F, bunching pair watch dominant birds take over the ants; G, pleading and wing-waving by a female on the ground; H, pleading female yells in the ear of dominant bird.

even if her mate is dominant. The dominant male, however, more often challenges alone and his female follows him at a distance or forages; the subordinate pair or family bunches. The dominant male often ignores his mate, even when she bunches with him and "nibbles" up at him, while the subordinate male nibbles and/or pecks down at his mate.

During bunching, the female or young bird nibbles up now and then to the downward-pointed beak of the challenging male of the family. If the female or young is above him, he tosses his beak up at times to meet its downward nibbling, then returns to beak-down challenging. Often caroling accompanies the nibbling, and then both the visual and auditory parts of the display resemble courtship feeding. In some cases, the male did caroling and the female stopped her screaming and wing-waving; perhaps caroling tends to stop such displays. The female, however, is sometimes the bird that carols during nibbling. To some extent the mutual nibbling causes the male to go into a more upright and hence more challenging pose; its effect is to incite him to attack or face the other pair more strongly than before. The process reminds one of "inciting" in ducks.

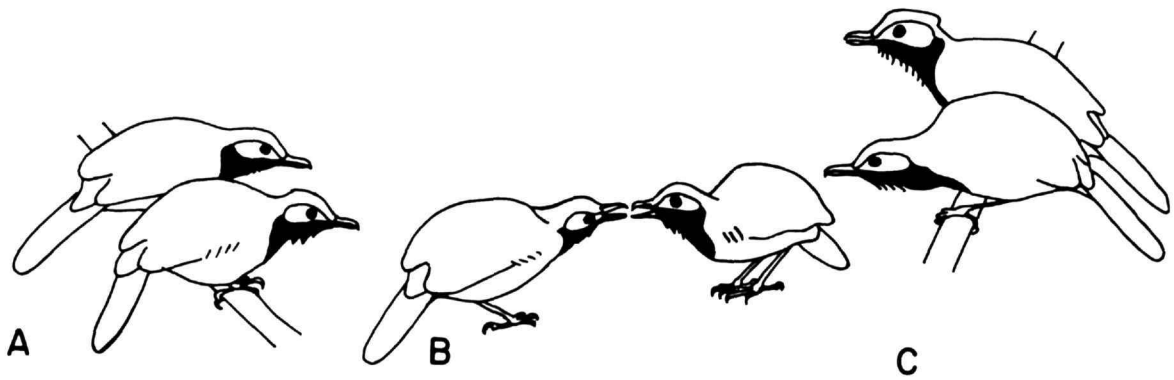

FIGURE 9.—Social submissive behavior: A, both of a pair cringe together; B, young female and mother nibble at each other when ousted by another pair; C, mother takes submissive pose near her slightly aggressive grown son.

If the subordinate bird is attacked despite its cringing, pleading, wing-waving, bunching, or nibbling, it usually gives a few screams or squawks and hops away with head low. At times a strained chirr emerges among the screams. Then it recovers and starts chirping to itself or grunting at Bicolored Antbirds or other competitors at some far corner of the ant swarm. At times it chirrs at the distant approach of the dominant competitor. Occasionally a subordinate male or family goes off with faint-songs, then loud-songs, and either finds another ant colony or returns to the same swarm later still evasively or cringingly subordinate.

AGGRESSIVE DISPLAYS

Ocellated Antbirds completely lack aggressive calls, except for an occasional chirr or chip, but have a distinct silent display. It may be called "challenging," although it is only moderately like that display in Bicolored Antbirds (Willis, 1967:49). The challenging Ocellated Antbird (Figure 10A)

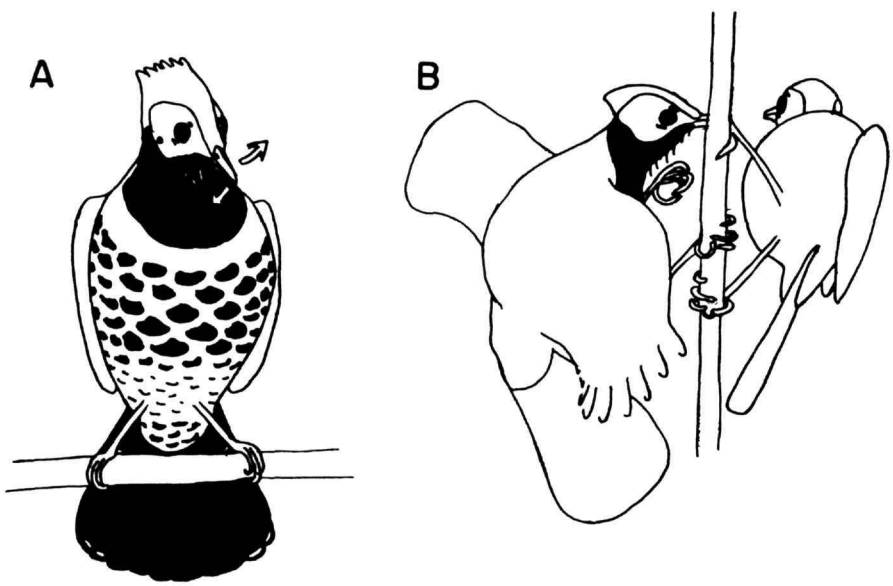

FIGURE 10.—Aggressive behavior: A, challenging; B, wings spread in pecking attack of bird that would not flee.

spreads the tail, stands high and upright with legs splayed, and periodically points the bill down at its chest (flexes the head toward the neck).

The toes are clamped on the perch; only insubordinate birds have the toes loose. The shoulders may come out slightly (Figure 11B). The body is spread, seemingly inflated rather than fluffed (Figure 11F). The throat feathers are ruffled, but this shows mainly at lower intensities when the bill is not strongly down. The face is bright blue, and its size is maximum because the feathers of the crown are sleeked back from it while the throat feathers are ruffled away from it.

When in this upright pose, the bird periodically lifts its bill to the horizontal with a jerky and ratchetlike motion, and lowers it again. It also turns its head from side to side. The whole display, especially these movements, probably shows the blue faces and dark eyes as giant "eye-spots" against the black bib. Meanwhile, the rusty nape feathers part from the feathers of the neck to give a hammerheaded appearance. The face and hammerhead are displayed when the bird turns its head from one side to the other, so that rusty, black, and blue parts of the head are conspicuously displayed in challenging. The gray crown does not seem to be used, except perhaps as a "facelike" gray field separating the blue "eyespot" facial areas. The black bib is outlined by rusty on the breast. Black ocellations spot the rusty belly below this (Figure 10A). The black tail is shiny and conspicuous and is another plumage character that is mainly displayed in challenging. The scaled pattern on the back, however, does not seem to be used in this or any other display and may be concealing coloration against the leaves of the forest floor.

The tips of the wings are sometimes spread a little (Figures 11A, B), but ordinarily the wings are not fully spread for challenging. Once, however,

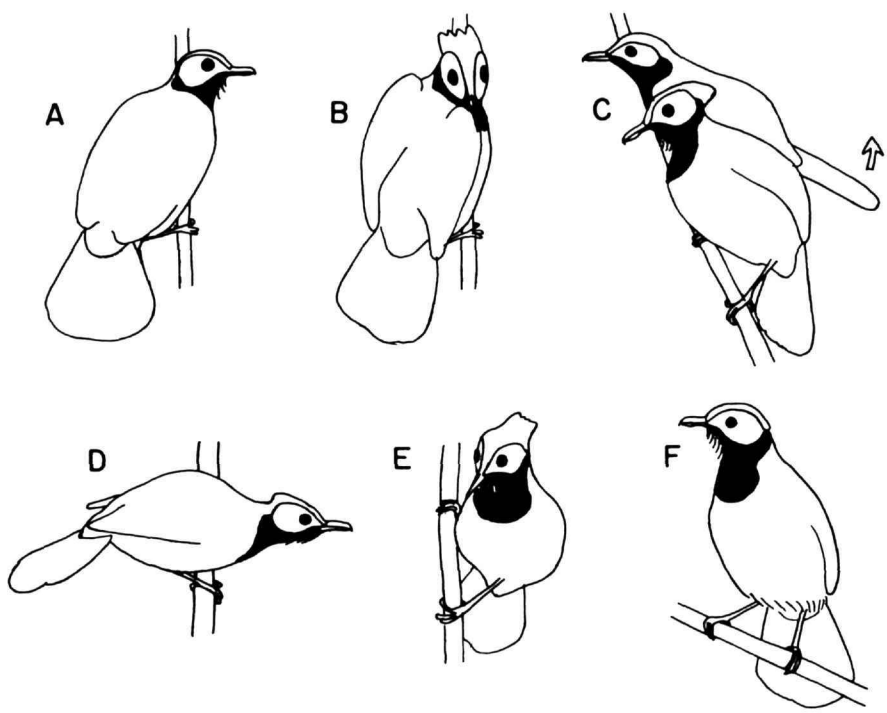

FIGURE 11.—Behavior of dominant birds: A, alert staring at an opponent (low intensity challenging; B, challenging over the shoulder at an opponent (note that the facial disks become giant eyespots); C, challenging at medium intensity, as female follows in bunching action; D, pointing at opponent of another or the same species before a supplanting attack; E, challenging from the front; F, low-intensity challenging (note expanded belly region).

two birds went for one prey and the two spread their wings up, gaped, and the larger bird grabbed the prey. Once, too, a dominant bird that failed to supplant another did a wing-spread (Figure 10B) as it then pecked the other off its perch.

Adult, settled males use challenging more often than do females or young males. Females and young males, when dominant, are more likely to ruff the throat, spread the tail, and supplant the opponent (Figure 11D). Challenging is best developed in confident, dominant birds; but the male of a bunched subordinate family may be recruited to challenge for a time by the nibbling and following of his mate or young (Figure 8E). Occasionally pairs challenge persistently and circle each other warily for several minutes.

After challenging and following a subordinate or insubordinate bird about for a few minutes, the silent dominant bird is likely to fly at or over it with an audible whirr of wings (normal flight is silent) and a ferocious series of bill-snapping, thus supplanting it. Usually the intruder squawks, whines, wing-waves, and flees; or it flees with loud-songs. If it does not flee, the dominant bird pecks at it from nearby and supplants it again. However, there were seldom the vigorous "gantlets" or series of supplantings seen among excited Bicolored Antbirds.

Occasionally, in 9 of 1500 encounters (Table 7), there was a brief screaming fight. This rate of fights is about 0.6 percent, or 2.4 times the rate for fights among Bicolored Antbirds (Willis, 1967:53). Ocellated Antbirds, however, have fewer intraspecific supplanting attempts than do Bicolored Antbirds; indeed, Table 6 shows that Ocellated Antbirds supplant or displace Bicolored Antbirds more often than Ocellated Antbirds supplant each other. Supplantings and fights are probably uncommon in Ocellated Antbirds because the well-developed system of submission usually keeps competitive situations from escalating into violence.

Fights are generally short but vicious, involving pecking and clawing but not much wing-beating. Perhaps the wings are too weak to be very useful. The defeated bird may scream loudly as it flees. One fight ended with the two females glaring at each other, heads sleeked but bodies and tails spread.

Dominant birds, at least well-fed ones, sometimes give in for a time to the wing-waving, pleading, and pecks of subordinate birds; this also reduces the incidence of fighting. The dominant bird gives a deep chirr and sputtering faint-songs as it is badgered by the frantic subordinate, then hops away. The next minute, however, it is likely to supplant the subordinate and take the position it vacated. It may also refuse to give in and may peck at the bird screaming in its ear, sending it hopping away. If the subordinate birds team up to oust a dominant one for a time, the dominant one may forage away from them for some hours; it is then difficult to say which bird is dominant. Later encounters tend to be more definite, however, in that one bird consistently challenges and chases the others about even when they bunch or plead.

Other Agonistic Behavior

Toe-looking (Figure 7) is often used by feuding Ocellated Antbirds; it is frequently associated with low-intensity challenging, and like challenging involves "arching" the head (flexing it toward the neck). Jerking the tail, bill-wiping, supplanting nearby Bicolored Antbirds instead of the opponent ("redirection activity"?) are often part of agonistic activity. A challenging bird loses its upright posture when it forages, but a cringing or wing-waving bird may flit the wings, flick the tail, bound about with head low, and chitter or whine even as it forages near the dominant bird. The subordinate may grunt at Bicolored Antbirds, but its grunts are very scratchy and quickly grade into whines if the dominant bird comes closer. Feuding Ocellated Antbirds sometimes chirr, chip, and sing during a series of chases or supplantings.

Many of these seem displacement activities, combinations of behavior patterns, or conflicting behavior patterns. Probably mixtures of any two patterns described in this report are possible, and in some other species such mixed patterns are important (Tinbergen, 1953). However, the mixed patterns of Ocellated Antbirds are variable and infrequent compared to the unmixed patterns.

Loud-singing (Figure 12A) is sometimes related to agonistic behavior. The dominant male at a swarm loud-sings more loudly than other males at the swarm when a distant bird loud-sings, and he may look that way (Figure 12B), or go off to meet the intruder. If I played recorded loud-songs, the

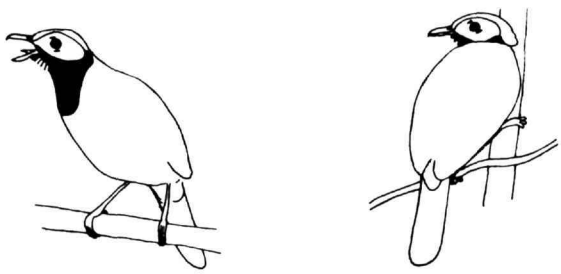

FIGURE 12.—Loud-singing male (left) gets a stare from a distant male (right) over the ants.

dominant male quickly came up loud-singing and circled me and the tape recorder. When two pairs are rather equally matched and a "bunching" battle with much challenging ends indecisively, one pair may leave with loud-songs and the other pair loud-sing back. The agonistic nature of loud-singing in these circumstances is somewhat uncertain, however, for birds frightened from a swarm of ants by the observer or departing it after the ants stop raiding often loud-sing, too. Possibly the dominant male may only be saying "come closer" when he loud-sings. Loud-singing seems primarily an attracting call in Ocellated Antbirds, as is described below. As Thielcke (1970:228) points out, only the reproductively stimulatory function of song has yet been proved; theories that songs ward off intruders need observational or experimental backing, although muted Red-winged Blackbirds have been shown to lose territories (Peek, 1971).

Reproductive Behavior

Ocellated Antbirds are monogamous and pair for life. I have no records of divorces among definitely mated birds, although a bird that loses its mate usually gets another one within a year or two. One young female did switch from one young male to another, but I was not sure if she had been with the first male long. Courtship involves three major activities: loud-singing, courtship feeding, and traveling with the mate.

LOUD-SINGING

A male that has lost his mate loud-sings (Figure 12A) repeatedly at the swarm of ants he is following or at a short distance from it. If the female answers, his songs become faint-songs or serpentine-songs; but if the female has disappeared he continues loud-singing for several minutes at a time. Such periods of loud-singing may occur at any time of day, but are more frequent in the early morning and late afternoon. Departure of a male from a swarm of ants to loud-sing persistently is almost a sure sign that the mate has disappeared; when she is merely off incubating he loud-sings only to answer distant loud-songs. The male loud-sings near presumed roosting areas, in the last light of evening, when he has lost his mate. Young males that have never had a mate do not perform such loud-singing, so far as I have been able to determine. Loud-singing brings in any other birds in the vicinity, and the male courts any female that appears.

COURTSHIP FEEDING AND COPULATION

As in many other antbirds, courtship feeding is the main courtship activity of Ocellated Antbirds. The male eats the legs off prey, chews the prey, looks about as if thinking, faint-sings or wanders with faint-songs (Figure 13B), and flies to the watching female. At times a lone male wanders with food, as if hoping a female will appear. The lone male may carol now and then as he carries food and end loud-songs with serpentine-songs.

From an initially rather upright and overbearing pose that may somewhat resemble challenging (the tail is spread, the legs splayed, the body upright and inflated, the stiff neck and throat ruffled, and the bill down), the male that finds a female carols and pokes the food down at her (Figure 14A). If she takes the food he loses the upright pose and becomes less puffed out, as was seen most clearly once when the two tugged back and forth at an insect for more than a second. She often crouches or is in a low pose (but her body and tail may be spread), her head low and extended on the neck so her bill points up.

If he holds back with the food, she carols a bit. Perhaps caroling overcomes agonistic tendencies. If he eats the food, she champs her beak, but usually he swipes it past her beak again. At times they seem to be fencing back and forth. She grabs the food and hops away quickly; he stands upright a moment, then champs or wipes his bill or not, and returns to foraging.

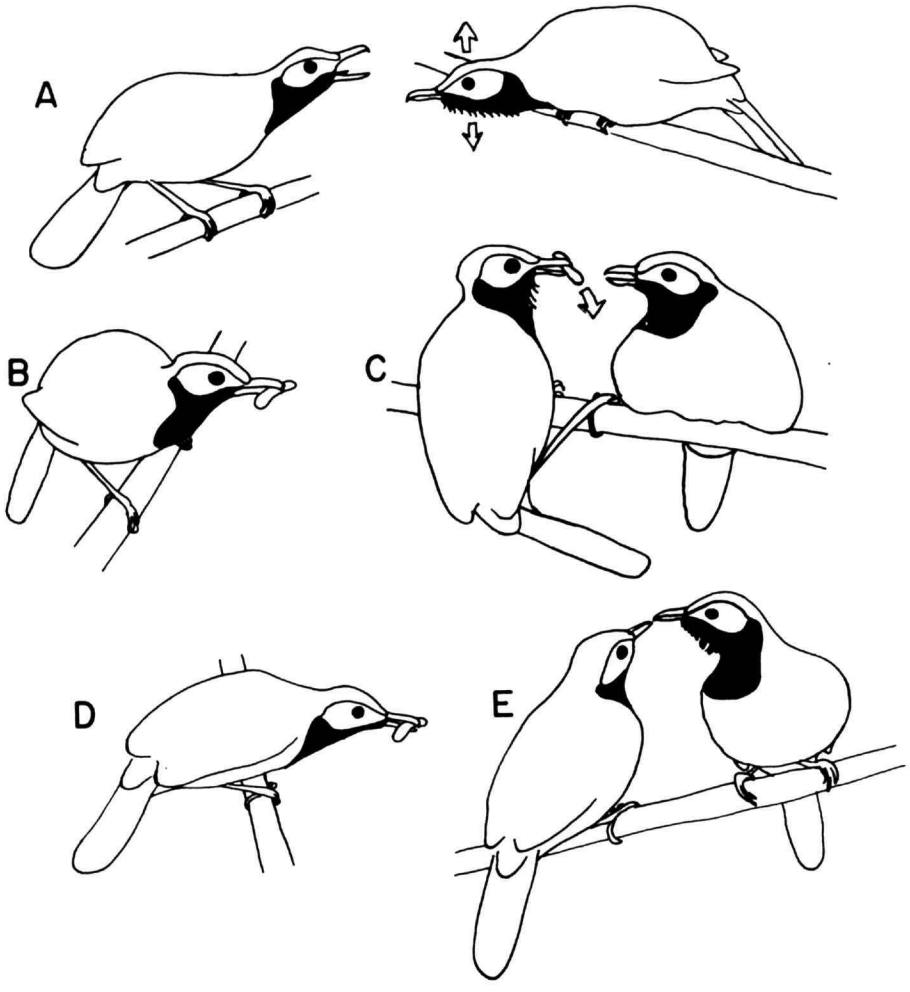

FIGURE 13.—Courtship feeding: A, female screams at mate (right), which bobs the head ritually; B, male faint-sings with food in bill; C, male feeds resting female; D, female takes low posture as she eats the food; E, female pecks at male bill when he stays and bobs the head after a courtship feeding.

After repeated feedings, the female stays on her perch, takes the food quickly (Figure 13C), and champs her beak as the male departs. At this time, there is little evidence of agonistic behavior and little caroling; the transfer of food is quick and simple. If the male stays near the female, she may give faint *chee* or *chee-chee* chirps and peck at him lightly (Figure 13E) as if still hungry; he usually returns to foraging as soon as she starts chirping. If he preens instead, she chirps now and then. At times a series of caroling and chirping notes follows a feeding as if the pair are talking to each other.

Rapid courtship feeding marks the early courtship process. One widower fed the mate of an incubating neighbor every minute or two with loud caroling and overbearing poses. The cringing female avoided the widower, however, except to grab his offerings of food. I have not directly observed the formation of a pair bond, except for a young female that met an eligible male a day at most before I found him feeding her busily (she had been at a distant ant colony until two days before). Probably the pair bond can be formed rapidly, for thereafter this young female stayed with that male.

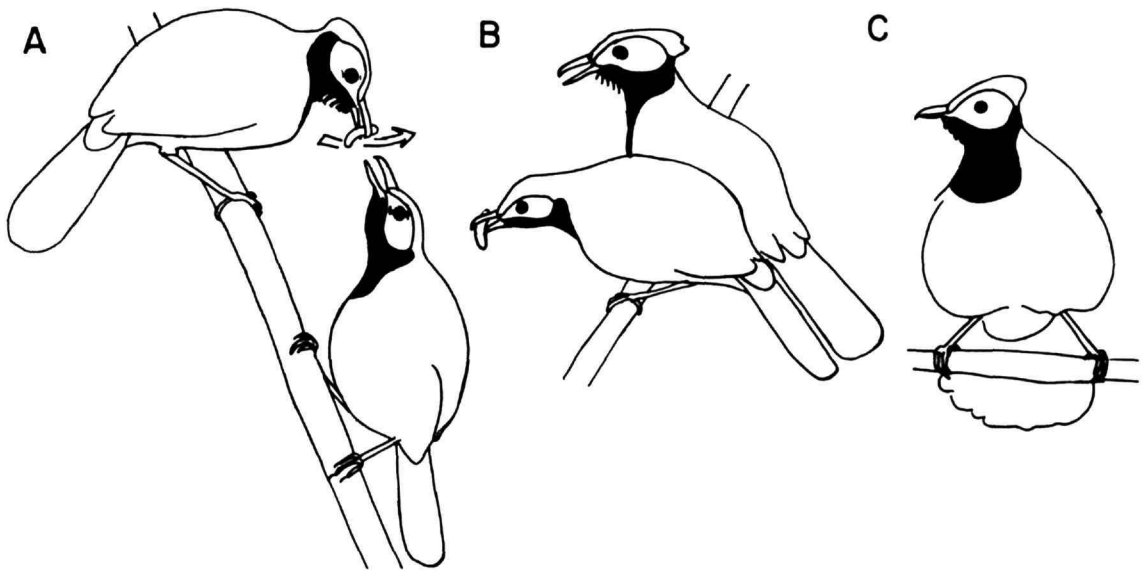

FIGURE 14.—Pre- and post-copulatory poses: A, courtship feeding with swiping the prey past the female bill; B, post-copulatory aggressive sidling to female; C, post-copulatory pose, rather like challenging.

During the subsequent months of the pair bond, courtship feeding is irregular, usually less frequent. Before each nesting, however, the male begins to feed the female regularly. She preens and rests in cover as much as 50 m behind the ants, and he ferries all her food. When the ants move too far ahead of her, he begins to serpentine-sing (Figure 15) as he returns to the ants after feeding her; often she moves with him to a new patch of cover closer to the ants.

After repeated feedings (Figure 14A) he tries to hop onto her back as soon as she lowers her head to eat the food. Usually she hops or flutters away,

FIGURE 15.—Male (left) serpentine-singing for female (right) to bring her to new resting site closer to ants.

tail-jerks, and chirps back at him. One male pecked at his mate when she did so, but fed her again after getting the food she dropped as a result. Another male toe-looked when his female hopped away. Finally, after many courtship feedings, the female stays for copulation.

In copulation, the male flutters the wings as he perches on the back of the female. His crown is sleeked, his throat ruffed, and he is somewhat puffed out as if aggressive. His bill is horizontal and his tail is closed as he tries to push it down on one or the other side of the female's tail. The caroling notes often continue during copulation and become low-pitched or hissing *cheahh* or *chwohh* notes from one bird. The female slips out from under after a second or two, or he flies off; he stands puffed out, spread-tailed, and ruff-throated (Figure 14C) on her or another perch, then preens briefly or returns to foraging. She carries off and eats his food, perhaps after ritually ducking her head his way a few times (Figure 14B).

The male sometimes feeds the female so frequently that she refuses to take his food. He carols as he swipes it past her bill several times, as if tantalizing her with the aroma. She may growl as she turns her head away. At times she takes the food and swipes it past his beak repeatedly; one bird

carols each time. Often she is in a somewhat challenging pose (upright, with body and tail spread, throat spread, and head somewhat arched on the neck). He spreads his tail and sleeks his head as he carols each time he tries to feed her; his posture becomes more challenging. If she takes and drops the food repeatedly, he flies down, picks it up, and returns to feed her repeatedly. He may chew the prey even more between attempts to feed her or take it to the ground for dissection. Finally he eats it himself or leaves her with it still in her or his bill. She may drop it and look down lazily, or gulp heroically. He probably eats any food he carries away, for he does not return from his foraging for a long time.

If the male does not feed the female often, she stretches and faint-sings, then moves to the ants and forages near him. She may give brief *chee* or *chee chee* chirps, or carol briefly, as he dissects food or carol or whine as she hops up to him. Often her caroling is a simple *chee chee chee,* without a drop in pitch. He may carol back, with a drop in pitch. Often he lowers the head and bobs it (Figure 13A). He resumes feeding her again. In the dry season, I have seen a female gape and whine at her mate repeatedly without his feeding her or giving way to her. Although, I have seen courtship feeding at every month of the year, there is less often feeding and more often female begging in the dry season.

Male to male pair bonds develop and sometimes persist for several years when no female is available. The two try to feed each other and often pass food back and forth several times. Neither accepts food the way a female would, which is probably one reason that the appearance of a nubile female breaks up the fragile male-to-male bond. There is much caroling, and many overbearing poses, when two males pair. Often the other bird is a son of the male involved, and the sporadic feedings are probably possible because some sons associate with fathers for several years. Occasionally such sons feed and attempt copulation with their mothers.

Traveling with the Mate

Pairs of Ocellated Antbirds stay together. They preen or forage from the same perch less than the width of a body apart at times. The tail of one may rest on the body of the other. Foraging birds hardly seem to notice each other even when they are almost touching (Figure 4A). Once I saw two birds cling with their feet alternating on the perch. Once a male nibbled the toe of a female above him and she moved up.

When other birds are present, the pair may carol or gape and nibble at each other's heads as if nervous. Often, too, they carol or chirp faintly (possibly agonistic?) as they come close together. The female sometimes has to whine and gape (plead) or wing-flutter to her own mate, especially if he is fighting with other Ocellateds. Occasionally he pecks back gently. When they go for the same prey together, the large male is likely to snap at the female and end up with the prey; but then he may feed most of it to the female. One male did steal food from his female and she pecked at him; later he supplanted her. This was in the dry season, however, and the pair were subordinate to another pair. In the dry season, there is much whining and caroling as the two come together, and they seem generally slightly agonistic; but they still stay close together. There are occasional supplantings, the female by gaping and pleading at her mate (who may chirr) and the male by simply supplanting her. When mates challenge each other on meeting, usually one nibbles toward the beak of the other, which nibbles back and loses its challenging pose too.

When a pair of Ocellated Antbirds moves, the two faint-sing back and forth. Faint-songs or serpentine-songs of the male often induce the female to leave her patch of cover or desert the swarm with him if a human comes near. Longer and louder songs bring them together if they get out of sight of each other for some reason. If the male finds a good antswarm or branch of the swarm, he often serpentine-sings repeatedly (Figure 15). The female quickly follows. If the male hesitates because other Ocellateds dominant to him are at the swarm, his mate may serpentine-sing and lead him in to a side branch of ants. Once, when a male was crippled, his mate loud-sang and led him in to the ants by going back to him repeatedly. In traveling, the male is more likely to be in the lead and to give inflected faint-songs or fragmented serpentine-songs. When the pair arrives at a tape recorder after playback of songs of Bicolored Antbirds, they chirp or carol briefly to each other as they look about. About the only time a pair separates is when one bird is on the nest.

Searching (for Nest Sites?)

Occasionally a timid pair of Ocellated Antbirds wanders through the forest away from or near a swarm of ants and behaves most peculiarly. The male alights low on buttresses of trees, peers down between them, and serpentine-sings on and on even though no ants are there. The female flies up and takes his place, then looks down at the space between the buttresses. Often one or both disappear between the buttresses before moving on warily to new buttresses. The female visits some buttresses and serpentine-sings, too, attracting the male.

Once I was able to see what happened, for the birds performed this activity at a swarm of ants. Male XG serpentine-sang repeatedly on a buttress of a small tree, flew 2 m toward his mate (MBRM), then returned to the buttress and serpentine-sang again. Then he hopped down onto the leaf litter between two buttresses and stopped calling as his mate flew 1.5 m away and looked at him. He sat very low, his bill inward toward one buttress (Figure 16A) for nearly a minute. The female wandered off and he broke the pose; he returned to foraging near her.

The Nest

The nest of Ocellated Antbirds is not certainly known. Neal G. Smith (pers. comm.) saw an Ocellated near a nest behind loose bark of a log on the Navy Pipeline Road in 1964; the two eggs went to Charles Sibley for egg-white protein analysis. The nest site, however, sounds like that known (Y. Oniki, pers. comm.) for Wing-banded Antbirds (*Myrmornis torquata*), which occur regularly on the Pipeline Road (Karr, 1971). Moreover, Skutch (1946) warns that antbirds often seem to be curious about nests that are not their own, so that only continued watching could have determined what species made this nest.

On 7 May 1961, I found a nest sunk in the ground between buttresses of a tree of *Quararibea asterolepis* on Barro Colorado Island, southwest of Balboa 3. The nest was partly protected by lianas across the buttresses and was a neat open cup of slender strands. One heavily speckled egg, larger than the egg of a Bicolored Antbird, was in the nest. Unfortunately, I saw no bird go to the nest (an antswarm with several Ocellated Antbirds was near the nest when it was found), and the egg disappeared from the nest a day or two later. On 13 June 1967, I found an empty nest in a similar place, northeast of Balboa 5.6, while watching a pair of Ocellateds searching for a nest site. The evidence that these were indeed Ocellated nests must rest on the facts that Ocellateds search for nest sites in such places, and that no other bird on Barro Colorado has such a nest and an egg that size. The

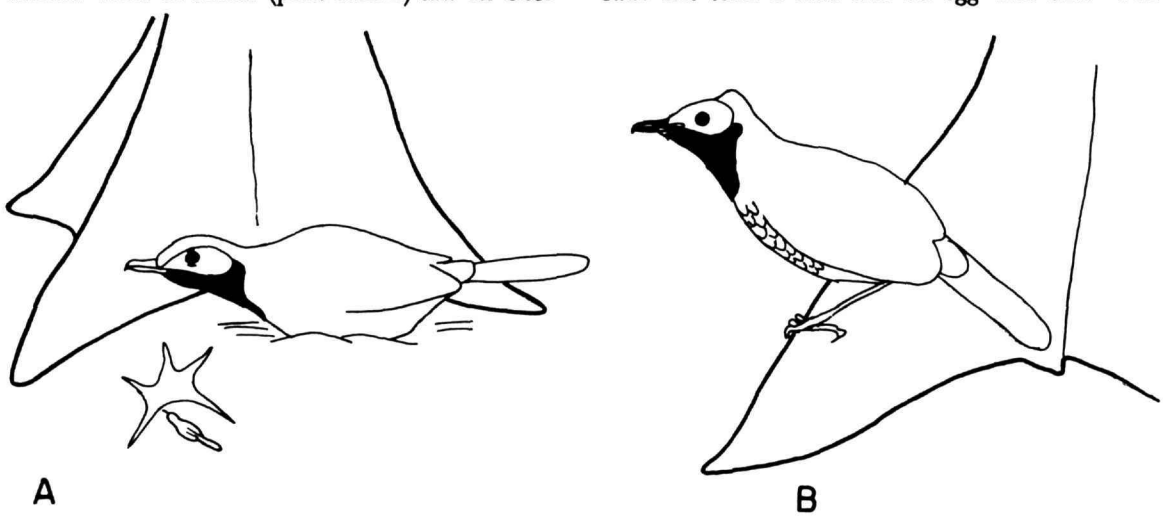

Figure 16.—Male (A) crouches in leaf litter between buttresses, probably searching for nest site. Small figure below gives top view. Fledgling (B) about three weeks out of the nest waits on tree buttress, a frequent hiding place.

nests of all other antbirds, ovenbirds, and woodcreepers on the island are known; no tanager or treetop bird is likely to nest in such sites.

Incubation and Brooding

It may seem presumptuous to talk about incubation and brooding when the nest is unknown, but watching pairs of Ocellated Antbirds at swarms of army ants shows that they are much like Bicolored Antbirds in these respects. Male and female Ocellateds both have brood patches when nesting.

Since one or two young eventually arrive at swarms of ants, we can presume that the clutch is two as in most antbirds, possibly one at times. Incubation is marked by the disappearance of the male for nearly all morning, as in Bicolored Antbirds. Presumably the female incubates all night and he incubates all morning without feeding at the swarm of ants. In one case, however, a male briefiy visited the ants before going to the nest about 8:00 AM. Between about 11:00 AM and 12:00 M, loud-songs in the distance elicit loud-songs from the female at the ant swarm. She flicks her tail, looks about, flies his way, and returns with grunts and loud-songs. The male sweeps in with a few chirrs at the observer and much caroling as he meets the female and she nibbles at him. Then he moves in over the ants and forages rapidly, as if famished. He preens quickly between rapid sallies for prey. The female rests, watches him and prey, and preens; but she does not forage much. The pair are together at the swarm for an hour or two about noon. The female departs with a few faint-songs. The male hardly looks her way. She arrives again in late afternoon, and he disappears. The afternoon periods are irregular in length, and the female sometimes leaves (probably for incubation) well before dark. Thus, the male has at least two incubation periods per day and the female at least two (including the night period).

During early brooding, the visits of male and female alternate, with the female foraging at the ants early in the morning. Presumably she broods all night, as do other female antbirds, and the male takes over in the early morning. Both sexes probably brood young, as in most antbirds. Each parent stays at the swarm of ants an hour or two at a time, then dissects a large prey item, eats projecting legs, and faint-sings as it looks about with the body or abdomen of the prey in the beak. It moves off in a straight line, faint-singing and looking around at each stop. It may stop and point the bill upward to rechew the prey. The mate arrives from that direction within half an hour, and forages vigorously. Occasionally the mate loud-sings in that direction and the foraging bird at the swarm answers, the mate moves in, there is a meeting with loud caroling, and the pair forage together for a time. As the young grow older they are brooded less, for both parents are at the ant swarm much of the time.

Care of the Fledglings

Bob-tailed fledglings eventually appear near swarms of ants. The small young hide on the ground between buttresses of trees, and later low in dense treefalls, and are difficult to flush. From their labored but not weak flight, from the lengths of their tails, and feathering of their bodies, and comparison of these characters with young of known age in other antbirds, I estimate that young Ocellateds are between two and three weeks old (age since hatching) before they arrive at swarms. I do not know whether they stay at the nest until this age or, as is more likely, move out of the nest at an age of about two weeks and are gradually moved toward the ant colony. I have not found parents and small young away from ants.

Parents ferry food to the hidden young much as before fledging. The parent's faint-songs, looking about, and movement directly toward the young allow the observer to approach it. The parent then chirrs violently, flies around, and the young freezes. One may flush it accidentally, at which the parent chirrs frantically. A few faint-songs or serpentine-songs, however, start the young one peeping and moving toward the parent. If the observer is nearby, the peeping of the young gets a loud chip or chirr from the parent, at which the young abruptly stops calling and freezes. Chased young fly well, high into liana tangles or other cover, and can be caught with mist nets but not by hand. The young follows the parent to a distant tangle, and waits there. I have not seen distraction displays.

The young peeps loudly before feedings and squeaks as it is fed. It sits, even in the leaves of the forest floor, and beats its wings downward. The parent may carol faintly as it feeds the gaping,

flutter-winged fledgling. If it gapes too violently, the parent turns the nape of the neck to it and resumes the feeding when it settles down. A chirr in its face sometimes shuts it up if it peeps loudly after the feeding.

As in Bicolored and Spotted Antbirds, if there are two young, each parent takes one. Once when a male was crippled, however, the female fed both young birds. If there is only one, the male parent usually helps or is helped by the female in feeding the young, but he is likely to start feeding the female again. She passes his food on to the young bird much of the time. At times a female with her young bird is at a swarm of ants a kilometer or so from the male with his young bird, but the family soon rejoins. The family normally is together over the ants.

Growth of the Fledglings

The smallest young seen had tails about 10–20 mm long, with vanes for 60 percent of that length. The legs were bare except for a circlet of pinfeathers at the "heels," and the undersides of the wings were bare back to the sheaths of the remiges. The body was fairly well feathered, but the head was rather bare. Black throat feathers and gray-tipped blackish crown feathers were just coming out. The face was dull and blackish, the gape angles and gape and tongue bright pale yellow. The base of the lower mandible was pale. In the hand, the young pecked and snapped, jerked the tail, struggled, and sometimes screamed.

By an estimated week out of the nest, the young bird has a tail half the adult length. The grizzled crown is sometimes fairly well feathered and sometimes bare anteriorly, and the young bird is nearly adult weight. By two weeks out of the nest, the tail is three-quarters the adult length. Some new adult feathers are on the chest. The tail is full length only at about three weeks out of the nest. New gray feathers of the adult plumage are appearing at the front of the crown, but the change to adult plumage is then very slow. Even at 12 weeks out of the nest the grizzled juvenal feathers still cover the rear crown. The face is turning blue by then, but it is still mottled with dusky and with whitish areas. The gape angles are still pale, but the bill is nearly completely dark.

By 18 weeks out of the nest there are often still some dark or pale areas on the blue face, and the gape angles are still pale, but the young bird is gray-crowned and has nearly completed body molt into adult plumage. The tail feathers are finishing molt, and specimens in various museums show that wing molt is also finishing as the last juvenal feathers disappear from the crown. The molt from juvenal to adult plumage is thus complete, rather than restricted to body feathers. By 21 weeks (five months) out of the nest it is difficult to tell young from adult. The process is thus much slower than in Bicolored and Spotted Antbirds, which molt into adult plumage in about five weeks after leaving the nest (Willis, 1967, 1972a) but do not go through wing or tail molt until the following year. Perhaps a dominant species can support an early wing and tail molt and give the young a better chance to survive the first year; survival of juveniles is better in Ocellateds than in the two other species (Willis, MS).

The young Ocellated Antbirds start feeding themselves as fast or faster than do young Spotted and Bicolored Antbirds. Young Ocellated Antbirds with tails half the adult length spend much time over the ants when the birds are undisturbed by competing Ocellated Antbirds or by predators. The young peer at the ants or peck clumsily now and then. By the time the young have tails three-quarters the adult length, they occasionally sally clumsily for their own prey. Sometimes they get only a bit of leaf or a twig and chew it briefly before dropping it. They tend to stand on the ground and hop or whirl in the middle of the ants rather than do neat sallies to the ants and back up, but they definitely get some tiny prey items. By four weeks out of the nest, even earlier than in Bicolored and Spotted Antbirds, the young Ocellateds are getting much of their own food. Their parents seldom feed them after this time. Perhaps their simple foraging method and dominant status make it possible for them to get much of their own food at an early age, while the variety of methods smaller and less dominant ant-following birds must use makes for slower maturation or learning of foraging techniques.

Young birds that are still being fed by their parents wait near them over the ants, gape and squeak *whaiaiaih* at the parents periodically, and sometimes carol and flutter the wings at them. The

parents gape and extend the head at them, turn the head away from the young each time it pleads, or retreat and champ the bill before the importuning young. When one young is fed, the other may come up and gape, turning the body back and forth as it lowers the head and tail in a rather submissive way. One young female dropped her food but was too naive to pick it up; the mother supplanted her with a vigorous snap! of the beak but then flew down, picked up the food, and fed the young female.

As noted earlier, parents commonly lure young away from a human observer by serpentine-singing or faint-singing, at least until the young are no longer being fed. The parent chirrs at the observer. Later, the young often follow the songs one parent is using for attracting the other. Young come up and beg when the father feeds the mother, and sometimes even beg from strange males on their way to feed their mates.

Young Ocellated Antbirds loud-peep frequently, and their peeping is beginning to change into faint-songs and loud-songs when they are four weeks out of the nest. The notes are a series of quavering peeps, however, when the parent is feeding the young occasionally. Young chirr and chip infrequently, and these notes are rather weak and falsetto until they are three or four weeks out of the nest. However, they crouch and hide readily at the chirrs or chips of adults. Grunting notes at other species are still falsetto at 4–12 weeks out of the nest. Loud squeaking notes of feedings tend to grade into whining and chittering as the parents start to reject the young birds.

Older young, foraging for themselves, occasionally gape and flutter to the parent. More often, however, they gape and nibble with the parent or whine, chitter, or plead with it to keep a good foraging site or bump the parent (even bodily!) off its perch. At times the young bird chirps or carols, *chee chee*. The older young hop about cringing or whining at times. Challenging is rare before the young are foraging for themselves. After this, young males sometimes gape and snap or challenge at their mothers (Figure 9c), who are subordinate to all males unless protected by their mates. Females usually tolerate their grown young, however, except for gaping and nibbling. Possibly the wing-fluttering and pleading of adult birds develop directly out of techniques used by young birds that stay near their parents. The male parent often supplants or even pounces on the young bird if it gets in the way of his foraging, but the chirrs of the female at the screeching of the young may stop his attacks short.

Clan Formation

Young Ocellated Antbirds continue to associate with their parents after the parents are no longer feeding them, and even after the young birds get completely adult plumage. This leads to the formation of one of the most complex familial societies yet reported for any bird. These are far more complex societies than those of Bicolored Antbirds, in which parents drive their young away as they get adult plumage. In Ocellated Antbirds, patrilineal "clans" develop around a successful pair, forming families in which young males and the mates they bring home are tolerated in and outside of breeding seasons for several years, in assemblages that can separate or come together as food supplies dictate. Four such families were observed over several years on Barro Colorado: around males XR, YX, XRYG, and YBXB (Figures 19–25).

The young female commonly stays with her parents for six to eight months, until the next breeding season after her hatching. Then she mates outside the clan (in the few cases known) and does not associate further with her parents. She has been wandering to swarms away from her parents occasionally since she was a few weeks old, but she readily rejoins them, with a little chittering and gaping at their heads to ward off occasional pecks, until she gets a mate of her own. She then becomes a member of his clan, unless he is a solitary male that has not stayed with his clan. Her adopted clan now tolerates her as a member of the loose family; however, she often has to display submissively when other males of the clan are nearby, in a way that her mate need not do. Also, she tends to stay close to her mate and bunch with him if other clan members become aggressive.

Young males occasionally wander off as solitary males, but often associate with their parents periodically for a year or more. Some submissive behavior is necessary, especially low-intensity chittering, cringing, gaping at the head of the adult male, and whining. At times the young male dis-

places his subordinate mother; however, usually the parents tolerate or ignore the young bird. Brothers and sisters also tolerate each other, even foraging a few cm apart. Sometimes they bob the head and gape at each other, then one retreats. Occasionally the adult male feeds a year-old young male, probably mistaking it for a female. Occasionally the young male feeds new fledglings of his parents, probably mistaking them for nubile females; however, his activity is altruistic in its results. Young born in different years tolerate each other, but older ones bob the head (Figure 17) or gape at young of the year in some encounters. Wing-fluttering is not often used, and bunching is done with the parents or siblings rather than against them. In other words, one can get groups of several birds bunching together against a neighboring clan. The bunching becomes unstable with more birds, so that clans of grandparents, parents, and several broods of young do not join closely.

Ocellated Antbirds are not very successful at nesting, and pairs that belong to a clan tend to wander off from it, but occasionally one can see eight or so birds of a clan at one good ant swarm. Typically the largest part of a clan present on any one day consists of two grandparents, one or two males of the previous year or two with a bride or two, and perhaps three young of the current year as offspring of the grandparents and of one of the young pairs. Other members of the clan may be at another ant colony. The clans are often more inclusive than one can see at any one swarm, for a few days later there may appear another young male of the previous year and his family, while one or more of the original group is at another ant colony for the time being.

Eventually, apparently, such clans break down into separate units as the "grandparents" isolate themselves more and more from related grandparents or siblings. Probably most of the birds of Barro Colorado Island are related to each other, but even among the 30 or so birds in my study area there seemed to be three major clans and one minor one. Probably, had I known the complete genealogies of the various birds, some peculiar spatial organizations of pair home ranges (see below) might have become more understandable. It seems that as the birds age, however, they tend to isolate themselves and to become the "grandparents" of separate clans. Normal attrition, in a bird that has a short life cycle (Willis, MS) and high predation on nests, probably insures that the loose clans must break apart as parents and siblings die off.

The development of these clans has not progressed to the degree of regularity one sees in family flocks of various birds, such as the Australian Bell Magpie, *Gymnorhina tibicen* (Carrick, 1963), or in Anis, *Crotophaga ani* (Davis, 1942). Possibly the group territories of these species evolved through a stage like that in Ocellated Antbirds. The lability of the clans of Ocellated Antbirds, however, makes them in some senses more social than flocks that keep together. Communication, particularly submissive behavior, is certainly more complex than in flock-forming jays (Brown, 1963). An assemblage in which the various members can split apart and come back together again, such as this one, seems to require greater individual recognition and social

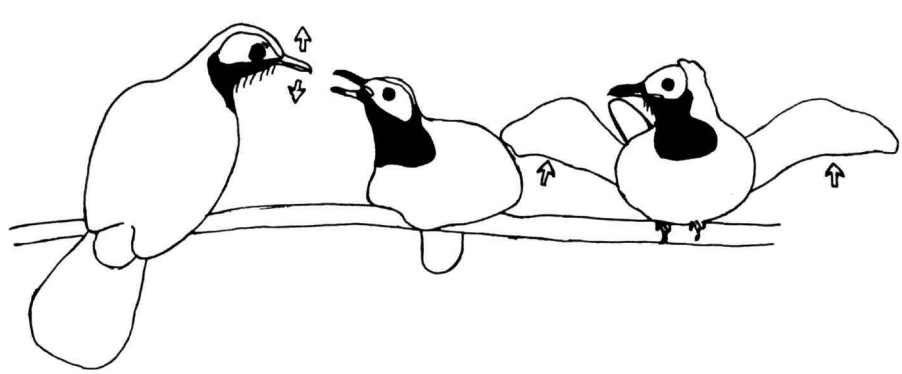

FIGURE 17.—One-year-old uncle (left) of two young birds bobs (threatening?) at one of them, which gapes and nibbles, while the other (right) wing-waves and tail-flicks as if expecting food (or submissive?).

interaction than an assemblage in which the members are constantly together or accept any new members. Brereton (1971) has noted a similar phenomenon in Australian parrots: birds of wet areas are territorial, birds of dry areas flock, and birds of intermediate habitats have intermediate spacing systems but more complex vocalizations than do birds of either extreme.

The clan of Ocellated Antbirds is a patrilineal one, in which exogamy is created by importation of females from outside the clan. Many mammals (Red Deer, *Cervus elaphus,* Fraser Darling, 1937; baboons, *Papio anubis,* DeVore and Hall, 1965) have matrilineal clans, in which males move from clan to clan and females stay with the clan of their birth. Perhaps female movement is favored if the pairs are to be monogamous, as in antbirds, while male movement is favored if polygamy or promiscuity is possible.

The clans of Ocellated Antbirds are rather like the loosely social clans in chimpanzees (Lawick-Goodall, 1968), which also unite and separate according to changes in food supply—fruiting trees in the case of chimpanzees.

Nest Survival, Renesting, and Breeding Seasons

Even though no nest has been found, knowledge of incubation routine shows that nest success is low and that individual pairs renest repeatedly throughout the rainy season (April to December) on Barro Colorado Island (Figure 18). We can estimate that incubation probably takes about 16 days and the nestling period 14 days, as in related antbirds; with building, a complete nesting probably requires some 37–40 days. Young are fed for some four weeks after they leave the nest, and then the parents nest again. The young of the first brood still are with the parents. Indeed, one young female accompanied her mother away from the swarm and came back with the father, in a pair that were feeding young in the nest. At times a pair will have two broods of dark-faced young, as the pair that had

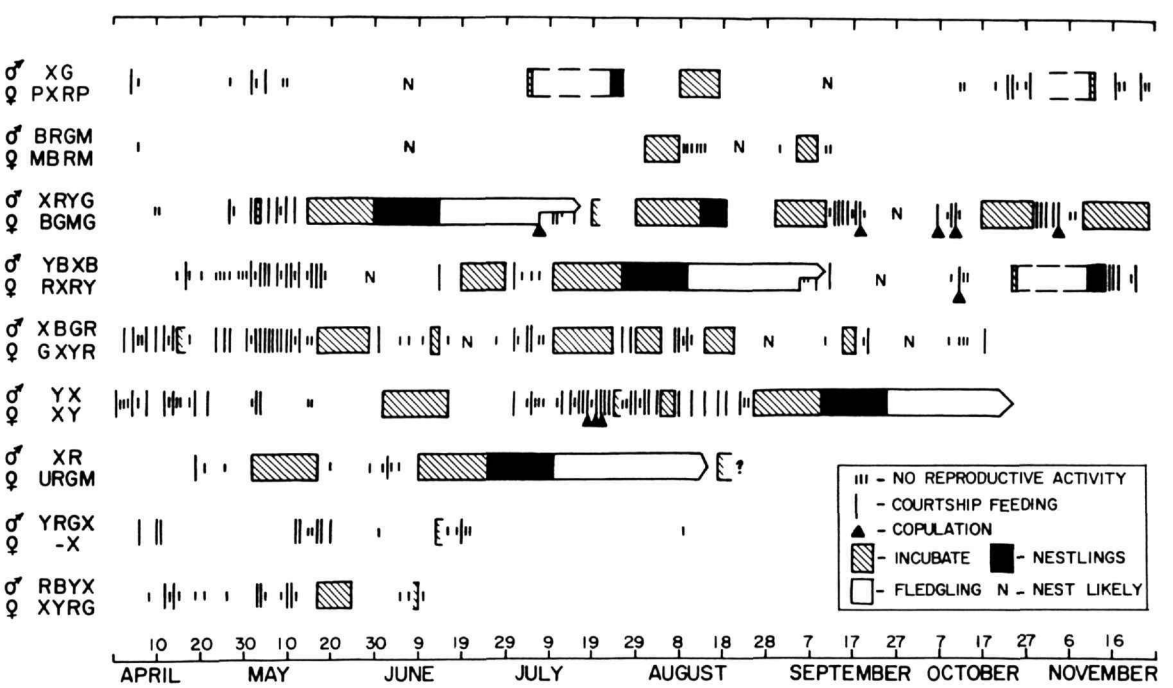

Figure 18.—Nesting of nine pairs of Ocellated Antbirds on Barro Colorado in 1961. Fledged young stay with parents during later nestings. Times of nests, not located, are estimated from the behavior of birds at ant swarms.

young 2 days and about 12 weeks out of the nest on 7 August 1965.

Young birds out of the nest are still being fed in January in some years, so that nesting certainly extends into December. The earliest young seen were ones about three weeks out of the nest on 2 June 1967. These young probably came from a nest in which eggs were laid about 5 April. With the long breeding season, it should be possible for pairs to rear three or even four broods in one year. Specimens of young birds from eastern Panama and western Colombia, where rains last all year, indicate nesting in January and February. In these regions, nesting may go on all year.

The poor success of nesting, as in many birds of tropical forests, means that few pairs actually raise more than one or two broods per year. From the nine pairs in Figure 18, 27 of 31 detected nestings, or 87 percent, were unsuccessful; there must also have been undetected nestings, such as ones in which eggs were destroyed within a day or two of laying. Willis (MS) estimates nest survival as 4.2 percent. (Detection of a nesting by watching parents away from the nest requires incubation at that nest for one or more days.) Since the four successful nestings produced only one young each, and the clutch size is likely to be two, only 4 eggs out of 50–60, or 7–8 percent, produced fledglings. Since none of these nests was visited by the observer, the possibility that the observer causes the high nest destruction often seen in tropical nests is eliminated; that is, nest destruction is not an artifact of observation.

Spatial Behavior

Spatial Distribution: Territoriality, Superimposed Pairs, and Superimposed Clans

As is the case for Bicolored Antbirds (Willis, 1967:93), two to four Ocellated Antbird pairs may be found at the same swarm of ants even during the months of breeding (Table 9). Coexistence once was thought to indicate nonterritoriality, but in Bicolored Antbirds coexisting pairs are still territorial (Willis, 1967:102). The pair on its own territory dominates others, which upon analysis turns out to be the only relevant criterion for territoriality—a territory is a space in which one animal or group dominates others that become dominant elsewhere.

TABLE 9.—*Records of pairs of Ocellated Antbirds at swarms of* Eciton burchelli *on Barro Colorado Island*

Month	*Wandering birds, no pairs* 0+	*Number of pairs of antbirds*			
		1	2	3	4
November 1960	–	6	–	–	–
December	–	6	6	3	–
January 1961	10	1	6	9	1
February	8	14	6	1	–
March	2	17	11	–	–
April	2	19	8	8	–
May	–	22	12	10	3
June	–	23	7	–	–
July	–	34	14	4	–
August	–	18	18	15	–
September	–	37	6	–	–
October	9	29	8	2	–
November	–	30	3	–	–
Total	31	256	105	52	4

Ocellated Antbirds, at low densities, show much the same type of territoriality as do Bicolored Antbirds. Figures 19 to 23 show maps of home ranges of several such males and their mates over the years. These ranges are much larger than in Bicolored Antbirds—about 1500 m across (area, 1.75 sq km) rather than 750 m across (area, 0.44 km²). The ranges of Ocellated Antbirds overlap extensively. When one pair near the edge of its range meets another pair well within its range, the latter pair dominates. When the same two pairs meet well within the range of the former pair, the former pair dominates. There have been several cases of these space-centered reversals of dominance, but not as many cases as I recorded for Bicolored Antbirds. Ocellated Antbird pairs tend to show flight or submissive behavior rather than attack and challenge, and the "main" territorial pairs thus tend to avoid each other. Moreover, the ranges and dominance "cores" or territories within those ranges are so large and diffuse that some main pairs never moved far enough peripherally to be subordinate.

When one of the main pairs disappears, a neighboring pair may move into its region as if it had earlier been prevented from doing so. Figure 21 shows that male MOPS and his mate moved into the region of male XRYG and his mate after the

latter pair disappeared between 1968 and 1969. The pair MOPS was moving from a region of low density of Ocellated Antbirds to the "escarpment" zone of higher density (see below), suggesting that they got a better habitat by the move.

The main pair of a region is usually the pair that comes up if one plays recorded loud-songs of Ocellated Antbirds in the forest. The male does not show signs of challenging, but he does loud-sing vigorously and look about as he sweeps past rapidly. The following female may echo his loud-songs. Then the pair moves away rapidly, unless there is a swarm of ants. (If one plays loud-songs of Bicolored Antbirds, by contrast, any pair of Ocellated Antbirds in the area is likely to move in without loud-singing, chirr at the observer, and stand about as if waiting for ants.) Loud-singing is not used regularly as a territorial call by Ocellated Antbirds, although they respond to loud-songs. More often, as noted earlier, the loud-songs are signals between mates or are used when a pair is scared away from ants or hunting a new colony of ants. (Since the main pair of a vicinity respond to wandering pairs by loud-singing, the latter often

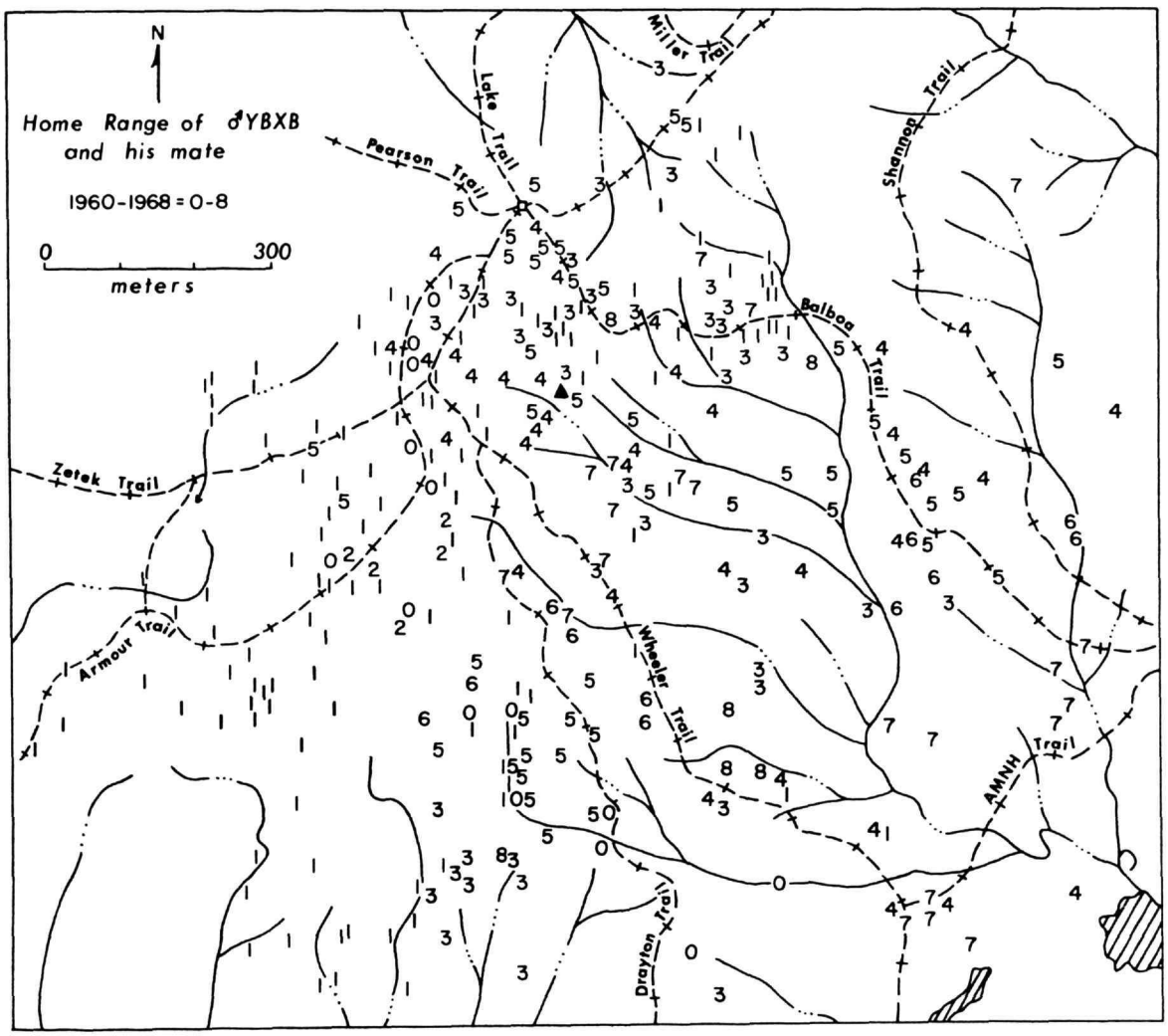

FIGURE 19.—Sites where male YBXB and his mate (1960–1963, RXRY; 1964–1968, GOBW) were seen at swarms of army ants. Location of a possible nest in 1961 is indicated by a triangle.

home on them. This might discourage use of loud-singing in territoriality, since neighbors would move in and compete.)

So far the Ocellated Antbirds are not very different from Bicolored Antbirds. However, Ocellated Antbirds in areas of high densities have, in addition to "main" pairs, what one can call "superimposed" pairs. The simplest class of superimposed pairs is that of a male young bird and his mate, which often occupy the territory of the father and mother as the nucleus of a clan. Figure 23 shows how young male RSWR stayed in the range of his father and mother, XR and XGBR. He was mated and had young in the area in 1964 and early 1965, as did his parents, thus forming a very large clan. XR did not chase him, and indeed RSWR helped XR in many disputes with neighboring pairs and clans. In late 1965, XR had disappeared and RSWR was mated with his mother, XGBR. The next few years he had other mates.

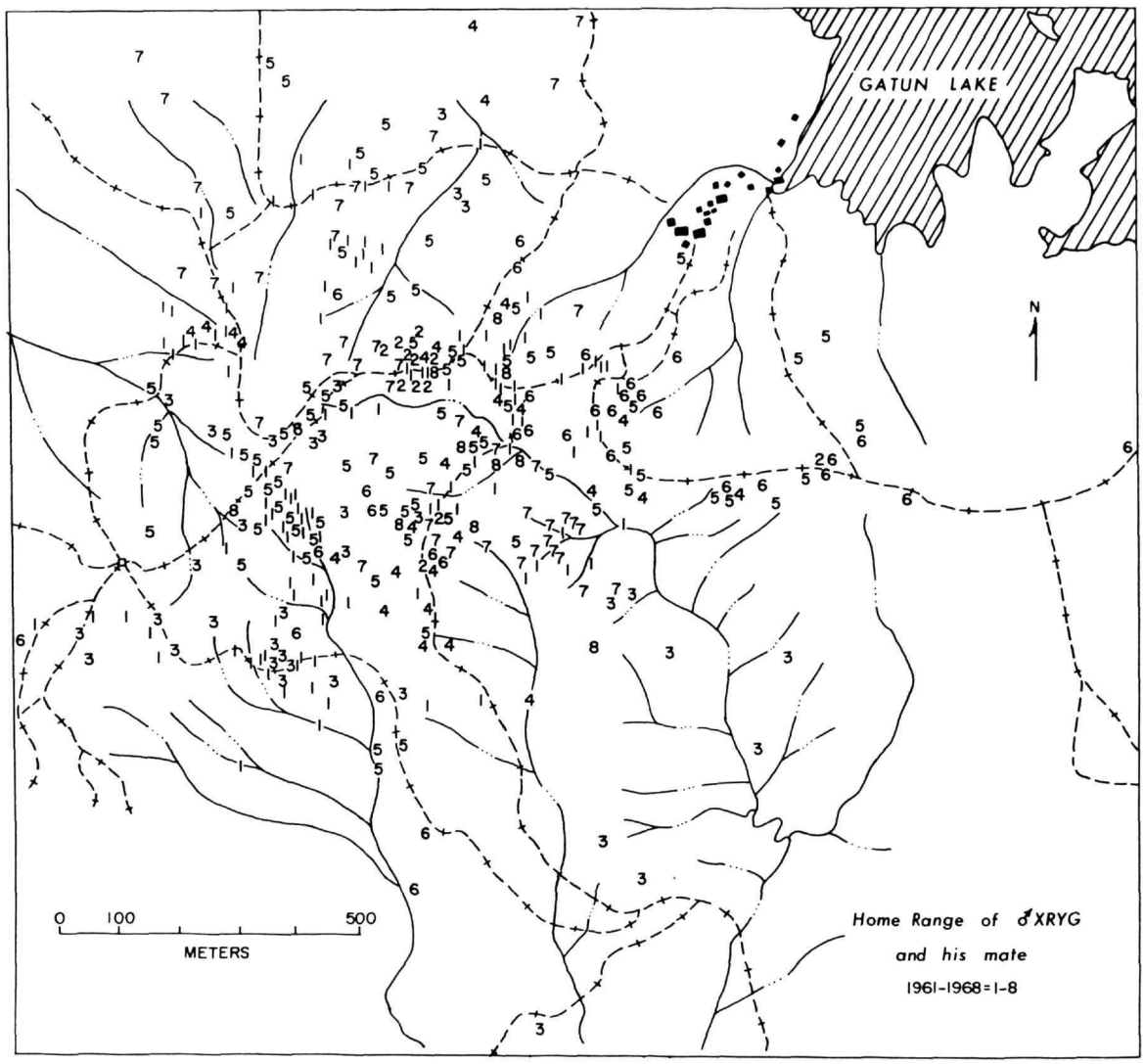

FIGURE 20.—Sites where male XRYG and his mate (1961–1963, BGMG; 1964–1965, PWBM; 1968, ZYOS) were at swarms of ants.

More often the superimposed young pairs of a clan fight a little with the father of the clan, but not as strongly as they fight with outsiders. When the young male loses his mate, he sometimes rejoins his parents as a threesome (see the section, "A Day at a Swarm of Ants"). Eventually he gets another mate and wanders more and more apart from his parents. Perhaps this leads to the second class of superimposed pairs, which are rarely dominant pairs that wander over the areas of main pairs or between the cores of home ranges of main pairs. Figures 24 and 25 show two such pairs, which tended to wander in slightly different areas from surrounding pairs but which can scarcely be said to have had separate dominance or territorial centers of their own. Male XBGR and mate unfortunately disappeared in late 1961; they seemed to dominate over other pairs in the canyon areas between Wheeler 20 and Balboa 10 and may have had a territorial center there; if so, however, they had to forage out of their territory much of the time in 1960-1961. Male YX and his mate, however, definitely centered almost on the same ranges as males XBGR and XR (Figure 25). Male YX tended to dominate XBGR when both were far southwest or northwest, but dominated male XR only on a few brief occasions when both were in a zone approximately 200 m southwest of Drayton 5.

The situation became more rather than less complex after XBGR disappeared, for YX in 1961 had a son (SS) which by 1963 got a mate and joined his parents to form a superimposed clan! Half the area of this superimposed clan was the northeastern half of the area of the clan based on XR and his many descendants, and half was the southeastern half of the home range of the developing clan of YBXB and his descendants. The result was that, from 1960 to 1967 or 1968, there was a high-density

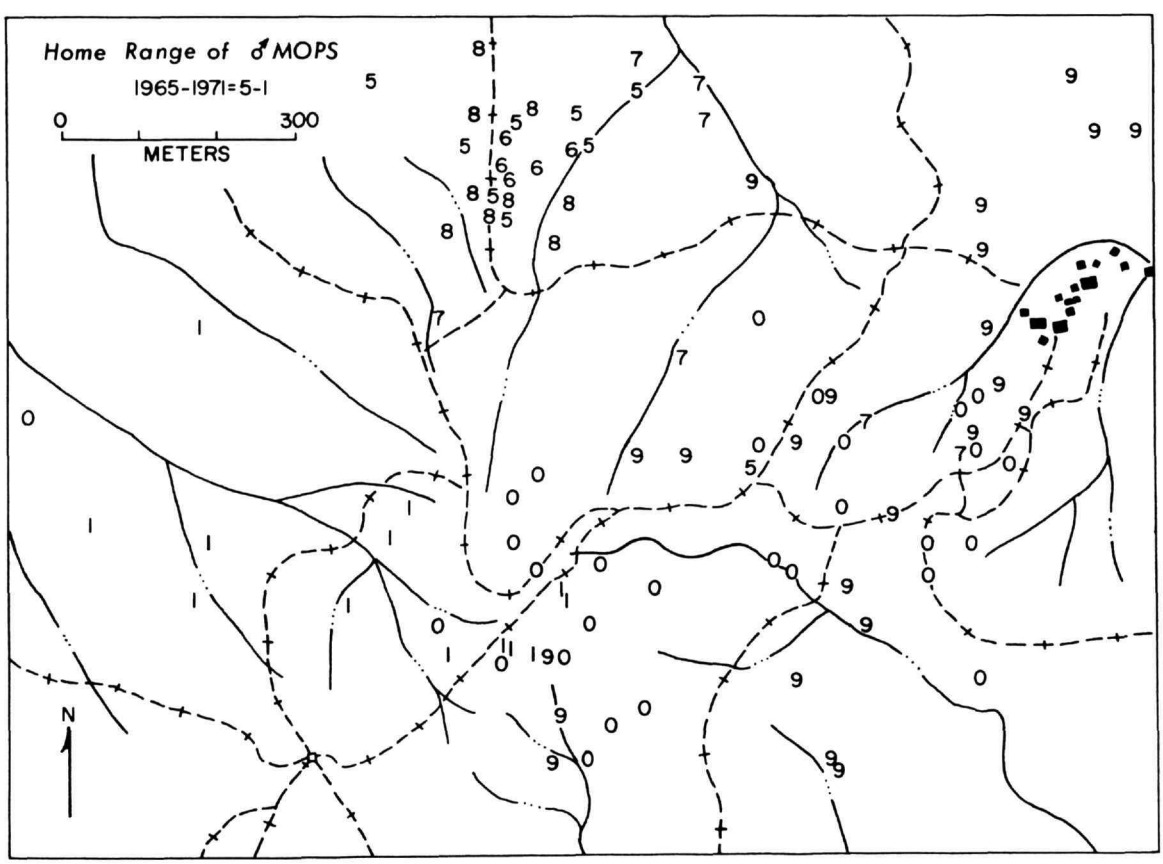

FIGURE 21.—Sites where male MOPS and his mate (1965–1969, SUSP) were at swarms of ants.

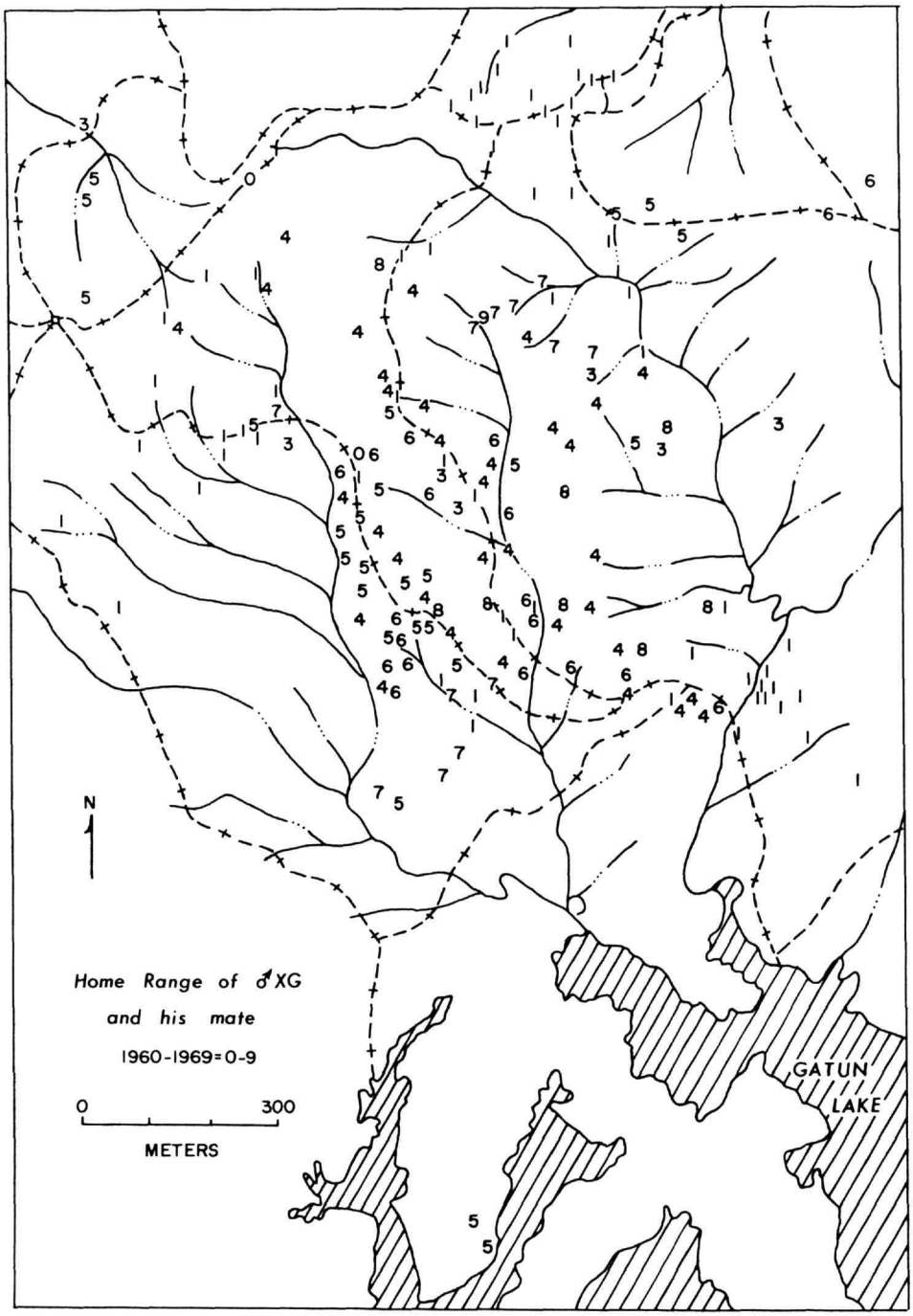

FIGURE 22.—Sites where male XG and his mate (1961, PXRP; 1963–1968, MBRM) were at swarms of ants.

zone for Ocellated Antbirds along the escarpment from about 400 m west of Drayton 10 to the area southeast of Wheeler 10. In this zone, there were clearly main pairs plus superimposed pairs, and some of both groups formed loose clans.

Superimposed pairs rarely occur in Bicolored Antbirds, except when a young pair has no territory during the first dry season they are together. In that species, each young "superimposed" pair manages to carve out a dominance area, perhaps a small one, by the first nesting season. In Ocellated Antbirds, however, locally high densities of nesting pairs were permitted by having pairs with little dominance (or dominance only over other superimposed pairs or over peripherally wandering main pairs) managing to coexist with pairs of normal (locally supreme) dominance.

ROLE OF FEMALES IN CLANS AND TERRITORIES.—Female Ocellated Antbirds, as has been noted, are smaller than males. Females play little part in territorial or agonistic encounters and are subordinate even to trespassing males unless their mates are there to bunch with. Females, especially ones whose mates are incubating, must cringe and whine and wing-wave to stay at a swarm of ants if males not of their clans are present.

A female dominates other females present if she is near her own area, or if her mate has established dominance over the mates of the other females. A subordinate female often can, of course, rush for the protection of her own mate or sidle cautiously near her son if a dominant female or male presses her.

The females usually stay near their mates or older sons, if these are present, and as a result have more or less the status of their mates or older sons. Young females are usually with their parents and take more or less the status of their parents. Other birds supplant very young females right under the noses of their parents at times, but then

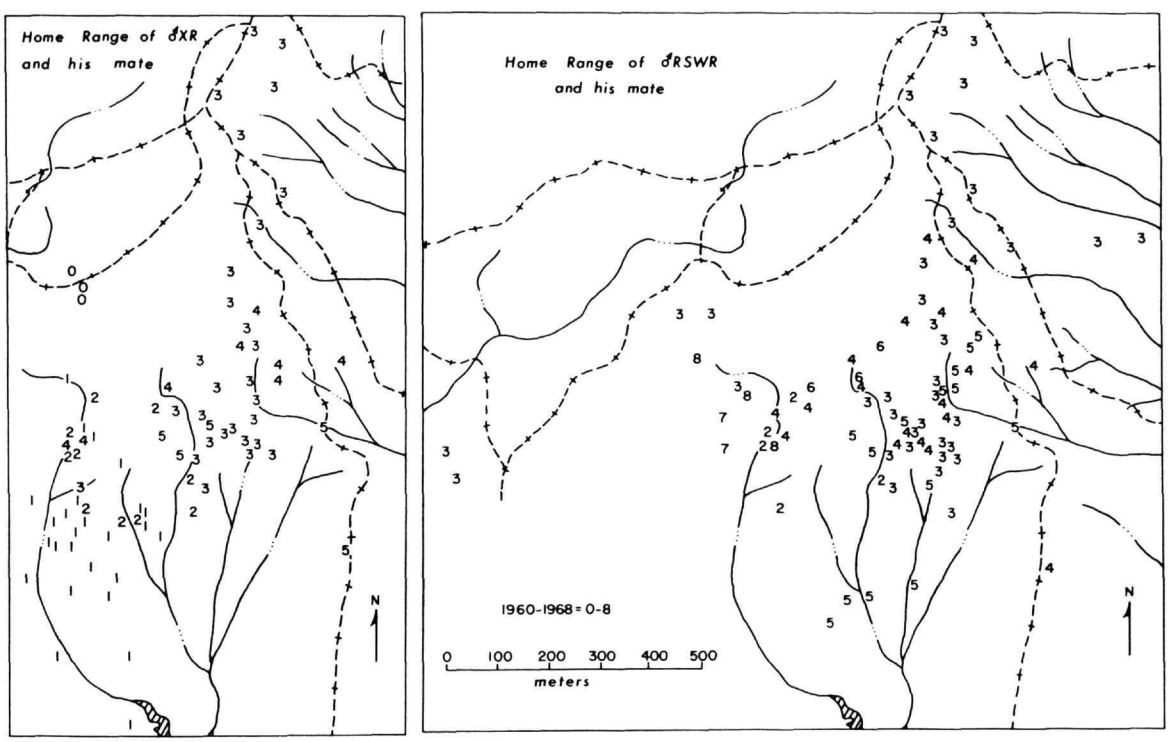

FIGURE 23.—Left, sites where male XR and his mate (1961, URGM; 1962–1965, XBGR) were at swarms of ants. Right, sites where male RSWR (the son of XR and XGBR, in 1962) and his mate (1963, RUOB; 1964–1965, GPMO; September 1965, XGBR; 1966–1967, SPYD; 1968, OWYS) were at swarms of ants.

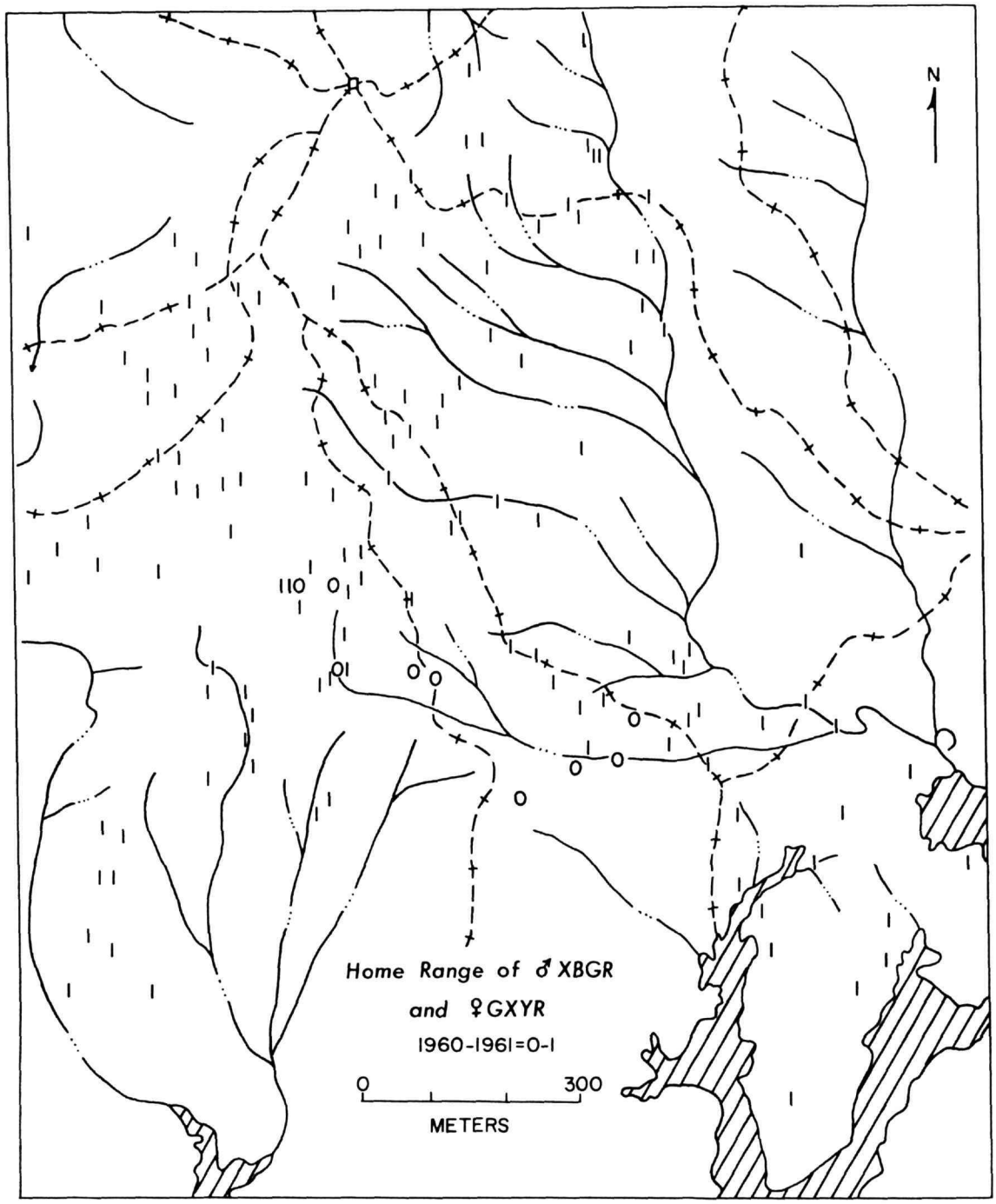

FIGURE 24.—Sites where male XBGR and female GXYR were at swarms of army ants until both disappeared, late in 1961. Note that this area overlaps that for males XR, YBXB, XG, and YX.

flee as the parent attacks. Later the young females may dominate the other birds, as long as the parents of the young females are not far away. Older young females, in adult plumage but still with their parents, often dominate neighboring females when the neighboring males are away. Clan formation thus helps protect both young and old females from competing antbirds, even when the female has to cringe to her son. Possibly this helps female survival, which is much poorer than male survival (see legends for Figures 19–25).

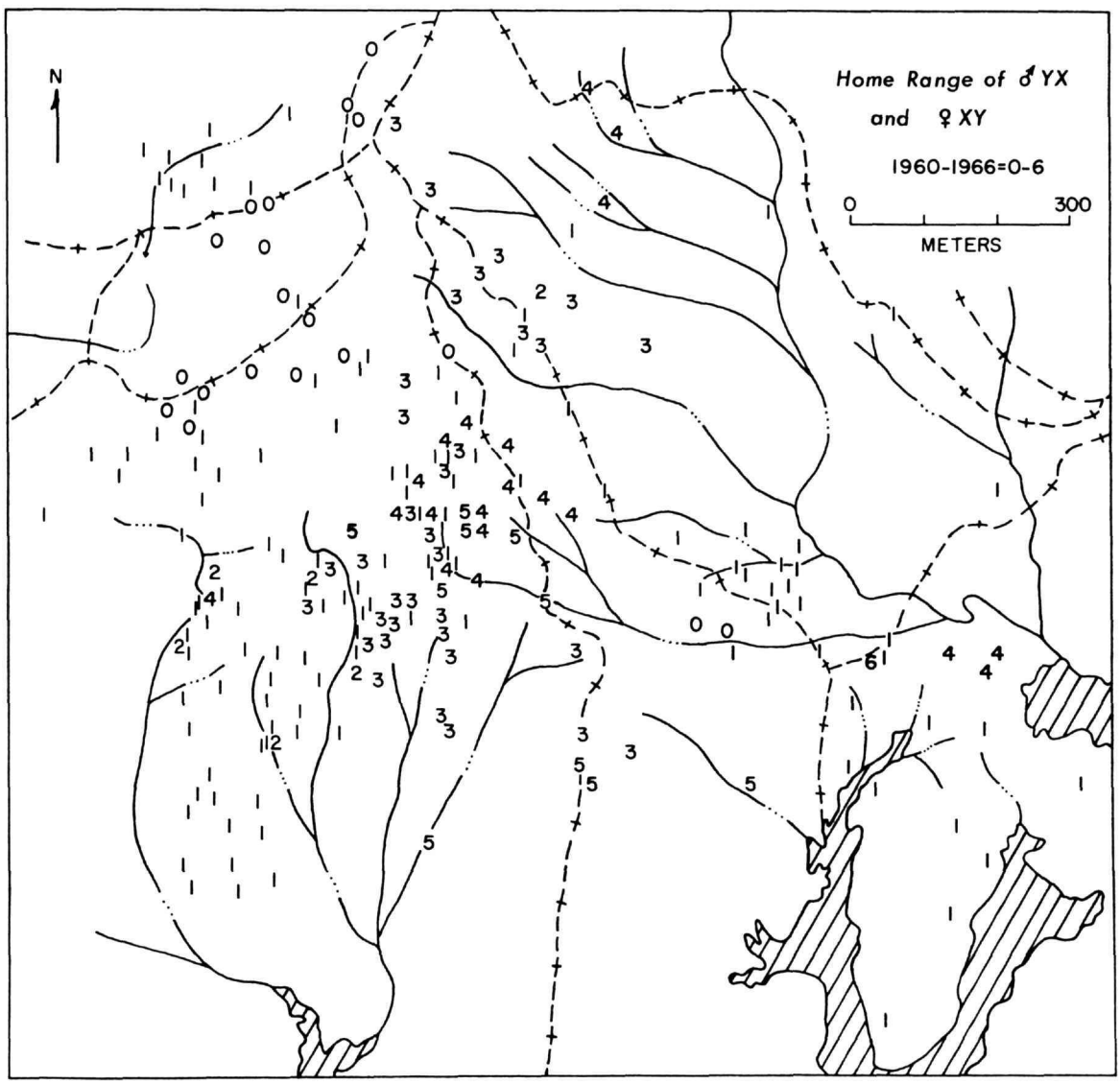

FIGURE 25.—Sites where male YX and female XY were at swarms of army ants until 1966. The area is almost the same as that for male XBGR, and overlaps that for males XR, RSWR, YBXB, XB, and several males not mapped herein.

Spatial Distribution: Escarpment Zones Versus Flat Areas

On Barro Colorado, Ocellated Antbirds concentrated over the years and formed clans mainly in regions of hilly terrain and toward the center of the island. The successful clans developed mainly in the escarpment region near the top of the island, in a zone Woodring (1958) shows as hard and slope-forming Bohio conglomerate. The flat top of the island, a basalt cap, has occasional pairs from the nearby escarpment zones but is not really good for Ocellated Antbirds. The flat Barbour Peninsula, which additionally is low woodland rather than tall forest, seems not to have the species. When ant colonies move that way or onto the peninsulas of Gigante Bay, the following Ocellated Antbirds soon return to colonies closer to the center of the island. Low woodland as such, however, is occupied if it occurs on varied terrain: the areas along Wheeler, Balboa, and Lathrop Trails on Barro Colorado Island; numerous areas on the Rio Agua Salud and the Navy Pipeline Road.

It so happens that most of the escarpment regions are toward the center of the island, so it is difficult to know if Ocellated Antbirds avoid peripheral zones and peninsulas or avoid flat areas. A slight tendency to avoid the flat basaltic cap at the center of the island and occasional following in steep zones right down to Wheeler Estero or to the laboratory clearing, however, suggest that the birds are not avoiding the edges of the island as much as they avoid terrain of low relief.

I am not sure if relief as such is important, except perhaps in providing a variety of habitats. Perhaps landslides and tree-fall zones along gullies, rapid release of minerals by erosion, and other aspects make an area of moderate relief more productive than a flat one (except a river floodplain, where deposits of eroded materials and periodic floods should also do so?). It seems to be a commonplace observation in tropical America that bird species diversities are higher in foothill zones than on the tropical plains. Ant-following birds reach their highest diversities in foothill zones, both in Panama and in the Colombian-Peruvian foothills of the Andes.

Even on small Barro Colorado Island there was a diversity gradient in professional ant followers between the escarpment zones and the flats. On the flats were mostly four generalized species—Plain-brown Woodcreepers, Spotted Antbirds, Bicolored Antbirds, and Gray-headed Tanagers—which also occurred (some in reduced numbers) in escarpment zones. On the escarpment, two large and dominant species—Ocellated Antbirds and Barred Woodcreepers—were added. In escarpment zones elsewhere in the Canal Zone, one adds also a very large species—Black-crowned Antpitta—and possibly three or four other species—Ruddy Woodcreepers, Rufous-vented Ground-Cuckoos, Barecrowned Antbirds, Immaculate Antbirds. The actual distributions of the last four species, however, require closer study.

The northern escarpment zones on Barro Colorado are mostly off my study area, but occasional visits to this zone suggest that only along Pearson Trail and southwest to the start of Standley Trail has there been a fairly high density of Ocellated Antbirds at times. The area never seems to have had as high a density of Ocellateds as the southern escarpment zone.

Population Densities.—Since there is a variable distribution of Ocellated Antbirds along the escarpment zones on Barro Colorado Island, it is difficult to calculate home ranges and population densities in any meaningful way. In the main study area, which included much of the flat basaltic cap of the island, the centers of home ranges of main pairs in 1961 were about 500 m apart. This would give about 250 hectares per main pair. Including birds of the previous year but not young of the year, there were in August of 1961 some 18 birds on the study area, or 7 per square kilometer. This is about 0.35 g per hectare, less than the 3 g per hectare of Bicolored Antbirds or the 7 g per hectare of Spotted Antbirds. In addition, Ocellated Antbirds are almost absent in the many flat areas off my study area, so that the total population on Barro Colorado Island in August, 1961, was probably only 45 birds (3 per square kilometer, or 0.15 g per hectare). By 1971 the population had decreased to 5 males and 1 female (Willis, MS), all in the escarpment zones; the species seems on its way to extinction on Barro Colorado Island.

Detailed Spatial Relationships—A Day at a Swarm of Ants

The "macrospatial" relationships of geographic

range, of habitat and niche, and of territoriality are reflected in but give only a frame for the picture of detailed relationships of distribution over swarms of ants, antagonistic or other interactions there, and of individual distances and the roles of males, females, and young birds competing with each other and with other species. Perhaps a description of part of a day at a swarm of ants will give a better picture of how the Ocellated Antbirds manage the complex spatial relationships of their lives:

The day is 23 August 1963, and a large nomadic colony of army ants is moving northward up the escarpment in tall forest just west of Drayton 4, an area so much in the center of Ocellated activity that I thought of it as "Ocellated Alley." It is a blue-and-white morning, with cumulus sailing through polygons of blue sky in the green ceiling of the canopy. It is still cool, but sunbeams probe downward from the polygons, for I am arriving late (8:56 AM) after an unsuccessful search for a lost colony of ants far to the northwest.

Loud *stiek!* alarm calls of a Plain-brown Woodcreeper mix with *stet* and *chip* alarms of a Gray-headed Tanager pair, then chirrs and *chip-ip!* of an Ocellated Antbird. The cause of the alarm is an agile little Semiplumbeous Hawk, bright white below, which flies from near the ants with a lizard (*Ameiva leptophrys*) in its talons.

Tame Bicolored Antbirds and Spotted Antbirds move out of my way with musical notes as I approach the ants, but the Ocellateds are still in a panic of chipping and tail-jerking. They hide well behind practically no ground vegetation except big trunks. The Ocellateds and other birds are long since used to me, for they scarcely chirred as I approached. A few weeks before my approach would have brought a storm of remonstrative chirring, but I have been following this colony for several weeks now.

As some seven Bicolored Antbirds move back in over the ants, a few of the Ocellateds present appear as if by magic. Male XR, the venerable boss of the clan, jerks his tail a little over the ants as his son of 1962, RSWR, faint-sings and wanders at the left end of the raid. Earlier this summer RSWR briefly had a mate, but she moved over to another male; he will not have another mate until next summer, when his first offspring will make this a three-generation clan. His mother, XGBR the mate of XR, is now near him at the left end. There are several other birds in the clan, probably other 1962 offspring of XR and XGBR, but most of them have not been around for several days. They must have found another colony of ants in the wide home range of the clan . The baby female of the clan, GOBW, is present but not evident at the moment; perhaps she is hiding in a tangle nearby. The daughter of XR and XGBR, she is now fed by them and by the amorous RSWR, who occasionally feeds his mother as well. However, GOBW will next year become the mate of YBXB, in the home range to the northeast, and over the next four years help him develop his clan; she will not associate with her parental clan again.

The Bicolored Antbirds occupy my attention for a long time, for the pair to the north is gradually becoming dominant over the pair to the south as the ants move north on two forks (Willis, 1967:98). I am only vaguely aware of the quietly foraging Ocellateds, mainly because they take the other fork of the swarm and force all the Bicoloreds to my fork and into disputes with each other.

Here comes female Ocellated XY, her head low and her whole posture humble, faint-singing. Her mate, YX, must be incubating this morning. Probably the clan of XR has chased her from the other fork of the swarm, for XY and her mate are subordinate. Three weeks ago, when the ant colony was statary off to the southwest, there were a few hours when it looked as if YX were dominant. He took silent and upright challenging poses, and XR and RSWR both moved out of the way humbly. The son of YX and his daughter-in-law were present then, for YX is the head of a superimposed clan. However, YX's glory did not last long; perhaps he was only dominant briefly because XR and his clan had been away the preceding few days.

The son and daughter-in-law of YX were having troubles; the son challenged but his mate was bunching up to and nibbling at him, as they faced but gradually retreated before even the young members of the other clan. This forced them next to YX, who was none too friendly; his son had to cringe and whine a little, and even so moved out of YX's way. RSWR came up and supplanted YX's son, who moved near YX again; RSWR challenged a little and moved off. Fifteen minutes later RSWR

was back, supplanting YX's daughter-in-law. Then XR joined RSWR in challenges to YX and his cringing son. YX's challenging was weak, and he faced XR rather than pointing the beak at him; XR supplanted him. YX could not even displace his own son a minute later; his son gaped, almost swallowing his head, and YX chirred in annoyance before flying off. A rain started YX and his mate to wandering, loud-singing, as the other clan took the few active sites of the ants. YX and XY took a left fork of the swarm, supplanting the female of yet another pair (10 Ocellateds were present in all). The next day YX was dominant again, but XR and RSWR took over again late in the day. The following day YX's son and daughter-in-law disappeared, and have not been around since. Probably they are at another ant colony, for in 1964 the mateless son will turn up with YX and his mate, and the three will clash with XR's clan much as they are doing this year.

For the last several days, YX and XY have been subordinate. YX can supplant most of the young males of the other clan, except RSWR when backed up by XR. The young males of the other clan, other than RSWR, however, deserted this colony a week or two ago. YX can supplant the female and young female of the other clan, and XY can supplant the young female, but this seldom helps much because the opposing females immediately bunch together with the males of their clan. So, today, XY moves near me and supplants a Bicolored Antbird, taking the center of this fork of the swarm. Other Bicolors quickly spiral in, however, and female XY has to grunt frantically and point her beak repeatedly to keep the barbarian horde out of her foraging zone. Perhaps hearing the sounds, in comes male RSWR and supplants her with a ferocious whirr of wings and snapping of the beak. She slinks off, in a very low cringing posture. XR and the baby female GOBW arrive. The baby is peeping persistently as she follows her father. He supplants XY again, and then feeds his own mate despite the frantic begging of the baby. RSWR feeds his mother. The four birds of the clan take a circle 2 m in diameter over the ants, and female XY wanders peripherally. RSWR displaces her once, but she mostly stays more than 2 m from the active clan. XR ignores her, as he usually does. Is she perhaps a daughter of his? I banded her, him, and YX together in one net nearly three years ago. But perhaps they have just seen each other often over the years.

The Ocellateds of the clan grunt at a brave male Spotted Antbird that briefly infiltrates their ranks, snaps up a small insect, and flees. All ignore an agouti wandering through. The alarm notes of a Black-chested Puffbird cause crouching and keening among the circling ring of Bicolored Antbirds, and a Rufous Motmot over the assemblage freezes bolt upright. There are occasional sounds of the large Barred Woodcreepers high near the Puffbird; the only two pairs of Barreds on Barro Colorado are feeding at this swarm today, but are working high probes of ants rather than coming low and ousting the Ocellateds and Bicolors as they sometimes do. The Gray-headed Tanagers are not challenging the five Ocellateds and seven Bicolors either, and like the two Plain-brown Woodcreepers are staying high. By the end of observations at 2:23 PM, I will have seen 29 birds of 9 species at this swarm, including a Slaty Antshrike briefly present. The Puffbird continues alarm notes. Is the Semiplumbeous Hawk back? With faint-songs, one of the Ocellateds lures the baby female into a thicket off left. I have not seen her fed today, but she is at the stage when she is still fed most of her food.

It is 10:00 AM, and male XR preens over the ants even as he grunts at the circling and bickering Bicolors. He flies over and feeds his mate, caroling briefly, then returns to the ants. She preens. They are probably getting ready to nest again. The Tanagers give up and leave; perhaps there are too many Bicolors and Ocellateds near the ground, and too few ant probes up trees. A Plain-brown Woodcreeper works the left fork, but its *stiek!* calls on my approach cause keening among the Bicolors and chipping from the Ocellateds, which vanish into cover. I watch Bicolor disputes for 30 minutes. When a band of white-faced monkeys on the ground ahead races up into the trees, an Ocellated chirrs loudly. It is sitting, resting, but jerks its tail upward. I watch a dispute between the Barred Woodcreepers overhead. The Tanagers left too early, for Plain-brown and Barred Woodcreepers are at an active ant probe up a tree trunk now. The Barreds supplant Plain-browns now and then as the battle moves back and forth. Rains inter-

rupt observations for an hour. I watch Bicolors after a *stiek!* outburst of Plain-browns sends the Ocellated clan to a thicket ahead, where four birds a meter apart panic in concert—tails are jerking up, stuttering chips and occasional chirrs burst out, and birds turn their heads sharply.

At 12:00 M here is male Ocellated YX with his mate. Rains interfere with my observations, but he seems to be foraging as busily as he can to make up for a morning of no food. His female disappears soon, probably to the nest. He supplants several Bicolors, seeming to head for them right away as if he knows a Bicolor will be in the best available position for foraging. He is at the right fork of the ant swarm, alone except for fighting Barreds and Bicolors. I check the left fork before I leave and find the other Ocellated group there. The female is resting in a vine tangle ahead of the ants as her son and husband work. The baby female is not visible. There is no sign of birds when I return at 5:30 PM to check the ant colony, but everybody except male YX is present the next morning at 8:20.

It was not an unusually exciting day for Ocellateds over the ants; in fact, most of my notes for the day had to do with the fights among Bicolors and Barreds. There were only five Ocellateds present much of the time, and only two pairs. However, several kinds of spatial distribution can be seen from the account: the main clan ousting the lone female of a superimposed clan; the later separation of the lone female and her mate at another fork of the ants; the aggressive role of the young male of the clan, and his probably sexual feeding of his mother and of his baby sister; the slowing of feeding after about 10:00 AM for members of the dominant clan, etc. It is a complex society, but knowledge of individual life histories explains many of the spatial arrangements one sees at a given ant colony.

Discussion

The life of the dominant antbirds at swarms of army ants on Barro Colorado Island is plainly not simple, but neither is it a bed of thorns. Ocellated ability to supplant most small antbirds keeps them out of competition, even if they are a constant nuisance—especially the abundant and persistent Bicolored Antbirds. Most large birds, such as motmots, Squirrel Cuckoos, and Barred Woodcreepers, are not suited for foraging on vertical perches near the ground like an antbird and are only sporadically troublesome to Ocellated Antbirds. As noted earlier (Willis, 1972a), the Ocellated Antbirds are usually able to take the front, low, and central zones where ants flush most prey and relegate Bicolored and Spotted Antbirds to concentric or peripheral zones. In the central zone, Ocellateds forage mostly in one simple way (sallying to the ground) that requires little maturation or practice—young birds soon forage for themselves.

The problems for foraging Ocellated Antbirds seem to come with intraspecific interactions and with other environmental restrictions. While there were a few pairs of Ocellateds in many parts of Barro Colorado, the birds concentrate mainly over the largest ant raids in the central escarpment zone—"Ocellated Alley." In this region, there were not only pairs or clans, but superimposed pairs and clans. As many as 10 or 12 birds were at some swarms of ants, and three pairs were commonly represented at a good ant colony even though four pairs rarely coexisted. Such concentrations have been noted rather often elsewhere in Panama and Colombia and probably have the same social organization.

At such swarms, intraspecific dominance hierarchies come into effect and seem to force out low-ranking birds—both in clans and outside clans. These low-ranking birds then must move to distant colonies, probably at some personal risk both from waiting predators and of loss of time and food. When a swarm varies in flushing power from day to day, the low-ranking birds probably have to move away from and to it repeatedly.

Probably the complicated social structure and submissive behavior of Ocellated Antbirds allow them to avoid some of the risks when subordinate birds have to move while yet insuring that they do move if a given swarm gets too crowded. The clan formation clearly could act as "kin selection," in the sense of Hamilton (1963), by favoring the offspring of a dominant pair. Instead of young being tossed out of the parental sphere to fend for themselves, they are tolerated for years (a bit churlishly if competition is rough). Young males stay with the parents and sometimes are waiting to take over that area when the old male dies.

They are far higher in the local hierarchy than they would be outside the protective influence of their fathers; even when he is subordinate they can stay near him and yell in his ear if he gets churlish. Of course, they often drop out and go to another swarm if the local competition gets really strong. In a few cases, the young males actually feed young birds of later broods.

Young females stay with their parents much of the time and are thus protected for several months after they begin to forage for themselves, rather than being at the bottom of peck orders for these months as in Bicolored and Spotted Antbirds. Survivorship of young female Ocellateds is higher (about 60 percent) than for young female Spotteds and Bicolors (40–45 percent—Willis, MS). The time between a young female's leaving her parents and her finding a suitable mate to protect her may be very short—a few days in the one case observed. In 1961, there was not the surplus of unmated male Ocellateds there has been in subsequent years; one female (XGBR) that lost her mate actually waited until January, 1962, to get a new one after the disappearance of his female. However, even under such circumstances a young female could probably stay with her parents for long periods. She could wander out periodically to check for males or to listen for the persistent loud-singing of one that had lost his mate.

Ocellated Antbirds have a complex submissive behavior and a simple aggressive one; Bicolored Antbirds tend the other way but have much aggression. Spotted Antbirds have practically no submissive behavior and have well developed and distinctive aggressive displays that they seldom need to use, for they drive out most intruders. Since Spotted Antbirds are less adapted to ant following and close meeting of individual birds than are Bicolored Antbirds, and the latter less well adapted to following and social life than Ocellated Antbirds, it is possible that this is an evolutionary sequence. The sequence starts with territorial birds that have aggressive behavior well developed; the aggression increases spectacularly as birds crowd together over ants; but more crowded birds replace aggression with submissive hierarchies. In other words, increased crowding beyond a point leads not to increased aggression but to the increased submission seen in Ocellated Antbirds.

Southwick (1970:5) notes similar increases and then decreases in aggression with mice and rats under increasing crowding; but in mice and rats the very overcrowded animals seem to become passive rather than react with increased submissive behavior. Perhaps passivity is not desirable for Ocellated Antbirds, which still have dominance hierarchies and a fair amount of aggressive behavior. Unlike fed rodents in cages, the Ocellateds must still forage for their own food near domineering other individuals.

Another way to describe the change is in terms of "overpopulation," which increases in the sequence from Spotted to Bicolored to Ocellated Antbirds. It may seem odd to talk about overpopulation for a bird that is so rare in tropical forests as the Ocellated Antbird; but it may tend toward overpopulation in concentrating over an extremely limited food resource. The evolutionary result of overpopulation and high interaction rates of competing individuals over army ants is at first increased aggression, as in Bicolored Antbirds. Later, the agonistic interactions decrease or become submissive ones. The possible evolutionary sequence, and even more the experimental one in rats and mice, suggest that overpopulated humans could go this way too: territorial, then highly aggressive, and finally submissive or passive to their local dictators or "main pairs." This might be especially likely where there are space limitations, as over army ants. Other types of social organizations, such as herds or flocks, seem not to develop such systems; or perhaps such organizations are the stage beyond the Ocellated stage.

The great development of submissive behavior in Ocellated Antbirds, and the slight development of aggressive behavior, probably facilitates clan formation as well as aggregation of unrelated birds. As a member of a dominant species, dependent on rich front and center places at ant swarms, the dominant individual Ocellated Antbird probably does not need very much intraspecific aggression to keep the small place it needs, at the center. However, the center is a small area, and the subordinate bird that stays nearby must confront the dominant one quite closely. In these circumstances, submissive behavior would be quite valuable—hence its hypertrophy. The hypertrophy would especially favor related animals, ones that

stay close to the dominant individual. The kin selection made possible by this is actually an advantage to the dominant individual, since his relatives are more likely to succeed.

Submissive behavior is also useful to female Ocellated Antbirds. They are smaller than males and never win direct contests. By bunching up with their sons or mates or parents, they can avoid extreme defeat. If no protecting bird is around, they can whine and be submissive and stay until the mate arrives from his tour of duty on the nest. Females, in contrast to young males, seldom deserted a swarm due to competition unless their mates or clans also did so.

It is difficult to know why female Ocellated Antbirds should be smaller and less dominant than males, unless this keeps them out of disputes or helps population control in the way suggested by Wynne-Edwards (1962). Female survival is poorer than male survival (Willis, MS). Perhaps the low status of females in peck orders insures that any excess females without mates will tend to die off rapidly and not use up food supplies. It may be better in a monogamous species to have a small surplus of males rather than of females, for a female that is not breeding is gaining only a little foraging experience while a male that is not breeding may be gaining status as well. Perhaps, however, the small female is better when the male has to feed her, using up less food. It may also be that the females use slightly smaller food than do males; but males and females often went for the same prey, and bill lengths seem similar. Could the male recognize the female by her small size, as Jehl (1970) suggested for sandpipers? In the declining populations of 1966 to 1971, males sometimes fed other males as if they did not recognize sex; recognition of sex seemed to be based on the fact that females accept food readily as adults, while males do so only as young birds. Male–male feedings were confused, for the fed male tried to give the food back.

The overlapping of home ranges in Ocellated Antbirds, and the presence of superimposed pairs and clans, is an overpopulation problem that goes beyond kin selection and clan formation. It seems that it was better for pairs of Ocellateds to stay in the escarpment zone on Barro Colorado, even though this meant they often had to compete with dominant pairs or clans not closely related to them. (Of course, all the 45 or fewer Ocellateds on Barro Colorado must have had many genes in common.) They did this rather than move onto flat areas like Barbour Point, where students and I saw many ant swarms but never saw Ocellated Antbirds. Given that a pair needs a wide foraging area to be certain of having a swarm of ants to follow each day, this makes it necessary to have superimposed pairs or else a system of dominance like that in Bicolored Antbirds (Willis, 1967:110) in order to get more than a few pairs of Ocellateds in the small escarpment zone on Barro Colorado. The dominance system of Bicolored Antbirds requires a great expenditure of aggressive energy, which may be too difficult when a territory would have to be four times as large as that of Bicolored Antbirds. Thus, given a habitat restriction and the need for a very large foraging range, it uses much less energy to be subordinate more or less everywhere (i.e., be a superimposed pair) rather than try to keep up a dominance area that may not have any ants on it much of the time.

The basic question then becomes, why are Ocellated Antbirds restricted to escarpment zones when the ants go all over Barro Colorado Island? MacArthur, Recher, and Cody (1966) speculated that restriction of birds to certain patches in seemingly homogeneous habitat, or rather the subdividing of a habitat into suitable patches on the basis of very small differences, is likely to be common in the species-rich tropical avifaunas; however, many antbirds do not show this pattern. Neither Bicolored nor Spotted Antbirds show this pattern to any great extent, except for some avoidance of precipitous slopes in the canyon west of Balboa Trail. Ocellated Antbirds, however, do show this pattern. They are almost as tied to certain areas on Barro Colorado as are motmots (*Electron platyrinchum* and *Baryphthengus ruficapillus*), which nest only in steep-sided gullies and hence are mostly in regions of gullies.

Are Ocellated Antbirds restricted by their nest sites? Since the nest has not been definitely discovered, there is a slight possibility that they may nest deep within motmot burrows or in fallen logs across gullies. However, I have never seen a mud-stained Ocellated, nor seen them show any interest in old logs. The two likely nests, and the pattern

of nest-searching, suggest that they nest between tree buttresses where lianas cross to give some protection. These sites are most common in areas of moderate slopes, since buttresses tend to protect trees against windthrow where the soil is shallow or wet (as by springs, which emerge on slopes) and where trees are exposed to the wind. Cativo-espavé forests (*Prioria copaifera—Anacardium excelsum*), such as the flats near Armour 10 and the flats near Wheeler 25, have few buttressed trees and seldom attract Ocellated Antbirds. Moreover, trees do not often fall in these areas and bring down lianas across the bases of other trees; the forest has a tall and virgin aspect compared to the rather sloppy and undisciplined look of forests in Ocellated Alley.

There are certainly some buttressed trees and liana crossings, however, even in flat areas of Barro Colorado Island. Moreover, small numbers of Ocellated Antbirds do use most such areas. I have noted the "undisciplined look" of forests in Ocellated Alley. These zones on Barro Colorado are very diverse, with patches of windthrown trees, of old forests and young, of rotting logs, of diverse slopes and rapid erosion, of springs and seepages, and a wide variety of other microhabitats one does not find in the rather monotonous flat zones. Is the very diversity of such zones, or some other factor, leading to greater food supplies or cover for Ocellateds in these zones?

At the moment, I can only suggest some differences that may be important to foraging Ocellated Antbirds between the regions where they are common and the regions where they are not. The zones where they are uncommon tend to be peninsular, peripheral, flat, and young forest; these forests have a strong dry season, abrupt leaf fall, and little leaf litter in the rainy season; these forests have few fallen trees and hence relatively open undergrowth; and these forests may have less light and release of soil nutrients than do slope forests.

Peninsulas should impede the free movement of army ant raids, which tend to reflect back and forth within a small peninsula and to repeatedly rework areas already passed over. I followed one ant colony for several months in the peninsulas of Gigante Bay, and found Ocellated Antbirds at the colony only at the start of its odyssey there. Although a pair of Ocellateds worked the base of the peninsula on Lathrop Trail and others worked the base of the Barbour Peninsula, we never found Ocellateds far out these peninsulas.

Simpson (1964) pointed out the "peninsula effect" for faunas of mammals, and it is well known for birds. This is the lowering of numbers of land species breeding in such areas as Florida, and is a subset related to the "island effect" of isolating a fauna or flora on an island—the smaller the island, the fewer the species that survive there (Preston, 1962). A peninsula or island is somewhat or completely isolated, and hence gets new animals of some species too slowly to keep up with total losses, especially if there are periodic habitat changes that prevent the animals from surviving on the peninsula or island indefinitely. Florida thus lacks tropical birds that it would have if it were connected to Central America, for periodic cold waves or effects of glaciation have eliminated many tropical species with little or slow replacement. Some introduced tropical species, such as Red-whiskered Bulbuls (*Pycnonotus jocosus*), Blue-gray Tanagers (*Thraupis episcopus*), and Spotted-breasted Orioles (*Icterus pectoralis*), are doing well and increasing the diversity.

In the context of Barro Colorado, the impeding of movement of army ants and the possibility that very long periods may be without ants—followed by periods of overworking when colonies do happen to enter the peninsula—may represent a "peninsula effect" like that of south Florida. Spotted Antbirds are on the peninsulas, but can forage away from army ants for long periods if necessary (Willis, 1972a). Bicolored Antbirds are also on the peninsulas occasionally (Willis, 1967), but have smaller foraging ranges than do Ocellated Antbirds and presumably can survive on smaller ant colonies or on ones that flush little food.

Ocellated Antbirds, however, live on the rather narrow Bohio Peninsula near Barro Colorado. Moreover, the eastern part of Barro Colorado, out to Barbour Point, forms a huge peninsula that is wide enough to support several pairs of Ocellated Antbirds. That it does not suggests that there are other things wrong with the peripheral areas on Barro Colorado than simple impediments to ant movement. Peripherality as such does not seem likely to cause problems, except perhaps for lake-breeding mosquitoes and for the fact that isolated

points on Barro Colorado are swept by the drying northeast trade winds in the dry season.

Mosquitoes carried fowl pox and avian malaria to Hawaiian birds, virtually eliminating them in the lowlands and leaving them only in the uplands (Warner, 1968). The mosquito *Anopheles albimanus* has become a real pest along the borders of the lake on Barro Colorado in the years 1965–1971, probably because the lake since 1964 has been stabilized rather than low in the dry season, which has permitted an explosive growth of the water weeds (*Hydrella* species) in which the mosquito breeds. The decrease in Ocellated Antbirds has mainly come in the 1965 to 1971 period. The loss has been characterized by high losses of females, which incubate long periods at night and afternoon rains, and probably do so between tree buttresses. I have found *A. albimanus* unusually common in such sites during rains and even at other times. These events, however, may be coincidental. Ocellated Antbirds have not shown signs of bird pox, except for occasional loss of the tips of toes, nor have I seen any listless as if malaria-infected or arbovirus-infected. They should have defenses against these diseases and against mosquitoes, probably including sleeping with the head in the fluffed back feathers as do other antbirds. Antbirds are probably not like the Hawaiian birds, which had never encountered mosquitoes before *Culex pipiens fatigans* was introduced in 1826, and hence had no behavioral or immunological defenses. Moreover, Ocellated Antbirds occur just across Gatun Lake on the Rio Agua Salud, where there should be many *Anopheles albimanus* (there certainly are plenty at nearby Frijoles). Thus, mosquitoes and diseases along the lake shore seem possible but unproved as reasons for the tendency of Ocellateds to favor upland zones on Barro Colorado Island.

The effect of the trade winds seems a possible reason for the seeming tendency of Ocellateds to concentrate on the south side of the island's hills, particularly in the sheltered upper parts of south-facing ravines from Shannon Trail across Drayton Trail. Although some birds were in the corresponding north-facing escarpment over the years, it was never an Ocellated Alley like the southeast side of the hill. The trade winds strike isolated points, such as the tips of Barbour Point, the tops of ridges, and northeast slopes of the island, with more vigor than one would suppose on reading how little wind there supposedly is in the tropical forest undergrowth. The most obvious effect is to dry out and crack the soil and leaves of the leaf litter, but there are probably effects on tree types and deciduousness as well. Such periodically dry zones perhaps produce fewer prey items for the ants and birds than do more protected zones. Sunlight and occasional wind would have the same effects on nearly all shores of the island, but especially on the northeast side.

The trade winds may also eliminate trees that are not resistant to being blown over, and thus eliminate one source of diversity in tree species and in undergrowth patchiness. Periodically, windstorms come up from the southeast and topple trees right and left on that side of the island. On 1 October 1961 a storm did so and created many treefall tangles that are just now growing up. Dennis Knight (pers. comm.) talked to an old resident of Barro Colorado who says that many of the trees of Barbour Point were leveled in a windstorm about 1919. Certainly Barbour Point is rather low forest today, and this may be one reason that Ocellated Antbirds do not occur there.

Ocellateds, however, seem to do well in equally low forest on Balboa Trail and across Shannon Trail. It seems doubtful that Ocellated Antbirds are restricted to tall forest. Much of the eastern half of the island is low forest and much of the western is tall forest (Bennett, 1963); but Ocellated Alley cuts almost perpendicularly across the boundary between tall and low forest. In the Pipeline Road Reservation, Ocellateds do well in low forest as well as high.

Low forest, however, may exacerbate problems of trade winds and dry seasons. I sampled leaf litter for insects from February to November, 1961, and found that areas of low forest tend to drop their leaves rapidly in the dry season, have a spectacular bloom of leaf-litter feeders as soon as the rainy season moistens the dry litter, then be rather bare-floored much of the rest of the rainy season (Willis, MS). Taller forests, especially on protected southern slopes, tend to drop their leaves more evenly through the year and to have arthropods more evenly throughout the year. Low forests are certainly "lighter forests" (Eisenmann, 1952) much

of the dry season, for they tend to lose more leaves and to be hot, dry, and light underneath. Unfortunately, I did not check leaf-litter insects in low forests on the side of Barro Colorado away from the trade winds to see whether such forests have less periodicity in leaf fall than do the exposed low forests I did check.

Low forest, especially in trade-wind zones, has other characteristics that may disturb Ocellated Antbirds. (Low forest on Barro Colorado Island is 50 to 100 years old and is 20–30 m in height, I hasten to add.) This forest tends to be very open underneath, with new fallen trees or tangles around former fallen trees. There is little cover, and Ocellated Antbirds seem very nervous when working in such areas. There is little ground cover from small seedlings or saplings, and only large patches of wild pineapples (*Ananas magdalenae*) where there is impeded drainage. Areas of impeded drainage and seeps occur, naturally, farther up toward escarpments in the areas where local landslides and windthrow also cause clutter in the undergrowth. Flat areas tend not to have this clutter. The clutter, besides providing cover for Ocellated Antbirds, may provide their prey with more food. So, the Ocellateds may have several reasons to avoid a flat, windswept, low-forested peninsula like Barbour Point.

Among other possible reasons for Ocellated Alley, drainage and soil and erosion may play a part. Flat areas tend to get sheets of water during extended rainstorms, and such sheets may carry off the leaf litter or drown some arthropods in it. The army ants are also interrupted or drowned. The sheet erosion probably carries off soil nutrients, too. Areas of greater slope tend to have crossing roots, buttresses, logs, and other clutter that keep the particulate matter back while allowing the water to run off quickly in natural gullies. Perhaps the impeded runoff and spring-emergent erosion one gets on slopes also releases nutrients to plants more quickly than in flat areas, resulting in greater productivity. (Flat areas along rivers are almost lacking on Barro Colorado; it is just a hilltop. The eroded materials go to fill up Gatun Lake only.) One also has to keep in mind that the steeper slopes on Barro Colorado are mostly Bohio conglomerate, while the flat basaltic cap and the flat peninsula of Barbour Point have different and perhaps better weathering and mineral characteristics. However, Ocellated Antbirds do not seem to do well in Bohio conglomerate on the low-forested, hilly, and narrow peninsulas of the northeast and windy side of the island.

In conclusion, likely reasons for high abundance of Ocellated Antbirds in the southeast escarpment zone on Barro Colorado are the absence there of drying effects of northeast trade winds on the leaf litter, the moderate clutter of the undergrowth in a steep and rarely windswept zone, and perhaps greater productivity of plants, leaf litter arthropods, and army ant colonies in a complex but not peninsular or isolated region. Mosquitoes from the lake may keep Ocellateds from peripheral areas, too.

That Ocellated Antbirds, dominant birds at the swarms, are so much more restricted to the "best" zones on Barro Colorado than are birds low on the interspecific peck order over ants, like Bicolored and Spotted Antbirds, is perhaps not surprising. Ocellateds are specialists, which because of their dominance never have to forage away from the central and best zones over army ants or forage in many different ways. They are not generalists and probably cannot take even a moderate deviation from optimum foraging conditions. Bicolored and Spotted Antbirds can use optimum foraging conditions, but most use less optimum conditions whenever Ocellated Antbirds are present. Bicolored and Spotted antbirds are probably able to use zones in which not another species but an unfavorable environment creates the suboptimum conditions.

Moreover, Ocellated Antbirds are large birds that require more food per unit time than do small birds, much as large Zebras (*Equus hemionus*) on the African plains (Bell, 1971) require more abundant foods than do small Thompson's Gazelles (*Gazella thomsoni*). Probably the Ocellateds must stay in zones where the ants flush food consistently rapidly, while Bicolors and Spotteds can persist even when ants flush little food. Size, while it gives dominance, probably forces animals like Zebras and Ocellated Antbirds to occur in low densities or stay in zones where food is very abundant. If there is indeed more food in Ocellated Alley, it would support large birds, and this would explain why the largest ant followers on Barro Colorado—

Barred Woodcreepers and Ocellated Antbirds—persisted on the alley into the 1960s. The disappearance of large species of ant-following birds during the 1960s and before (in the case of Rufous-vented Ground-Cuckoos) suggests that either the food supply of the escarpment is no longer sufficient or that predation is too severe (Willis, MS). In either case, dominance and specialization clearly carry risks as well as advantages, for the large and dominant ant-following birds have been the first to disappear.

Dominance over other species and the moderate demands of an environment that fluctuates considerably seem possible reasons why Ocellated Antbirds have developed a social system like that of chimpanzees. Dominant species can group without attracting dominant competitors. If they are occasionally in an environment that makes grouping valuable, such as a group of fruiting trees for chimpanzees or a good ant colony for the antbirds, they will develop grouping tendencies. If, however, the environment forces the animals apart at other times, they will form loose or facultative groups. Mexican Jays (Brown, 1963) probably can form regular groups because the environment never gets bad enough to force birds off their territories, even though groups are necessary so that a large enough area can be occupied to include suitable winter as well as summer habitats. If the environmental fluctuations are slightly greater than for Mexican Jays, the Ocellated or chimpanzee social structure preserves some kin advantage while permitting grouping. If even greater animal movement is needed, in a more fluctuating environment, it becomes valuable to separate up or to join huge herds, as in Hamadryas baboons (Crook, 1970) or budgerigars (Brereton, 1971). Such anonymous flocks (Lorenz, 1963) are social in terms of numbers but lack rich communication and internal structure. Thus, an occasionally rich environment seems to lead to the mixture of kinship groupings and isolated movement in chimpanzees and Ocellated Antbirds.

Ocellated Antbirds resemble chimpanzees in having a highly developed system of calls and displays, with an emphasis on submissive behavior. It may be that the complex communication developed in a loose clan system was a starting point for human language. Anthropologists have until recently assumed that humans developed mainly as group-territorial animals like baboons. However, baboons (DeVore and Hall, 1965) and gorillas (Schaller, 1963), seem relatively uncommunicative in their groups; one wonders why language would develop in such a system. Struhsaker's (1967) list of the number of calls for various primates suggests that forest and savannah species, mostly grouping or territorial species, have fewer calls than do the less tightly knit groups of the forest edge (chimpanzees, vervets, *Macaca fuscata*); open-country species have especially few calls. Brereton (1971) reports similar trends for Australian parrots. It may be that the grouping species have more mimicry or graded calls, and hence have a more complex communicatory system than their low number of discrete calls would suggest. However, graded calls occur among the clan-forming species as well; the songs and the submissive calls of Ocellated Antbirds are examples of graded calls. If human language arose from graded calls (Marler, 1965), more study of open-country animals is needed to see if their vocal repertoires include more graded calls and more complex ones than are found in such animals as chimpanzees. Since humans probably started hunting in forest-edge situations rather than in direct competition with the hyenas, lions, and hunting dogs of open country, a chimpanzee-like social structure seems more likely than a troop structure; the lack of vocal communication of open-living groups is another argument in favor of clans. Possibly human language arose as submissive or socially facilitory calls, rather than as aggressive calls or play calls as had been suggested by earlier primatological work.

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