POPULATIONS AND LOCAL EXTINCTIONS OF BIRDS ON BARRO COLORADO ISLAND, PANAMÁ[1]

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Abstract. A 1960–71 study of populations of color-banded ant-following antbirds of three species on a tropical-forested lowland reserve, Barro Colorado Island, showed that the small species (Spotted Antbird, *Hylophylax naevioides*) remained stable at about 20 pairs/km². A medium-sized species, the Bicolored Antbird (*Gymnopithys bicolor*), decreased from about 3 pairs to 1.5 pairs/km². A large species, the Ocellated Antbird (*Phaenostictus mcleannani*), declined from 1.5 pairs/km² to near extinction—only one female remained in early 1971. Two of three other species that regularly follow army ants showed relatively stable populations, but a third large species (Barred Woodcreeper, *Dendrocolaptes certhia*) declined from two pairs to local extinction. Prior to 1960 a very large ground-cuckoo that follows ants had already become extinct there. Thus, the three largest of the seven original species that regularly followed ants were gone or nearly gone by 1970. The decrease in numbers of regular ant-following birds was not made up by increases in occasional followers.

Detailed studies of antbirds showed no clear reasons for declines, except that annual mortalities of adults were high in Ocellated Antbirds (about 30%) compared to Spotted Antbirds (15%–17%) and nest losses perhaps higher in the former (96% compared to 91%). Nest mortalities were slightly lower (88%) and adult mortalities intermediate (about 25%) in Bicolored Antbirds. Female Ocellated Antbirds had higher mortalities than males. The antbirds renest repeatedly during long nesting seasons, up to 14 times per year for Ocellated Antbirds. However, to replace females of this species under Barro Colorado conditions 19 nestings per year would be needed.

Concurrent listing of all birds of the island showed that 45 species of breeding birds, 22% of the avifauna present when the island was made a reserve, had disappeared by 1970. No new species replaced them. Of the lost species 13 are forest birds, in danger if forests are cut elsewhere. The other species, second-growth and forest-edge birds, have been crowded out by growth of the forest.

Loss of species from this tropical reserve, especially the part apparently caused by the small size and isolation of the reserve, poses problems for conservation and ecological studies of tropical biotas. It is suggested that large future reserves have corridor zones to each other, that is, that intensive human use not preempt too much area nor interrupt immigration of animals or plants from one refuge to another.

Key words: Antbirds; conservation; dispersal; extinctions; forests; islands; mortality; natality; parks; populations; tropics.

INTRODUCTION

The dynamics of bird populations of tropical forests are of considerable theoretical and practical interest. High nest-mortality rates (Ricklefs 1969) suggest high adult survival, which could mean emphasis on "*K*-selection," the perfection of adult longevity even at the expense of low reproductive rates. Sensitivity of birds to human or other disturbance of the tropical ecosystem also depends on population characteristics. The dynamics of bird populations also help determine persistence and rates of spread of arboviruses like Venezuelan equine encephalomyelitis (M. Gochfeld, *pers. comm.*).

The population dynamics of tropical birds are little known. Snow (1962*a*) found in Trinidad a low mortality rate, about 11% per year, in 38 adult male White-bearded Manakins (*Manacus manacus*), a species of second growth. He estimated indirectly a similar mortality rate for the Golden-headed Manakin (*Pipra erythrocephala*), a Trinidadian forest bird. By contrast, Morel (1964) found high adult mortality in the Firefinch (*Lagonosticta senegala*), a bird of open country. Fogden (1972) estimated 10% mortality per year for a few individuals of many forest species on Sarawak, an island with few predators on adult birds.

Local extinctions of tropical birds have also had little study. The disastrous extinctions of native Hawaiian birds (Berger 1970) have started studies by the U.S. Fish and Wildlife Service, but detailed population studies have not yet been made. MacArthur and Wilson (1967) suggest that patterns of species diversity on islands are explainable as equilibria between immigration and extinction rates. Diamond (1971) found a loss and gain of at least one species per 3 yr on Karkar, an island off New Guinea; the rate was roughly the same as on Santa Cruz Island

[1] Manuscript received October 8, 1972; accepted August 15, 1973.

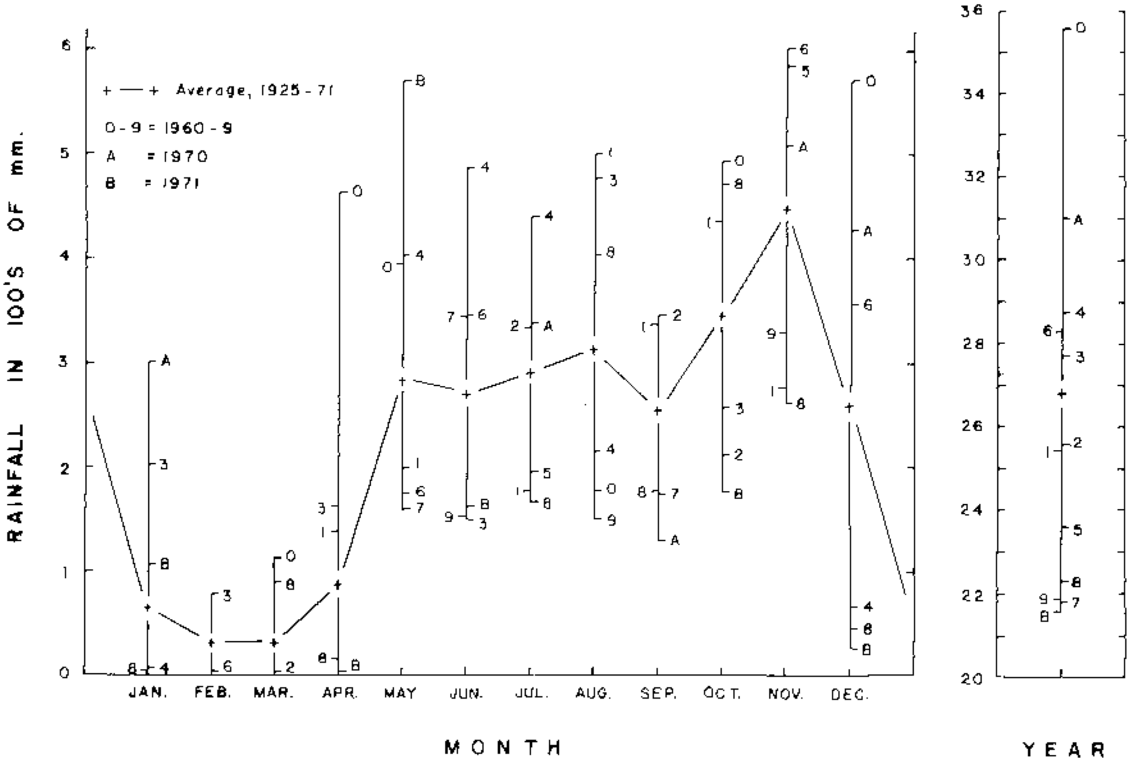

FIG. 1. Average rainfall on Barro Colorado Island, 1925–71, and variability 1960–71. Monthly rainfall is indicated only for extreme years. Absolute variability of rainfall is highest in rainy months, but especially in April–May and December–January; the rainy season can thus vary in length from 9 months (1960, 1970–71) to 7 months (1968, 1971). The only year with 6 months well below normal is 1968; 1969 is the only year with no month well above normal.

off California. He also suggests (Diamond, *pers. comm.*) high losses of "land-bridge" birds on other islands near New Guinea in the millennia since they were connected to it in the last glacial period.

Three species of birds that follow army ants (*Eciton burchelli* and *Labidus praedator*) in the lowland forest reserve of Barro Colorado Island, Panamá Canal Zone, are easily captured, marked, and resighted (Willis 1967, 1972*a*, 1973*a*): Spotted Antbirds (*Hylophylax naevioides*), Bicolored Antbirds (*Gymnopithys bicolor*), and Ocellated Antbirds (*Phaenostictus mcleannani*). Three other species regularly follow army ants, but are less easily captured: Gray-headed Tanagers (*Eucometis penicillata*), Plain-brown Woodcreepers (*Dendrocincla fuliginosa*), and Barred Woodcreepers (*Dendrocolaptes certhia*). In 1960–61 I studied the annual cycles of these birds. From 1961 to 1970 I returned for a few months each year to do a 10-yr study of their population dynamics. I concentrated on the three species of antbirds in a study area at the center of the island. In December, January, 1970–71, five college students helped search all of Barro Colorado for birds. During each study period I listed birds of other species seen. Other ornithologists visiting the island also recorded presence or absence of birds. This report gives the results of the 10-yr study and the final census.

METHODS OF STUDY

Birds captured in mist nets were marked with individual combinations of colored celluloid legbands. The bands were read through binoculars thereafter, except for occasional individuals recaptured in nets. I tried to avoid recapturing birds, for about one bird in 200 breaks its leg or wing in nets. Even though most of these few birds recovered rapidly and survived well, a few were not seen again. These individuals are not counted in the analyses of population dynamics. Band loss was rare, and birds were marked with two or four bands so that loss of a band or two was easily detected. The birds pecked at bands for a few minutes after being released, but seemed undisturbed by them thereafter. I saw no evidence that any birds developed foot trouble because of bands, although there were a few cases of loss of foot or broken leg for unknown reasons; foot, leg, and also wing problems have occurred in unbanded birds. Such birds, banded or not, sometimes survived years afterward.

TABLE 1. Professional ant-followers of Barro Colorado Island

Species	Weight in grams	Dominance	Foraging height	Habitat
Rufous-vented Ground-Cuckoo	350(?)	1	Ground	[a]
Barred Woodcreeper	65	2	High[b]	Escarpment
Ocellated Antbird	50	3	Low	Escarpment
Plain-brown Woodcreeper	40	4	High[b]	General
Bicolored Antbird	32	4	Low	General
Gray-headed Tanager	30	5	High[b]	Flats
Spotted Antbird	18	6	Low	General

[a] Extirpated by 1960.
[b] These species move down at times, especially if larger birds are not present (Willis 1966).

STUDY AREA AND CLIMATE

The main study area on Barro Colorado Island included approximately the central 4 km^2 of the island (Willis 1967: Fig. 3) and sampled most of the vegetational and geological zones. Barro Colorado (9° 09′ N, 79° 51′ W) is a 15.6-km^2 hilltop of lowland evergreen forest. It was separated from nearby forests in 1910–14, when Gatun Lake rose behind a dam on the Chagres River to form the central part of the nearby Panamá Canal. Before 1923, when the island became a biological reserve, a few settlers cut down patches of forest. Much of the eastern half of the island is medium-height forest, probably under 100 yr old; much of the western half is tall forest, probably mature but almost certainly not virgin (Bennett 1963). Kenoyer (1929) and Standley (1933) discuss the vegetation and successional stages on the island.

Elevations range from 164 m to 26 m at lake level. A flat basalt cap slopes westward from the summit, surrounded except on the west by a steep escarpment zone of Bohio conglomerate, which extends onto peninsulas near the laboratory clearing. A flat main eastern peninsula (Barbour Point) is Caimito formation (Woodring 1958). The escarpment and flat areas differ in birds, as noted below.

In a strong dry season (January to April) only 7.9% of the average annual rainfall of 2,678 mm falls. There is great annual and monthly variability (Fig. 1). Some dry seasons have periods of high rainfall, and nearly always dry periods occur in the rainy season. Allee (1926) notes that temperature near the ground, where ant-following birds work, is very stable; there is little wind, even in the dry season. Some areas of undergrowth, particularly ridges and shores facing the strong northeast trade winds of the dry season, are rather windy. The leaf litter and forest floor dry out especially rapidly in these areas, but all areas eventually dry out in prolonged dry periods at any time of year.

Windstorms and landslides periodically fell trees in the forest. A major windstorm on October 1, 1961, felled scattered groups of trees all over the island, creating treefalls in which Chestnut-backed Antbirds became very common by about 1966 (Willis and Oniki 1972). Local residents (fide D. H. Knight) report a storm in 1919 that felled much of the forest on Barbour Point and may account for the low forest there today. Several landslides in November 1959 created small zones of second growth in escarpment areas on the island. However, most of the forest is maturing gradually.

PROFESSIONAL ANT-FOLLOWERS

In the region of Barro Colorado Island there were originally 11 or more species of birds that follow army ants for most of their food. One of these "professional" ant-followers, the Ruddy Woodcreeper (*Dendrocincla homochroa*), is a casual visitant from the Pacific foothills. Two others, the Immaculate Antbird (*Myrmeciza immaculata*) and the Black-crowned Antpitta (*Pittasoma michleri*), were local in the wetter Caribbean foothills. A fourth, the Bare-crowned Antbird (*Gymnocichla nudiceps*), occurred in Caribbean second growth. None of the four was recorded from Barro Colorado in the 1920's and 1930's in the earliest ornithological studies (Chapman 1938, Eisenmann 1952); none has been recorded subsequently.

Of the remaining seven species (Table 1) the very large ground-cuckoo *Neomorphus geoffroyi* was collected and later observed on Barro Colorado Island to 1935. It is never numerous anywhere; probably the total population on Barro Colorado was a few pairs. Elsewhere from Nicaragua to Brazil these birds are often in riverine or slope forests, usually in areas crowded with treefalls and vines. Perhaps mature forest is unsuitable for them. The remaining six species (Table 1) were still present when I began work on Barro Colorado in 1960.

On Barro Colorado, Barred Woodcreepers and Ocellated Antbirds stayed mainly in escarpment zones toward the center of the island. All or nearly all individuals were on the study area. Gray-headed Tanagers were mainly in lighter woodland on the eastern half of the island. The other species were generally distributed, except that Spotted Antbirds were rare in the most precipitous canyons.

The three antbirds seldom cross open areas and

TABLE 2. Pairs of antbirds per square kilometer on 2- to 5-km² study areas, Barro Colorado Island, 1961–70

Year	Spotted Antbird	Bicolored Antbird	Ocellated Antbird
1961	22.2	3.16	1.92
1962	20.1	2.92	—
1963	18.7	2.48	1.79
1964	18.3	2.72	1.42
1965	18.6	2.47	1.11
1966	20.2	1.63	0.84
1967	19.9	1.56	0.72
1968	21.5	1.18	0.90
1969	19.3	1.42	0.40
1970	21.6	1.46	0.13

probably never cross Gatun Lake to or from Barro Colorado. The other species fly strongly across open areas and may cross the lake. No bird banded on Barro Colorado has yet been seen on the mainland or vice versa, but there has been little study on neighboring areas. Barro Colorado is 500 m or more from mainland forests. Diamond (*pers. comm.*) found most forest birds, even strongly flying ones, absent on a forested island only 55 m off the coast of New Guinea. Tropical birds of the undergrowth disperse across barriers extremely poorly compared to birds of northern or open habitats.

General Population Trends

Gray-headed Tanager populations remained near one pair per square kilometer from 1961 to 1971. Banded individuals rarely persisted more than 2 or 3 yr, although one female banded in 1961 was still alive in 1971. Turnover of pairs was high, and many new birds appeared each year.

Plain-brown Woodcreeper populations were stable at about six to seven individuals per square kilometer (Willis 1972*b*). Settled individuals often survived many years; three of four females banded in 1961 were still alive in 1970. There was a large population of wandering birds, which usually disappeared within a year or two after banding. Turnover was high except in the settled birds.

Two pairs of Barred Woodcreepers were in the escarpment zone on the study area in 1960; another bird appeared in 1962. Probably there were no other birds on the island, and previous records of the species were few (Eisenmann 1952). One pair and the lone bird disappeared between 1964 and early 1965. The other pair separated, one bird to the south escarpment until 1966 and the other to the north escarpment (a kilometer or so distant) until 1969. The 1971 census found none on the island.

The populations of the three species of antbirds in the study area from 1961 to 1970 are shown in Table 2. Spotted Antbirds were common and had stable populations. Bicolored Antbirds decreased to half

TABLE 3. Nest and fledgling success in three species of Antbirds on Barro Colorado Island

Item	Spotted	Bicolored	Ocellated
Minimum nest success (%)	9	12	(4)[a]
Number of nests with one fledgling (A)	8	1	(6)
Number of nests with two fledglings (B)	11	2	(4)
Number of fledglings/successful nest	1.6	1.7	(1.4)
Average days out of nest at discovery (t')	22	18	23
Number of broods of one at discovery (A')	38	7	10
Number of broods of two at discovery (B')	44	10	6
Average brood size at discovery	1.5	1.6	1.4
Percentage of fledglings surviving ($1-p$)	95	93	(90)
Complete brood loss by discovery (C, %)	2.2	2.6	(6.4)
Average days out of nest at banding	20	19	32
Percentage of fledglings surviving to banding	(95)	(93)	(88)

[a] Records in parentheses are estimates. See Appendix 1 for calculations and symbols.

the original density by 1968 and rose slightly by 1970. The 1971 census found 11 pairs, two male-male pairs, and several unmated males. Probably there were about 60 birds on the island, including some 20 pairs. Ocellated Antbirds were at this population level in 1961, for there were some 12 pairs on the study area. The 1971 census showed one pair and four unmated males on the island, all in escarpment zones on or near the study area.

In summary, of six professional ant-followers the largest disappeared between 1961 and 1970, and the next largest was nearly gone by 1970. The fourth declined to half the original density in this period. The third, fifth, and sixth seemed to have stable populations. Numbers of ant swarms remained about the same, so in 1970 there were fewer professional ant-followers per swarm than in 1960.

Many other species of birds take less than half their food—usually less than a tenth—by following army ants. There were no spectacular increases in ant-following by most of these birds. One large lakeshore species, the Greater Ani (*Crotophaga major*), turned up at several swarms at the center of the island in 1971. The large Rufous Motmots (*Baryphthengus ruficapillus*) also turned up more frequently in January 1971 than in January 1961. However, these increases did not fill gaps very well—there were similar numbers of "nonprofessional" birds in 1971 and 1961.

These changes apparently did not occur on the mainland, across Gatun Lake. In extensive humid forests of the Navy Pipeline Road, numbers of Barred Woodcreepers, Bicolored Antbirds, and Ocellated Antbirds per swarm from 1965 to 1971 were as high

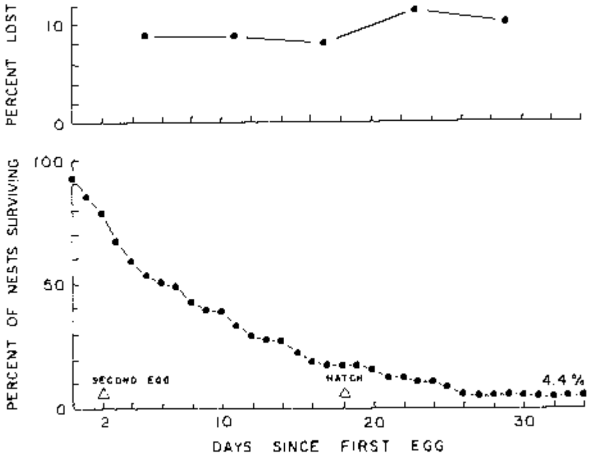

FIG. 2. Survivorship of 74 unvisited nests of Ocellated Antbirds (below); same data shown as mortalities per day for 6-day periods (above). Status of nests inferred by watching the parents at swarms of ants, by methods explained in Willis (1973*b*). Mortalities estimated at 8% on day 0 (the day the first egg is laid) and day 1 (the day between the laying of the two eggs), or nearly the average daily loss for day 2 (the day the last egg is laid) to day 7; survivorship of these antbird nests cannot be determined directly at unvisited nests until regular incubation begins on day 2.

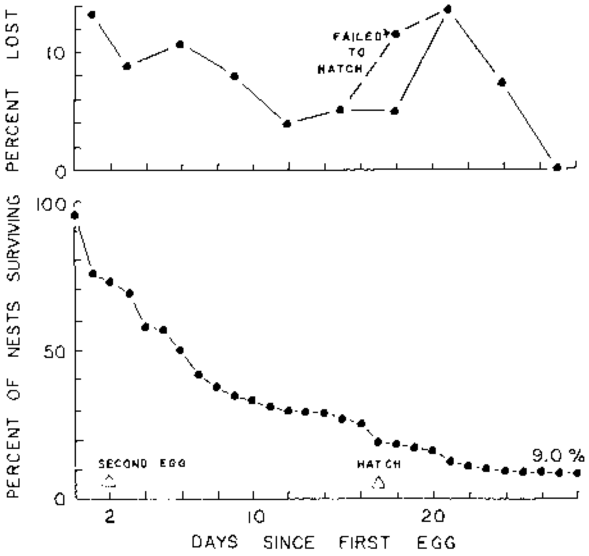

FIG. 4. Survivorship of 102 visited nests of Spotted Antbirds (below); same data shown as mortalities per day for 3-day periods (above). The dotted line shows mortality when five nests that never hatched are counted as lost on day 17; the solid line nearby omits these five nests for comparison.

or higher than on Barro Colorado in 1961. Numbers of Plain-brown Woodcreepers, Spotted Antbirds, and Gray-headed Tanagers per swarm were always lower than on Barro Colorado. These three species were more common in dryer forests toward the Pacific side of the Canal Zone.

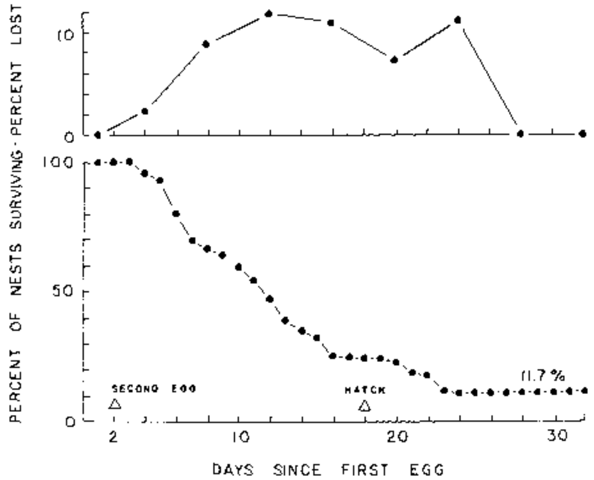

FIG. 3. Survivorship of nests of Bicolored Antbirds (below); same data shown as average daily mortalities for 4-day periods (above). Sixteen visited nests tabulated before day 2; 61 unvisited nests tabulated as well after day 2 (see Willis 1973*b* for a comparison of unvisited and visited nests).

Population Dynamics of Antbirds

More detailed data are available on the changes in populations of the three species of antbirds. Three factors determining population dynamics—mortality, natality, and movements—will be discussed.

Mortality

Losses of antbirds are divisible into four categories: losses of nests and nestlings, losses of fledglings before banding, losses of first-year birds, and losses of adults. In some species losses differ in the last two categories between males and females or between breeding and nonreproductive birds.

Losses of nests.—As is usual for forest birds in and outside the tropics (Snow and Snow 1963), nest success is very low in all three antbirds (Table 3). Success seems unusually low in Ocellated Antbirds, if the rough estimates are correct. Details of survivorship for the three species, based on a modification (Appendix I) of the method of Ricklefs (1969), are shown in Fig. 2–4.

A few eggs and sets of eggs of Spotted Antbirds did not hatch; in some cases one egg instead of two was in the nest. In most cases these sets were predated. Two eggs in each of five nests of Spotted Antbirds failed to hatch on day 17 or thereafter and were eaten later by predators (Fig. 4). The failure of these nests may have been due to infertility, etc., or to a predator scaring the female off the nest at night; they could be considered "predated" nests if the last were true. Occasionally an antbird nest loses an egg

TABLE 4. Losses of three species of yearling antbirds

Item	Spotted			Bicolored[a]	Ocellated[b]
	Male	Female	Both		
Average age at banding (days)			20	19	32
Maximum age at banding (days)			53	65	85
Number banded	43	49	92	36	30
Percentage lost by April 15	52	75	64	58	47

[a] Females and males not distinguishable externally until about 6 months old. Three of seven known young females and one of 10 known young males were lost from January to August following the year of hatching.
[b] Males and females alike externally until breeding. Female survivorship probably about the same as male, for young stay with parents until the next breeding season (females and some males) or later (other males) and are protected by them. Parents not hostile to independently foraging young as in Spotted and Bicolored Antbirds.

or nestling, so that average brood size at fledging is less than 2.0 (Table 3). Possibly some of the lost young starved, as Ricklefs (1969) suggests, but genetic failures and capture by predators are among the other possibilities.

Losses of fledglings.—Fledglings seldom disappeared after they were flying well and easily located, but losses must have been moderately high in the first few days after they left nests. At that age the young were very well concealed, usually with separate parents. They were too difficult to detect to get daily observations of survivorship without inordinate time and increased risk of attracting the attention of predators. Losses of fledglings to time of discovery and time of banding are therefore estimated in Table 3 by the methods in Appendix I. Survival from fledging to time of discovery, probably not less than 90%, suggests that many Ocellated Antbird nests fledge only one young (57%, if survival to discovery is 90%).

Losses of first-year birds.—Many young birds are lost between the time of banding and the next April 15, at the start of their first complete breeding season (Table 4). "Loss" includes emigration of individuals from the study area as well as actual mortality. It is only possible to estimate roughly how many young birds wandered off the study area and survived. Very few of these young birds were detected in later years, even though they must stay on the island. The 1971 census showed a very steep decrease in banded birds at increasing distances away from the study area for Spotted Antbirds (a few birds last seen as fledglings were detected off the study area, but no others), a moderate decrease for Bicolors, and no Ocellated Antbirds off the study area (even though they had sometimes been off the study area in 1960–61).

If 7%–10% of the yearling antbirds moved off the study area to places where they were not detected again, true mortality rates in the 1st yr would be about 55% for Spotted Antbirds, 50% for Bicolored Antbirds, and 40% for Ocellated Antbirds. In this case, rates for females should be about 60% in Spotteds, 60% in Bicolors, and 40% in Ocellateds; rates for males should be about 50% in Spotteds, 45% in Bicolors, and 40% in Ocellateds.

Losses of adult birds.—Losses of birds that have already passed April 15 in their first breeding season are lower than in yearling birds (Table 5). The emigration of these birds from the study area is small, mostly of peripheral birds, so that loss rates are fairly close to true mortalities.

Territorial and unmated adult male Spotted Antbirds seem to have a mortality rate twice as high as mated males. Unmated males sing and wander

TABLE 5. Losses of adult antbirds[a] per year

Item	Spotted			Bicolored			Ocellated		
	Male	Female	Both	Male	Female	Both	Male	Female	Both
Mated, territorial birds									
Number present at start year	534	469	1,032[b]	93	82	280[b]	68	67	160[b]
Number lost by next year	96	91	195	28	28	80	14	25	48
Percentage lost per year	17.6	19.4	18.8	30	34	29	21	37	30
Unmated, territorial birds									
Number present at start year	29	—	—	8	—	—	7	—	—
Number lost by next year	10	—	—	2	—	—	3	—	—
Percentage lost per year	34	—	—	25	—	—	42	—	—
Unmated, nonterritorial birds									
Number present at start year	—	—	—	83	—	—	18	1	19
Number lost by next year	—	—	—	20	—	—	6	0	6
Percentage lost per year	—	—	—	24	—	—	33	0	32

[a] Excluding a few peripheral banded birds that could not be checked a year later.
[b] Grand totals, including unmated, homosexual, or father-son associations as well.

around their territories and nearby territories, and their lower survival may be the price paid for advertising and for not having a mate to help keep the lookout. The loss rate is intermediate between that for settled adults and that for 1st-yr birds. The fairly high rate for adult unmated males eventually brings numbers of males into balance with numbers of females, offsetting high losses of 1st-yr females. Unmated males on territories ranged from two or three in most years (2%–5% of censused territories) to seven in 1964 (9.2%) and eight in 1970 (8.3%).

Unmated male Bicolored Antbirds had, by contrast, lower losses than mated ones (Table 5). Males that stayed on territories and formed a homosexual bond with a wandering male had especially low losses, 8% (1 of 12). Such males feed each other back and forth, dominate the ant swarm in their own area, and help each other look out for predators. All these advantages except feeding of the male accrue to mated birds, too, but the latter must travel to nests to build, incubate eggs, and feed young and thus lose in food, energy, and safety. Unmated birds can stay at swarms and need not lose in these ways, but are sometimes at the bottom of dominance hierarchies and are not as well fed and safe as homosexual and territorial birds (Willis 1967). Territorial females should survive better than their mates, for they do less work at nests or in care of young and incubate only in the rainy afternoon and evening, whereas males must incubate in the morning, when ants flush most food. Moreover, females often dominate their mates, waste less time chasing trespassers, etc. However, the territorial females do have to lay eggs and to incubate at night and may be predated by mammals more often (Willis 1973*b*). Table 5 suggests higher rather than lower losses for females.

Loss rates of Bicolored Antbirds varied from year to year. Male losses were unusually high in 1963 (13 of 24), female losses in 1963 (5 of 10), 1964 (4 of 7), 1966 (4 of 7), and 1968 (3 of 6). In 1969 female losses were low (zero of 6). Total losses of adults were low in 1962 (5 of 34) and 1969 (3 of 22), high in 1963 (18 of 34).

Possibly high losses in 1963 were due to high rainfall in January (Fig. 1). In 1970 a high January rainfall caused failure of flowering, then failure of November fruiting, and mass starvation in ground mammals (R. Foster, *pers. comm.*). The mammals tore up palms, in which Bicolored Antbirds often nest. Mortality and starvation of mammals also led ground omnivores and rodent-eating owls and hawks to seek new sources of food. Unfortunately, no naturalist was watching in late 1963. If approximately 10% of the "lost" Bicolors were wandering off the study area, as seems likely, true mortalities were about 20% for males and 25% for females.

TABLE 6. Nestings per month of study and percentages of successful nests (in parentheses) at different months

Month	Months of study (1960–71)	Species		
		Ocellated	Bicolor	Spotted
March	0.8	—	[a]	—
April	1.0	1.0 (0)[a]	3.0 (0)	1.0 (0)[a]
May	1.3	7.7 (10)	6.2 (12)	4.6 (33)
June	4.0	4.2 (38)	4.5 (29)	5.5 (27)
July	8.1	3.3 (12)	3.1 (0)	5.7 (9)
August	6.5	2.9 (15)	2.6 (23)	4.2 (7)
September	1.8	3.9 (25)	3.9 (20)	4.4 (50)
October	2.2	2.7 (20)	2.7 (33)	0.5 (0)[a]
November	1.7	1.2 (0)[a]	[a]	—
December	1.1	[a]	[a]	—

[a] Successful nests are known from these months, based on observation of known-age young out of the nest later. A nest is counted in a given month if the second and last egg were laid in that month, and if I was actually studying the birds on the day of laying that egg.

Mated male Ocellated Antbirds had lower losses than did unmated but territorial widowers (Table 5), perhaps because the latter sing loudly and wander widely around ant swarms looking for mates, and also have no mate to help keep the lookout. The few widowers that had accompanying sons had normal loss rates (1 of 3). Females had higher losses than males; perhaps some were lost because they incubate at night. They are often subordinate to trespassers when their mates are incubating and must forage peripherally or look for other ants; more might starve or be predated at such times.

If 5%–10% of the lost birds were wandering off the study area each year, true mortalities would be about 30% for adult females and unmated territorial males, 15% for mated males, and 25% for unmated wandering males.

Natality

Losses among these antbirds are made up by repetition of nesting, two eggs each time, over the course of long breeding seasons each year (Willis 1967, 1972*a*, 1973*a*).

Breeding seasons.—Table 6 indicates the total number of nests discovered or nestings detected per month of observations. Numbers in parentheses give the percentages of discovered nests that were successful for that month, omitting nests that were still occupied when I left. Midseason nests seemed less successful, in part because I usually visited in June to August and often left nests that may have been successful later. Broods of fledglings out of the nest seemed less frequent from midseason nests of Spotted Antbirds (Table 7). Fledglings in Table 7 come, in each case, from eggs laid 60 days previously.

No nesting has been detected in January and February, the early months of the dry season on Barro Colorado Island. Leaf litter is abundant, but probably only impedes capture of the few invertebrates present

TABLE 7. Broods of fledglings observed per month of study at different months

	Species		
Month	Ocellated (26)[a]	Bicolored (30)[a]	Spotted (35)[a]
May	—	[b]	—
June	0.2	—	2.7
July	1.1	0.6	3.5
August	0.8	0.9	4.6
September	1.1	—	2.8
October	0.9	1.8	2.3
November	0.6	0.6	5.3
December	0.9	0.9	[b]
January	0.4	0.8	—
February	0.5	—	—

[a] Age of young in days.
[b] Broods of fledglings of the indicated ages must have occurred in these months, based on observations of younger fledglings before or older young afterward. Observations are counted only if I was actually studying the birds on the day when fledglings reached the indicated age.

TABLE 8. Average number of days required for nesting by three species of antbirds

	Species		
Item	Spotted	Bicolored	Ocellated
Interval[a]	4	8	(4)[b]
Building	7	4	(3)
Laying	3	3	(3)
Incubation	15	15.5	(17)
Nestlings	10.5	13	(15)
Fledglings[c]	40	55 (45?)	28
Nest unsuccessful[d]	15	17	(13)

[a] From loss of previous nest to start of building.
[b] Data in parentheses are estimated.
[c] From fledging of young to start of building a new nest.
[d] From start of building to loss. See Appendix I, Part C, for calculations.

(Willis 1974). Invertebrates are few in the dry month of March, and only one Bicolored fledgling (in 1966) came from a nest started that month.

Rains normally start at the end of April, starting a "vernal bloom" of leaf-litter invertebrates that crests in June (Willis 1974). Regular nesting starts in all three species in April. The earliest clutch for Ocellateds was completed about April 14, 1961, the earliest for Bicolors (except the 1966 record) April 15, 1961, and the earliest for Spotteds about April 17, 1961. All pairs of antbirds are breeding May to September. As some pairs fledge early young and take care of them, the number of nests but not of breeding pairs goes down in June to September except in Spotteds. There an increase in unsuccessful nestings at midseason meant that each pair without fledglings was nesting more often. Leaf litter and invertebrates are becoming rare on the forest floor in August (Willis 1974), perhaps leading to low nest success and lowered numbers of nests.

Leaf fall increases gradually from August on (R. Foster, *pers. comm.*), leading to a weak "autumnal bloom" of invertebrates (Willis 1974). Spotted Antbirds stop nesting in early October (last clutch completed October 11, 1961). Some Ocellateds and Bicolors start clutches even in the heavy rains of November and 1st wk of December. Young out of the nest in January 1965 came from clutches completed about December 2, 1964, for Bicolors and December 4, 1964, for Ocellateds. In an average year the season of laying eggs must be about April 18 to October 10 (175 days) for Spotteds and April 15 to December 1 (230 days) for Bicolors and Ocellateds.

The heavy rains (Fig. 1) of early December 1960 and of December to early January 1970–71 did not induce any antbirds to extend their breeding seasons. Since little litter falls until a sharp peak after 2 wk of dry season (Foster, *pers. comm.*), there is little food for antbirds even if rains last late. It is uncertain whether the antbirds start breeding early when the rainy season starts early, as in 1960, but in that year unusual numbers of yearling antbirds were out of the nest. Perhaps, as in other birds, a refractory period occurs late in the annual cycle, but breeding can begin early in the cycle if conditions are favorable. Fogden (1972) proposes that breeding can start in Sarawak birds at any time when they reach a state of good nutrition, but does not mention refractory periods.

Nesting periods.—A successful nesting requires about 75 days for Spotted Antbirds, 80 or 90 days for Bicolored Antbirds, and 70 days for Ocellated Antbirds (Table 8). In extreme cases these periods were 10 days shorter or longer; then new nests were started a week or so before or after fledglings of the preceding brood were independent. Intervals between an unsuccessful nest and the start of a new one probably add to the requirement for a complete nesting (except the first of the year) by 4–8 days.

Intervals between a successful nest and the start of a new one are short in Ocellated Antbirds. They are dominant, and young birds are foraging for themselves with the simple techniques required at 28 days out of the nest. Moreover, young often associate in clans with young of previous nestings or years and need not have their parents about to give the alarm.

Spotted and Bicolored Antbird young are foraging for themselves only at about 35–42 days out of the nest, perhaps because these are small and subordinate antbirds that must develop a variety of foraging techniques whenever domineering larger antbirds are present. Some Spotted young were still following their parents when the latter started a new nesting, but others were independent for 1–2 wk. The average period between successful nests (Table 8) is thus about the average time to independence of the earlier brood. The period of 55 days for Bicolors is based on one case, and that pair may have had an unsuccessful nest that was not detected. Young are normally feeding independently at 42 days out of the nest, even though they usually stay with their parents 1–2 wk longer.

Nestings per season.—Knowing the average lengths of time for successful and unsuccessful nestings, the intervals between them, and the breeding season, one can calculate the possible number of nests during a season if pairs breed without stopping.

If a pair of Bicolored or Spotted Antbirds has only unsuccessful nests, or only one successful nest at the end of the season, it will have on the average 10 nests per year, but an Ocellated pair will have an average of 14 nests. Detected nests for single pairs have not ranged above 6 or 7 per season, but I have not watched a single pair carefully for more than about three-quarters of a season. Oniki[2] found a pair of Slaty Antshrikes that had 3 unsuccessful nests in 60 days, so there could be 12 in 240 days. I found some Bicolored and Ocellated pairs nesting at this rate.

If a Spotted or Bicolored Antbird has one successful nest in the early or middle season, it can have 7 nests that year. An Ocellated pair can have 10 or 11 nests. The maximum number of successful nests per season is 3 for Spotted and Bicolored Antbirds, 4 for Ocellated Antbirds. Chances of the last are only 1 in 390,625 (1 chance in 25 to the power 4), even if some local or experienced pairs are unusually good at producing successful nests.

Age and location.—In some species, particularly birds that forage off their territories, old birds are better at rearing young than are young ones. The greater success of late nests in my study could suggest that birds gain experience during a year, but it is more likely that predators are less active then; May nests are also more often successful. Morton (1971) found that predation on nests of Clay-colored Robins (*Turdus grayi*) in the Canal Zone was higher in June and July than earlier in the year (that species does not nest after June or July), even though food supplies and weights of young were highest in June and July. In general, I found little evidence that old antbirds were more successful than young ones. A few old males seemed to find the key to repeated successes, but most never did.

Young female Ocellated Antbirds sometimes have fledglings their 1st yr but are unsuccessful in later years. The few males that mate their 1st yr have not been known to produce young then. Some old males at the island center were repeatedly successful in breeding; perhaps they were able to build up their clans because they found safe foraging and nesting areas. Other males up to 9 or more years old, mostly nesting toward the edges of the island, were never very successful.

Spotted Antbird males and females sometimes produced fledglings in their 1st yr of breeding. Others seldom or never produced offspring, even over several years. Two males that were unusually successful (five, perhaps more, broods out in as many years) lived in areas where later pairs were generally unsuccessful, but in another case two successive pairs in one area were relatively successful. Most of the successful birds lived along small ridges with numerous small gullies where nests were often concealed. Some birds renested successfully in one or two small areas in their territories, but not all nests in these areas were successful. However, the evidence for greater success with age and area is not very strong.

Nesting success of Bicolored Antbirds does not seem to be be correlated with age or area. Possibly pairs toward the periphery of the island, away from the main escarpment zones occupied by Ocellated Antbirds, succeed better; six broods came from the center of the island out of 52 known nests and three from the periphery from 15 known nests. Young females and 2nd-yr males sometimes raise fledglings their 1st yr of nesting.

Movements

Few territorial adult antbirds moved off their territories to other areas (Table 9, part C6). A few peripheral birds probably wandered off the study area and were recorded as "lost" birds. Even adding to part C6 an estimate for these moving but lost birds, I doubt that total movements would surpass the following: 10% for male Spotteds, 15% for females; 15% for male Bicolors, 25% for females; and 10% for male Ocellateds, 20% for females.

Birds that stayed with the same mate usually stayed in much the same area (Table 9, part D1). Birds that were "divorced" (part D2), "widowed" (part D3), or "bachelors" (part D4) moved more commonly. Divorces and rematings were especially likely to be connected with movement. Females went to a new mate and a new area more commonly than did males. Often the female went to a neighboring male after he lost his mate, leaving her own mate without a female for the time being; perhaps some females or their nests get more food or survive better if a new area or male is available. In Bicolored Antbirds two males that had poor dominance over neighbors (i.e., small territories) accounted for four of the seven divorces.

Widowed birds moved fairly frequently, especially female Ocellateds. The female of this species is smaller than and subordinate to males and must quickly find a new mate if she is not to lose in foraging. Since local males of this clan-forming species are

[2] Y. Oniki. MS. The ecology and behavior of Slaty Antshrikes (*Thamnophilus punctatus*) on Barro Colorado Island, Panamá Canal Zone.

TABLE 9. Movements of individual territorial antbirds

Item	Spotted			Bicolored			Ocellated		
	Male	Female	Both	Male	Female	Both	Male	Female	Both
A. Total number of birds	376	331	707	69	54	123	57	42	99
B. Stayed at home (numbers)									
1. Same mate next year (S_1)	249	249	498	36	36	72	36	36	72
2. Different mate (D_1)[a]	19	8	27	4	1	5	0	0	0
3. Lost mate (W_1)	64	34	98	12	7	19	15	1	16
4. No mate (B_1)	11	0	11	9[b]	0	9	4	0	4
5. Total staying (M_1)	343	291	634	61	44	105	55	37	92
C. Moved off home area (numbers)									
1. Same mate next year (S_2)	3	3	6	0	0	0	1[c]	1[c]	2
2. Different mate (D_2)[a]	11	22	33	3	6	9	0	0	0
3. Lost mate (W_2)	10	15	25	5	4	9	1	3	4
4. No mate (B_2)	5	0	5	0	0	0	0	1	1
5. Status unknown	4	0	4	0	0	0	0	0	0
6. Total moving (M_2)	33	40	73	8	10	18	2	5	7
D. Percentages									
1. Moving if same mate (S)	1.2	1.2		0	0		3	3	
2. Moving if new mate (D)	37	73		43	86		—	—	
3. Moving if lost mate (W)	14	31		29	36		6	75	
4. Moving if no mate (B)	31	—		0	—		0	100	
5. Moving (M)	8.8	12.4		12	18		4	12	

[a] Old mate still alive ("divorce and remating").
[b] Includes four with male partners (two "pairs").
[c] Moved closer to center of island (the favored zone for Ocellateds) when pair in that direction disappeared.

likely to be mated, related to her, or young, she is more likely to find an unrelated single male with a good territory if she moves. The female Spotted Antbird is also subordinate to the male, although no smaller, and loses to trespassing neighbors if she has no mate. However, Spotteds need not forage over army ants all the time, so the widow can often hide in remote corners of her home area until a suitor appears. Bicolored Antbird females, by contrast, often dominate their mates and trespassers, and widows can often pick up a new mate from the many old bachelor males about. Movements of widows and widowers are similar, about as frequent as in widow Spotteds. Both sexes of Ocellateds and Bicolors normally travel widely off the home area and are quite likely to gain a mate on a neighboring area. Since moving off a familiar home area must increase danger from predators and problems in finding food, it is perhaps still to be expected that many widows and widowers stay at home.

Bachelor adult females are rare in these antbirds, for only in 1 yr (1961) was there a surplus of 1 out of 12 females in one species (Ocellateds). Bachelor adult males are usually fairly numerous, especially in Bicolors. Bachelor males of Ocellateds and Bicolors never moved off their home areas. They range so widely that they can pick up any widow from several neighboring home ranges, and in addition Ocellated widows move exceptionally and quickly home on the songs of an unmated male. If a bachelor male moves peripherally in his area or off it, he quickly goes to the bottom of the peck order and confronts more danger and difficulty in finding food. The male Spotted must confront more of these problems if he moves off his area, for prior to loss of mate he has little experience off his area. He also may not find the sedentary widows. Some bachelor Spotteds were males on territory for the 1st yr and may have picked relatively poor sites where they could not hold a female long enough. In such cases, moving to a new area would help.

Distances of movement were mostly short. Territories of Spotted Antbirds are about 200 m in diameter, of Bicolors about 400 m, and of Ocellateds about 500 m. Birds almost never moved the center of their activity more than one or two territorial diameters away, except in the case of widowed female Spotteds,

TABLE 10. Territorial turnover rates for antbirds

Item	Spotted			Bicolored			Ocellated		
	Male	Female	Both	Male	Female	Both	Male	Female	Both
Movements (%)[a]	8.8	12.4	10.3	11.6	18.5	14.6	3.5	11.9	7.1
Losses (%)[a]	18.8	19.4	19.1	27.4	34.1	30.3	22.7	37.3	29.6
Total	27	32	29	39	53	45	26	49	37

[a] Includes homosexual birds and birds without mates as long as on territory.

which sometimes moved a kilometer away. Young and other nonterritorial birds wandered more widely at times, but were "reflected back" by the water edge of Barro Colorado (details in Willis 1967, 1972*a*, 1973*a*).

Population changes

Territorial turnover rates.—Annual turnover rates of territorial or settled birds are the probabilities that given birds will not be on their territories a year later (Table 10). They thus include movements and losses, the latter caused by deaths and an unknown number of movements to areas where birds were not detected again.

Turnover rates for all these antbirds were high, especially for male and female Bicolors and female Ocellateds (Table 10). To some extent these rates reflect the declining populations of these two species. The turnover rates, none less than one in four, show that even tropical forest birds can have rather changeable populations. Annual turnover rates for Spotted Antbirds varied considerably (Fig. 5), as did those for Bicolors and Ocellateds. The seeming decline in turnover for Spotteds during the 10 yr may represent relaxation of competitive pressure from the declining Ocellated and Bicolored Antbirds, but the density of Spotteds did not increase (Table 2).

Population fluctuations.—Turnover is only one part of population dynamics; losses or gains of pairs are another, for these determine the fluctuations of populations (Table 11).

Most antbird areas with a mated pair were occupied by a pair the next year, especially in the stable population of Spotted Antbirds. In that species many

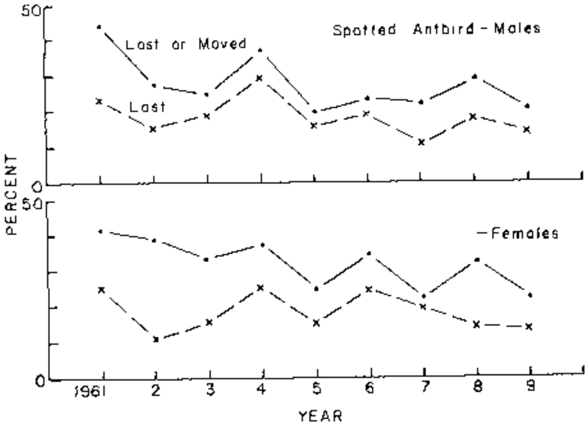

FIG. 5. Percentages of male and female Spotted Antbirds lost or lost plus moved each year from 1961 to 1969. Loss is probably too high in 1961 and too low in 1962; in 1962 peripheral birds were not censused as effectively as in other years.

areas that had only a male were occupied by a pair the next year. Few empty areas of any species gained a pair the next year; probably most such areas, either from small size or from some defect in food or safety, were not very suitable for nesting by a new pair. In declining populations, however, many areas became unoccupied, and swarms of ants wandered without resident birds or pairs. Even in Spotted Antbirds, sudden lack of a pair at a moving swarm of ants was often a result of temporary local vacancy; the neighbors only moved in at times.

The idea of "empty areas" surprises many ecologists familiar only with birds of northern or open

TABLE 11. Population losses in antbirds

Item	Spotted		Bicolored		Ocellated	
	Number	Percentage	Number	Percentage	Number	Percentage
A. Areas with male and female						
1. Total	506	100.0	86	100	72	100
2. Pair following year	465	91.8	64	74	57	79
3. Male alone next year	14	2.8	5	6	5	7
4. Became empty	27	5.4	17	20	10	14
B. Areas with male only						
1. Total	17	100	12	100	7	100
2. Pair following year	14	82	4	33	2	29
3. Male alone next year	2	12	7	58	2	28
4. Became empty	1	6	1	9	3	43
C. Empty areas						
1. Total	119	100	46	100	34	100
2. Pair following year	22	18.5	8	17	3	9
3. Male alone next year	5	4.2	1	2	0	0
4. Remained empty	92	77.3	37	81	31	91
D. Total areas						
1. Starting with birds	523	100.0	98	100	79	100
2. Lost the birds	28	5.3	18	18	13	16
3. Ending with birds	522	100.0	88	100	69	100
4. Started empty	27	5.2	9	10	3	4

TABLE 12. Mortality versus natality for female antbirds

Item	Species		
	Ocellated	Bicolored	Spotted
(a) Fraction of nests producing fledglings[a]	(0.041)[b]	0.115	0.085
(b) Number of fledglings per nest	(1.4)	1.7	1.6
(c) Fraction of females	(0.5)	(0.5)	(0.5)
(d) Fraction of fledgling females surviving	(0.9)	(0.93)	0.95
(e) Fraction of immature females surviving	0.6	0.4	0.4
(f) Number of nests per year	19.4	6.9	6.2
(g) Adult female mortality	0.30	0.25	0.16

[a] See Appendix I, part C, for estimates of losses during building.
[b] Records in parentheses are estimates.

country. To a degree, an empty area for these birds is split up by neighbors. If the neighbors visit the empty area, they ordinarily set up dominance systems or chase trespassers and thus incorporate it into their own territories. However, an animal can efficiently eat or dominate only so much. A new antbird or pair usually occupies the area with little argument from neighbors. Tropical birds like these tend to approach the barnacle type of site use because "basal space" is held much or all of the year and because neighbors tend to live many years and to center activity in their own spaces. There is not the change in year-to-year distribution of birds that one often finds in birds that occupy an area seasonally. Looking at "empty spaces" helps in discussing declines and increases in populations, as well as in determining what sites are marginal for a species. Since tropical birds often have patchy distributions (Karr 1971), trying to detect why areas stay empty different lengths of time may eventually be useful.

If a Bicolored Antbird or Ocellated Antbird area had only a male, it was likely to retain only the male or to become empty the next year. Few females of these species were hatched each year, and these mostly filled vacancies in areas with pairs the preceding year. Empty areas rarely picked up a single male of any species, even more rarely than they picked up a mated pair. Probably the empty areas are more marginal in food or in other respects when a male has to defend and keep the lookout alone than when he has a mate.

The balance between areas that ended empty and ones that began empty is broken for Bicolored and Ocellated Antbirds (Table 11, D). The detailed data illustrate but do not suggest reasons for the general decline in these species noted in Table 2. It is possible to present data documenting the decline in several other ways. However, little additional information is to be gained, especially since the mathematics of decline to extinction quickly make data "not significant" except for the decline.

Mortality and survival for females

Mortality and survival for females of the three species of antbirds are summarized in Table 12. The survival of young females must equal the loss of adult females if the species is to survive, so abcdef = g. The unknown is f, the number of nests per year for the average female to replace herself. Spotted and Bicolored Antbirds require only 6 to 7 nests per year to replace female losses; this is well within the limit of 7 to 10 possible nestings per female calculated earlier. Bicolored and Spotted Antbirds should be able to nest enough in areas where the rainy (nesting) season is shorter than on Barro Colorado, even in areas with 6 mo of rain, as long as mortalities are no higher than on Barro Colorado.

The average Ocellated Antbird female would require some 19 nests per year to replace herself. As noted earlier, only 10–14 nests per year seem possible. In areas with rain all year, the possible number of nests (assuming one success and no refractory period) would be 24, which would create a surplus. Apparently Ocellateds with the mortalities on Barro Colorado have to nest much of the year. Wherever they could not do this, they would decrease over time or be restocked by immigrants from better areas. If nest survival were 6.1% rather than 4.1%, only 13 nests per year would be required. However, possibly Ocellated Antbirds have nest and adult mortalities in many areas near the maximum, and they manage to survive because they are dominant and live mostly in rain forests, making nesting possible nearly all year.

DISCUSSION

Given the low nest and adult survival rates for Ocellated Antbirds, it is no surprise that Ocellateds declined on Barro Colorado during the 1960's; it is surprising they lasted so long there. Possibly nest and adult mortalities were unusually high in the 1960's. Could the study itself have had this effect? Since no nests were located, it seems unlikely that nests were affected directly. The only possible way would be if nest success were lowered because birds were disturbed by my watching them over ants. This could also have increased mortality. If so, one would expect lower natalities and higher mortalities in years when I watched the birds for long periods—1961 and 1965. Actually, however, adult mortalities were highest between 1968 and 1969, and natalities did not seem low in 1961 or 1965.

High mortality in 1968 could have resulted from low rainfall from 1967 to 1969, if low rainfall led to low arthropod numbers. There may have been less nesting and more traveling looking for suitable ant colonies in 1968. As it was more difficult for me to find ant colonies in June 1968, ants may have survived poorly that year. During the study period 1968 was also the only year when the rainy season was only 7 mo long and truncate at both start and close, and it was the only year with 6 mo of well below normal rainfall (Fig. 1). Out-of-season rains can also have disastrous effects, like the previously mentioned rain of January 1970; perhaps the early rain of March 1968 started breeding that stressed adults in the dry month of April. Possibly predation increased in 1968 also, as generalized predators scrambled for any available prey.

Bicolored Antbirds should not have decreased in the 1960's, according to Table 12. Perhaps the calculations, based mainly on 1961 data, overestimate nest success and underestimate adult mortality for the other years. Also, adult mortality may be higher at the edges of Barro Colorado, siphoning birds off the study area. A decrease of 50% did occur, but it is difficult to know why. Removing a percentage point here and there, especially on nest survival, could have disastrous effects difficult to detect without a huge sample size.

Spotted Antbirds fit the available data fairly well, although it is possible that they nest more than 6.2 times per year and that they have greater mortalities than estimated. If the mortality of young females is as "low" as indicated in Table 4, the species would have some leeway to take care of occasional bad years or to export a surplus to less prolific or more dangerous corners of the island.

All three antbirds have higher adult mortalities than the 11% Snow (1962*a*) found for males of a second-growth manakin in Trinidad. His data on a forest manakin (1962*b*) are from such a patchy forest (at Simla) and so indirect (111 of 200 netted birds were in female plumage, suggesting 11 were 1st-yr males) that I wonder if mortalities were 11%. Fogden's (1972) composite data for Sarawak suggest mortalities about 10%, but that island has few predators on adult birds. Since Bicolored and Ocellated Antbirds did not maintain their populations on Barro Colorado with adult mortalities above 25%, it may be that normal mortalities of forest birds are 15%–25%, and that some unusually safe birds like male manakins on leks or birds on predator-free islands keep mortalities below 15%. However, because some tropical birds have high nest mortalities is no reason to assume that they have low adult mortalities, or differ greatly from northern birds with respect to *K*- or *r*-selection. They may, like these antbirds, nest many times each year in a fecund race with death.

It is distressing that many birds on Barro Colorado Island, despite its protected status, seem to be losing their races. Appendix II lists breeding birds that have disappeared from the island since it was set aside as a reserve in 1923. Other birds may have disappeared, but were not recorded by the early visitors to the island. Some species now present were not recorded by Chapman (1938) and other early explorers, but they are mostly small flycatchers that probably were overlooked. (One such small flycatcher, *Myiornis atricapillus*, is noisy and common, but has not been reported by any visitor other than Paul Slud and me; experience with calls of tropical birds can change recorded species diversities in censuses.) Since these birds were probably present, there were originally some 209 breeding species on Barro Colorado (Eisenmann 1952). Of these species 45, or 22%, have disappeared without replacement; several others, like Ocellated Antbirds, seem on the way out. A few species have invaded from time to time, but no successful colonizations have taken place so far (except among lake birds).

Thirty-two of the vanished species, about 71%, are birds of second growth. Such birds wander widely and probably would reappear on the island if part of it were cleared. Most of them are common in second growth elsewhere in Panamá and are in little danger of extinction. Thirteen species, however, are birds of woodland or forest. Their disappearance from nature reserves like Barro Colorado may presage their extinction if Latin Americans ever cut down tropical forests and leave only isolated forest reserves.

Eight of the 13 vanished forest species nest or forage mostly on or near the ground (John Terborgh, *pers. comm.*). These species may have disappeared because the monkey, coatimundi, and opossum populations of Barro Colorado are unusually high. Apparently not enough natural predators of mammals survive on this small island to keep numbers low in the absence of human predation. However, despite the monkeys some arboreal birds like Slaty Antshrikes[3] are doing well. The ground-living birds also might have the most difficulty flying to Barro Colorado across Gatun Lake, and that, rather than ground predators, could be the reason why their populations are not replenished. Black-faced Antthrushes, for instance, are common on Buenavista Point across the Panamá Canal, but have disappeared from Barro Colorado.

Two classes of causes could have led to the decline or disappearance of bird species on Barro Colorado: the growth of the forest, or the isolation and small size of the island. Horn (1971) has shown that monolayer trees take over from multilayer ones as a forest grows. The frequent observation of foresters that productivity slows in the mature forest thus has an evolutionary basis. Monolayers produce less leaf lit-

[3] See footnote 2.

ter, reducing productivity of leaf-litter arthropods, so fewer birds could survive near the ground in an old than in a new forest. However, on Barro Colorado frequent treefalls mean that monolayers never dominate in most areas (Robin Foster, *pers. comm.*). Certainly, the loss of birds of second-growth and forest edge seems to be attributable to growth of the forest. Possibly the growth of the forest also has led to opening the undergrowth and providing less food and cover for birds there. However, one wonders why birds restricted to forest, like Barred Woodcreepers and Ocellated Antbirds, should disappear during forest maturation.

The "island effect," the fact that islands have a small fraction of the species found in a larger or less isolated area, is well known (Preston 1962, MacArthur and Wilson 1967). To a certain extent, it is caused by lack of habitats on small areas—particularly a riverless, exposed hilltop like Barro Colorado. It is impossible to have a big river or an alpine habitat on a small island, for instance. It is also due to the lack of a range of habitats on small areas, so birds cannot move back and forth in extreme years. Barro Colorado lacks the range of rainfalls found in an area like the Canal Zone; in an unusually dry year Ocellated Antbirds could disappear and never be replaced by the offspring of birds that had survived on the wetter Caribbean side of the Zone. Other species could be eliminated from Barro Colorado by an unusually wet year, and not be able to reinvade from the dryer side of the Isthmus. There are few refugia in a small place in a difficult year.

Preston (1962) shows that the exponential decrease in species in decreasing fractions of a mainland area is about the 0.15 power of area, whereas islands of the same absolute sizes show decreases as the 0.30 power of area and are well below mainland fractions. Presumably an island has a lower immigration rate because species cannot get there easily and a higher extinction rate because the animals that do get there die off in local fluctuations from which they could escape or find refugia on the mainland (MacArthur and Wilson 1967).

The antbirds are clearly unable to immigrate to Barro Colorado or escape from it. They simply do not cross water gaps, even of a few hundred meters. Different species occur on different banks of the major rivers of the Amazon (Willis 1969). Antbirds are missing on oceanic islands around South America and are nearly gone from "land-bridge" islands formerly connected to the mainland, such as Margarita and Trinidad off Venezuela and the Pearl Islands (R. MacArthur, *pers. comm.*) and Coiba (Wetmore 1957) off Panamá. They are like the forest-dwelling "land-bridge" birds that Diamond (1971) has found do not cross water gaps in New Guinea. Birds like these disperse poorly even overland, for no professional ant-following antbird has made the passage to the mountains of northern Venezuela; in that region, as on Trinidad, woodcreepers are the main ant-following birds. In such regions the "peninsula effect" (Simpson 1964) clearly lowers numbers of ant-following species the way the island effect does.

Extinction rates of forest-dwelling birds are low on Barro Colorado, about 0.3 forest species per year. This is about the same rate as on Karkar, a much larger island off New Guinea, for all species. However, the extirpated birds on Barro Colorado are not being replaced. This is a documented example of what happens when a "park" or "nature reserve" is separated from surrounding natural vegetation, even if not subjected to human interference significantly. Skutch (1971) documents a similar loss of species from the forest on his farm in Costa Rica.

"Ecological truncation," as in many other island situations, adds to the seriousness of the island effect. Large or specialized species go first—Ground-Cuckoos, then Barred Woodcreepers, then Ocellated Antbirds. Perhaps truncation occurs because large birds or specialists tend to have large territories with few individuals per unit area, and chance dry years or predators or genetic defects can wipe out most of a population. Where birds are limited to certain areas on the island, the limitation of Ocellateds to the escarpment zone for example, they are even more at the mercy of local events.

Even an occasional successful year helps little if it puts populations up over the normal level. Emigration cannot occur; the young stay around and encourage K-selection for adult longevity rather than r-selection for reproductive rates. The next time a catastrophe occurs, there are no rapidly breeding birds about. Moreover, the crowded birds or other animals cannot emigrate and must turn to alternate foods—which they may drive to extinction, destroy, or trample, or reduce to such a level that neither they nor species that normally feed on such food can survive. Specialized species disappear from parks, and only the "sparrows" are left—small, generalized birds that are jacks-of-all-trades.

A number of other problems are possible with islands—for instance, pests can occupy edge zones and reduce the total area available to birds, as mosquitoes did in carrying disease to lowland forest birds in Hawaii (Warner 1968). The Hawaiian events suggest the possibility that unusually high numbers of the lakeshore *Anopheles albimanus* kept Ocellated Antbirds from breeding near the lake shores after 1965. Apparently the mosquitoes increased after 1965 when the Panama Canal Company started to maintain the lake at a high level even in the dry season and *Hydrella* lake weeds, where these mosquitoes breed, increased. Certainly, the *Anopheles* concentrated in the daytime between the buttresses of trees in just the places where these antbirds probably nest (Willis 1973*a*). This kind of "edge effect" is the only known factor besides a low-rainfall cycle that changed at about the time of the main decrease in Ocellateds.

To determine if forest growth or the island effect is the cause of extirpation on Barro Colorado, birds of an extirpated species could be reintroduced. If they do not disappear quickly, forest growth and related factors are unlikely to have caused extirpation. If they disappear quickly, the experiment could be repeated a few times to see if the first time just happened to be a bad year. There is always the remote possibility that a species can survive before and after some critical stage of forest growth but not in the interim. However, this should also be observable on mainland areas.

Possibly the true causes of the decline of the Ocellated Antbird have not and will never be understood. Failure to detect causes in a 10-yr study suggests that causes can be difficult to detect in a tropical forest even with much effort. However, perhaps it matters less why animals in tropical parks disappear than it does that animals do disappear for practically undetectable reasons. We then realize that conservation theorems of general validity are needed rather than, or in addition to, specific techniques. Specific techniques, or "managements," can work well for a few species but are likely to have different effects on other species. These effects may be desirable in some cases, but not for an ecological study rather than an ecological experiment. Cutting half the forest on Barro Colorado would preserve many birds of second growth, for instance, but would probably have traumatic effects on the rest of the avifauna—the forest area would be even smaller and might lose even more species. The resulting truncation would probably make it difficult to learn why certain forest animals or plants behave as they do—their major competitors and predators might be gone.

One conservation theorem that seems generally valid is the Malthusian theorem, that food supplies grow arithmetically but populations geometrically. Translated into human terms, this has led to the suggestion of stable and limited numbers of people in time. The Barro Colorado observations suggest to me that the "island effect" points to another important theorem: arithmetic loss of space leads to geometric decline in the value of the remaining space. Translated into human terms, the "island effect" suggests that stable and limited human use of space will be necessary if we are not to lose many possibly valuable species of animals or plants or many important biological discoveries in a sea of humans, "rats, cockroaches, and sparrows." It matters little in conservation if we limit numbers of people in time, but do not also limit their intensive use of space. Limitation of human use of space will be most effective in preserving natural biotas if natural areas are not isolated islands in lakes or seas of humanity but instead are linked by corridor zones. Production of Ocellated Antbirds could then shift temporarily to the favorable end of a gradient if their usual reserve was subjected to temporarily unfavorable conditions. In a sense, the animals could then manage their populations while we manage our own.

Acknowledgments

I appreciate the help especially of the staff of the Smithsonian Tropical Research Institute. Five students from Oberlin College, Steve Anderson, Ronn Kistler, Steve Kistler, Jeff Strassenberg, and Douglas Wechsler, helped with the 1970 and 1971 census. Robin B. Foster's information on plant and litter cycles was invaluable. Yoshika Oniki, my wife, helped in many ways. Support was lacking in 1967 and 1968, but in other years the National Science Foundation, Woodrow Wilson Foundation, Frank M. Chapman Fund of the American Museum of Natural History, Sigma Xi, and Oberlin College contributed to a study no one foundation would have supported.

Literature Cited

Allee, W. C. 1926. Measurement of environmental factors in the rain-forest of Panama. Ecology **7**:273–302.

Bennett, C. F., Jr. 1963. A phytophysiognomic reconnaissance of Barro Colorado Island, Canal Zone. Smithson. Misc. Collect. **145**:1–8.

Berger, A. J. 1970. The present status of the birds of Hawaii. Pac. Sci. **24**:29–42.

Chapman, F. M. 1938. Life in an air castle. New York.

Diamond, J. M. 1971. Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. Proc. Natl. Acad. Sci. **68**:2742–2745.

Eisenmann, E. 1952. Annotated list of birds of Barro Colorado Island, Panamá Canal Zone. Smithson. Misc. Collect. **117**:1–62.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis **114**:307–343.

Horn, H. S. 1971. The adaptive geometry of trees. Princeton Univ. Press, Princeton, N. J. 144 p.

Karr, J. R. 1971. Structure of avian communities in selected Panamá and Illinois habitats. Ecol. Monogr. **41**:207–233.

Kenoyer, L. A. 1929. General and successional ecology of the lower tropical rain forest of Barro Colorado Island, Panama. Ecology **10**:201–222.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N. J. 203 p.

Morel, M. Y. 1964. Natalité et mortalité dans une population naturelle d'un passereau tropical, le *Lagonosticta senegala*. Terre Vie **3**:436–451.

Morton, E. S. 1971. Nest predation affecting the breeding season of the Clay-colored Robin. Science **171**:920–921.

Preston, F. W. 1962. The canonical distribution o

commonness and rarity. Ecology 43:185–215, 410–432.
Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1–48.
Simpson, G. G. 1964. Species density of North American recent mammals. Syst. Zool. 13:57–73.
Skutch, A. F. 1971. A naturalist in Costa Rica. Univ. Florida Press, Gainesville. 378 p.
Snow, D. W. 1962*a*. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. West Indies Zoologica 47:65–104.
———. 1962*b*. A field study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad. West Indies Zoologica 47:183–198.
Snow, D. W., and B. K. Snow. 1963. Breeding and the annual cycle in three Trinidad thrushes. Wilson Bull. 75:27–41.
Standley, P. C. 1933. The flora of Barro Colorado Island, Panama. Contrib. Arnold Arbor., Harv. 5:1–178.
Warner, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70:101–120.
Wetmore, A. 1957. The birds of Isla Coiba, Panamá. Smithson. Misc. Collect. 134:1–105.
Willis, E. O. 1966. Competitive exclusion and the foraging behavior of Plain-brown Woodcreepers. Ecology 47:667–672.
———. 1967. The behavior of Bicolored Antbirds. Univ. Calif. Publ. Zool. 79:1–132.
———. 1969. On the behavior of five species of *Rhegmatorhina*, ant-following antbirds of the Amazon basin. Wilson Bull. 81:363–395.
———. 1972*a*. The behavior of Spotted Antbirds. AOU Monogr. 10.
———. 1972*b*. The behavior of Plain-brown Woodcreepers. Wilson Bull. 84:377–420.
———. 1973*a*. The behavior of Ocellated Antbirds. Smithson. Contr. Zool.
———. 1973*b*. Survival rates for visited and unvisited nests of Bicolored Antbirds. Auk 90:263–267.
———. 1974. Seasonal changes in the litter fauna on Barro Colorado Island, Panamá. Ecology (in press).
Willis, E. O., and Y. Oniki. 1972. Ecology and nesting behavior of the Chestnut-backed Antbird (*Myrmeciza exsul*). Condor 74:87–101.
Woodring, W. P. 1958. Geology of Barro Colorado Island, Canal Zone. Smithson. Misc. Collect. 135:1–39.

Appendix I.

Calculations of Nest Survival, Fledgling Mortality, and Unsuccessful Nesting

A. Nest survival

Nests that survive to the next day and those that do not are tallied separately for each day. Surviving nests are divided by the total number to find the fraction surviving that day. The fraction for the 1st day is multiplied by the fraction for the 2nd day to get the graphed fraction of survival or percentage (Fig. 2–4) for the 2nd day; the graphed fraction is multiplied by the fraction surviving on each day thereafter. Nests are not counted before detection even when certainly occupied earlier.

Since survivorship of nests is somewhat lower at the center of the breeding season (Table 6) in these antbirds, and since many of my visits to Barro Colorado were near the middle of the breeding season, I have weighted data for Fig. 2–4: all tallies are divided by the number of the same months I studied the birds from 1960 to 1971. A tally for a July nest is divided by 8.1, for an April nest by 1.0, etc. Otherwise I would estimate survivorship too low, because I was most often present at a time of year when nests are least successful. (Unweighted data change final survivorships downward 1% or less in these cases.) Nests in 1961 tended also to be unsuccessful early in the year, perhaps abnormally so, but correction for a possible downward bias here does not seem warranted. Figures 2–4 probably represent minimum estimates of survivorship.

B. Fledgling mortality from brood sizes

Let A be the number of broods with one fledgling and B the number of broods with two at time t, say fledging. Let A' be the number of broods with one fledgling and B' the number with two at time t' (see Table 3). If p is the probability of a fledgling dying in the interval between t and t', then $1-p$ is the probability that it survives that interval. The number of broods of one reduced to none is Ap, the number of broods of two reduced to none is Bp^2. By the binomial theorem the number of broods of two reduced to one is $2B\,(p)(1-p)$. Then

$$\frac{A'}{B'} = \frac{A - Ap + 2\,Bp - 2\,Bp^2}{B - 2\,Bp + Bp^2}$$

The method assumes that each young in a brood of two survives as well as each young of a brood of one. For these antbirds this seems fairly likely. One fledgling goes with one parent, the other with the other parent. If there is only one young, the other parent often does not feed or care for it. Usually, therefore, one fledgling gets no more care or little more care than does each of two. Where fledgling survival differs with brood size, p is an average of the separate probabilities of loss.

C. Average time for an unsuccessful nesting

If the percentage of nests lost on a day i from the start of building is p_i, if i ranges from 1 to N (the day a new nest is started, on the average), and M is the total percentage loss from day 0 to day N, the average number of days preempted by an unsuccessful nesting is

$$\frac{\sum_{i=1}^{N} ip_i}{M}.$$

For antbirds, original data from Fig. 2–4 and Appendix I,A are used, but losses of nests before egg laying and complete loss of broods thereafter must be incorporated. Desertion of nests has never been noted, but some 5% seems possible; this would be 0.7% per day for Spotteds and 1.3% per day for Ocellateds and Bicolors. Complete loss (C) of fledglings to time t' (as in B) is

$$C = \frac{Ap + Bp^2}{A + B}.$$

Complete loss of fledglings for these antbirds is in Table 3. No complete loss was noted between day of discovery and day of independence of fledglings, but a small amount may be expected, so that the complete loss for Spotteds and Bicolors would be about 2.5%–3%, for Ocellateds 7–8%. If so, M for Ocellateds would be about 96%, for Bicolors about 89%, and for Spotteds about 92%. If one then assumes that most of the complete losses of broods took place in the first few days out of the nest, the average numbers of days per unsuccessful nesting are those given in Table 8.

Appendix II.

Breeding Birds That Have Disappeared From Barro Colorado Island

(g = nests or forages on or near the ground;
s = low second growth or edges of woodland;
* = disappeared as breeder between 1960 and 1970.)

*Little Tinamou (*Crypturellus soui*) gs
Roadside Hawk (*Buteo magnirostris*) s
Harpy Eagle (*Harpia harpyja*)
*Barred Forest-Falcon (*Micrastur ruficollis*)
*Red-throated Caracara (*Daptrius americanus*)
*Bat Falcon (*Falco rufigularis*) s
Great Curassow (*Crax rubra*) g
Marbled Wood-Quail (*Odontophorus gujanensis*) g
*Blue Ground-Dove (*Claravis pretiosa*) gs
Rufous-vented Ground-Cuckoo (*Neomorphus geoffroyi*) g
Tropical Screech-Owl (*Otus choliba*) s
Common Potoo (*Nyctibeus griseus*) s
Rufous-breasted Hermit (*Glaucis hirsuta*) s
White-vented Plumeleteer (*Chalybura urochrysia*) s
Blue-crowned Motmot (*Momotus momota*) gs
*White-necked Puffbird (*Notharchus macrorhynchus*) s
Cinnamon Woodpecker (*Celeus loricatus*) s
Red-crowned Woodpecker (*Centurus rubricapillus*) s
*Barred Woodcreeper (*Dendrocolaptes certhia*)
Buff-throated Automolus (*Automolus ochrolaemus*) g
Barred Antshrike (*Thamnophilus doliatus*) s
Streaked Antwren (*Myrmotherula surinamensis*) s
Black-faced Antthrush (*Formicarius analis*) g
*Thrushlike Manakin (*Schiffornis turdinus*) gs
Gray-capped Flycatcher (*Myiozetetes granadensis*) s
*Short-crested Flycatcher (*Myiarchus ferox*) s
Sulphur-rumped Flycatcher (*Myiobius sulphureipygeus*)
Black-tailed Flycatcher (*M. atricaudus*) s
N. Royal Flycatcher (*Onychorhynchus coronatus*)
Brownish Flycatcher (*Cnipodectes subbrunneus*)
Bay Wren (*Thryothorus castaneus*) s
Buff-breasted Wren (*Thryothorus leucotis*) s
*Black-bellied Wren (*Thryothorus fasciatoventris*) s
*Southern House Wren (*Troglodytes musculus*) s
White-breasted Wood-Wren (*Henicorhina leucosticta*) g
*Song Wren (*Leucolepis phaeocephalus*) g
Nightingale Wren (*Microcerculus philomela*) g
*Clay-colored Robin (*Turdus grayi*) gs
Chestnut-capped Warbler (*Basileuterus delattrei*) s
Thick-billed Euphonia (*Euphonia laniirostris*) s
*Crimson-backed Tanager (*Ramphocelus dimidiatus*) s
*Yellow-rumped Tanager (*Ramphocelus icteronotus*) s
White-lined Tanager (*Tachyphonus rufus*) s
Buff-throated Saltator (*Saltator maximus*) s
*Black-striped Sparrow (*Arremonops conirostris*) gs