The Living Bird, tenth annual (1971): 185-242

AN ECOLOGICAL STUDY OF THE BIRDS OF THE LOWLAND PINE SAVANNA AND ADJACENT RAIN FOREST IN NORTHEASTERN NICARAGUA

THOMAS R. HOWELL

This study concerns the avifauna in an extensive area of pine savanna that lies on the lowlands of the Caribbean slope in northeastern Nicaragua and eastern Honduras. This distinctive habitat, which supports only one species of pine, *Pinus caribaea,* is completely isolated by many miles of broad-leafed tropical rain forest or moist forest from the pine "ridges" of British Honduras and the highland pine forests of Honduras and Nicaragua (Figure 1).

General Ecology of the Pine Savanna

To summarize briefly from Parsons (1955), Radley (1960), Taylor (1963), and Munro (1966), who discussed the geography and some aspects of the ecology: the lowland pine savanna extends over approximately 9,200 square kilometers (calculated from a map in Radley) to 10,000 sq km (Munro, 1966) in Nicaragua, and about 6,600 sq km (from map in Monroe, 1968) in Honduras. Pines and grasslands occupy the greater part of the flat or gently undulating terrain that is generally less than 200 meters above sea level. The broad-leafed forest extends into the savanna along numerous watercourses and forms islands in low-lying areas throughout. I estimate that the incursions of broad-leafed forest occupy about one-fourth of the region; Parsons (1955) estimated one-third.

The savanna region corresponds fairly closely to an area of yellow-red latosols and hydromorphic soils associated with Pleistocene sediments; Radley (1960) considered it Pliocene; I have no precise dating of sediments. Within the area, the pines usually occupy expanses of very poor soil with little or no humus and only a relatively thin topsoil of sand, gravel, and clay overlying a deep bed of heavy, impermeable clay. The broad-leafed forests grow primarily in alluvial soils but can and do invade the poorer soils usually occupied by pines, and pines will grow in the richer soils if not shaded out in the seedling stage.

Frequently the boundaries between the pine savanna and rain forest are abrupt (Figure 2), but sometimes the pines and broad-leafed trees intermingle in a narrow zone. There are also extensive grasslands where trees and shrubs are sparse or lacking altogether.

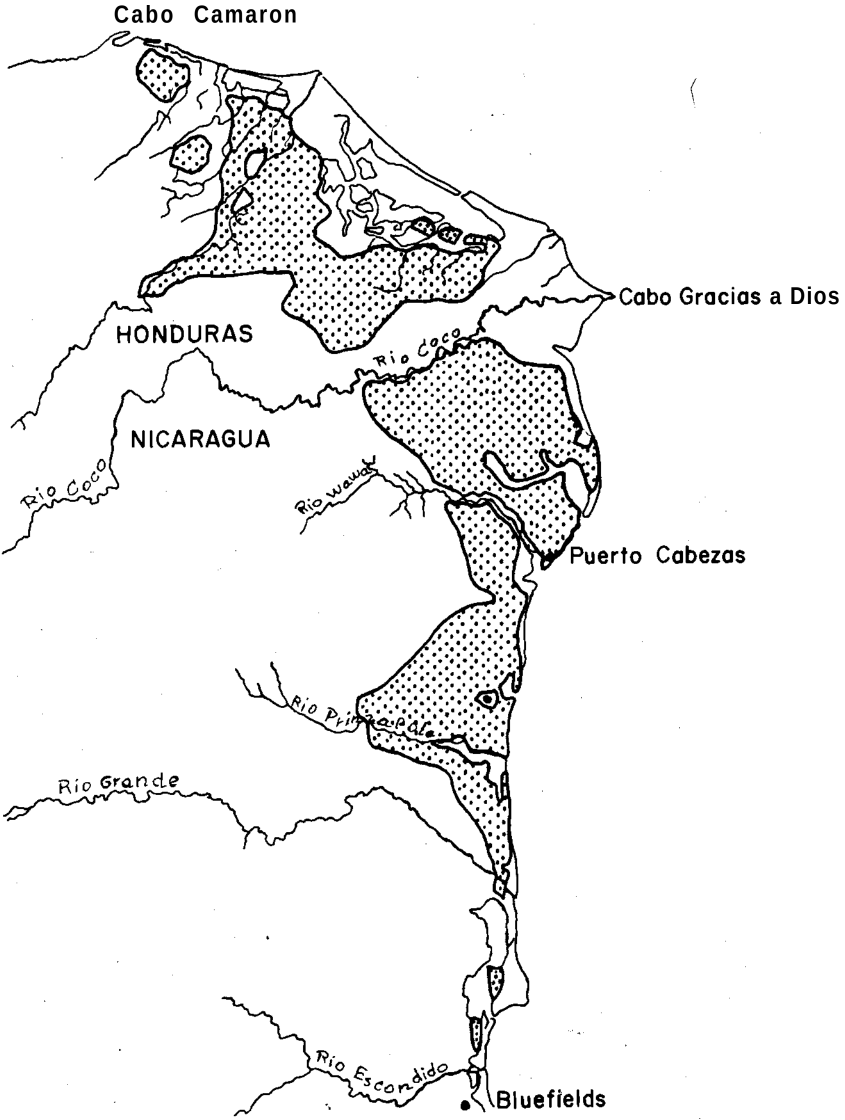

Figure 1. Eastern Honduras and Nicaragua in Central America showing the extent of lowland pine savanna (stippled area).

The humid, tropical climate has an average daily temperature of about 25" Centigrade and the minimum temperature is rarely below 20°C. The annual rainfall of 2,600 to 3,500 millimeters makes this savanna one of the wettest in the world. Talbot (1964) gives 1,270–1,524 mm for Africa, and Blydenstein (1967) records 1,700 to 2.000 mm for most of the llanos of Colombia "...increasing sharply near the base of the mountains to over 4,000 mm at Villavicencio." In the Nicaraguan pine savanna, a relatively dry season starts in February and extends through April, with March and April usually the driest months. Average rainfall records, compiled at Puerto Cabezas on the Caribbean coast, for the two dry months are: 1927–1950, March, 61.2 mm; April, 50 mm (Parsons, 1955); 1955–1959, March, 36.8 mm with extremes of 1.3–72.1 mm; April, 41.1 mm with extremes of 10.2–108.7 mm (Radley, 1960).

The precipitation varies locally so that, even in the dry season, rain falls over some part of the savanna almost every day. The areas where broad-leafed forest and pine savanna are contiguous probably receive the same amount of rain, but the soil penetration, run-off, and evaporation rates must differ considerably in the two habitats.

Even in March and April, numerous creeks flow throughout the savanna, and some small ponds appear to be permanent. However, most of the area of pines and grass dries out after a few sunny days, and grass fires, once started, spread rapidly.

The Nicaraguan pine savanna has been logged continuously since the 1920's, and almost no large pines remain in easily accessible regions. A good stand of pines may include trees up to 25 meters high; the rings of the larger felled trees indicate an age of about 70 or 80 years.

The age of the pine savanna is unknown and somewhat controversial. Parsons, Radley, Taylor, and Munro, as well as Denevan (1961) and Johannessen (1963), agree that the pine savannas owe their continued existence to periodic burning. The unsettled questions are whether the savannas originated through the clearing and burning of the broad-leafed forest by man, and if so, when the process began, or whether the savannas are the results of blowdowns by hurricanes, followed by lightning-started fires, possibly before the occupation of the region by man. Certainly, within historic times, man-made fires have maintained or extended the area of the savanna by destroying the encroaching broad-leafed seedlings and leaving the larger pines that are able to survive repeated burnings of the grassy understory (Figure 3).

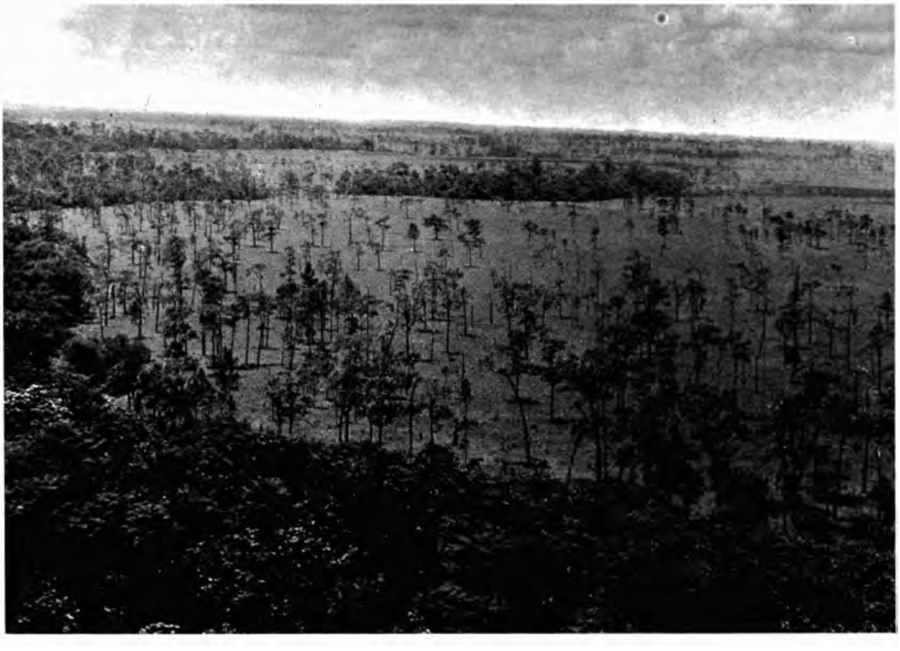

Figure 2. Rain forest-pine savanna interface, northeastern Nicaragua. Note the abrupt boundary here between the pine savanna and the rain forest (bottom of photograph).

Figure 3. Recently burned portion of pine savanna, showing damage to small pine seedlings and lower branches, (but undamaged crowns) of larger trees. Note rapid regrowth of grasses. Man-made fires are important in maintaining the savanna and preventing encroachment of broad leafed trees.

Ornithological Interest of the Pine Savanna

The pine savanna is of ornithological interest because: (1) it includes the southern limit of naturally occurring pines in the Western Hemisphere; (2) it includes the southern limit of the ranges of several pine-adapted species of birds, such as the Grace's Warbler (Dendroica graciae), Red Crossbill (Loxia curvirostra), and Chipping Sparrow (Spizella passerina); and **(3)** its isolation has led to the differentiation of several endemic subspecies of birds (Howell, 1965).

The region is of ecological interest because the pine forest is a very ancient and extensive vegetational association in the northern hemisphere and constitutes a distinctive temperate-zone habitat to which many organisms, including birds, are specially adapted. Although pines have penetrated tropical latitudes throughout the world, in the New World tropics they usually appear in montane regions, such as the Mexican plateau and the Central American highlands, where the climate tends toward temperate. The Nicaraguan-Honduran savanna, however, lies in lowlands between 12'10' and 16° N Lat., where the climate and general environmental conditions are entirely suitable for the well developed tropical rain forest that surrounds and interdigitates with it. In effect, the lowland pine savanna constitutes an irregular "island" of temperate-zone habitat set down in humid tropical surroundings.

The transition from a lush tropical forest with an abundance of cotingas, manakins, and antbirds to the pine savanna with a scattering of Common Meadowlarks (Sturnella magna), Common Bluebirds (Sialia sialis), and Chipping Sparrows is startling. This juxtaposition of primarily tropical and primarily temperate avifaunas offers a rare opportunity for a comparative study of the abundance, diversity, and ecologically relevant behavior of the resident birds under identical macroenvironmental conditions. The fact that the same day length, seasonal change in climate, elevation above sea level, and the basic soil conditions exist in both the savanna and broad-leafed forest narrows the range of environmental parameters that the investigators must consider in accounting for the differences in the avifaunas of the respective habitats.

Aims of the Study

The principal questions that I have considered are:

(1) What are the precise qualitative and quantitative differences between the avifaunas of measured areas of tropical pine savanna and adjacent broad-leafed forest?

(2) Within the tropical savanna, what are the differences between the bird populations in areas of pine with little understory and few seedlings, areas of pine with abundant seedlings of different heights, and treeless areas of grasses, sedges, and a few shrubs?

(3) Are the differences in bird populations in the various habitats'predictable on the basis of the different foliage profiles, as proposed by MacArthur and MacArthur (1961)?

(4) How do the bird populations of the tropical habitat compare, in numbers of species and numbers of individuals, with bird populations in temperate-zone habitats?

(5) Does competition between bird species influence their restriction to different habitats?

(6) Considering the composition of the avifaunas of the different habitats, what may one infer about competition, niche size and degree of niche overlap, and inter- and intraspecific partitioning of resources?

(7) How do the proportions of non-passerines to passerines and suboscines to oscines differ in the two habitats and how may one interpret the differences?

(8) What is the ecological effect of wintering North American migrants on the resident birds in both habitats?

(9) What historical factors may have been responsible for the differences in the avifaunas of the two habitats?

(10) What relevance do the answers to these questions have to the subject of latitudinal gradients in bird species diversity?

Methods

I visited the savanna region from 2 to 4 February 1955, 22 January to 20 February 1962, 16 January to 1 February 1963, 11 to 27 August 1965, 10 to 26 March 1966, 18 November to 1 December 1966, and 15 to 30 April 1967. Thus, I was present in both the wet and dry seasons, when the migrants were there from the north, and when breeding birds not resident the year round were present.

I studied intensively three areas — two in the pine savanna and one in the rain forest — and investigated less thoroughly two other savanna areas- one with a sparse growth of pines and one with grass and no trees.

For measuring the foliage characteristics and the bird species diversity of the different areas, I used the method described by MacArthur and MacArthur (1961). This permits direct comparison of my data from Nicaragua with the results obtained by MacArthur and his co-workers in temperate North America and in Panama (MacArthur *et* al., 1962; MacArthur, 1964; MacArthur *et* al., 1966). Appendix 1 presents a brief resume of this method and some minor modifications that we used to suit local conditions.

From measurements of vegetation density at different vertical levels, MacArthur and MacArthur (1961) calculated Foliage Height Diversity (FHD) for each of their study plots. From censuses of breeding birds in these plots, they calculated Bird Species Diversity (BSD) using the same equation as for FHD (see Appendix 1). When they plotted FHD against BSD for each of their plots, the results yielded a series of points that clustered about a straight line. A consideration of plant species diversity in relation to bird species diversity did not reduce the scatter of points or provide a better fit by a straight line. The authors concluded that BSD could be predicted, at least in certain temperate zone habitats, from FHD alone without considering the species composition of the vegetation. Their equation is $\mathrm{BSD} = 2.01\ \mathrm{FHD} + .46$. However, MacArthur (1964) pointed out that in the case of certain habitats and with some birds of specialized food habits, the proposed relationship between FHD and BSD might not hold. In a later section, I present measurements of FHD and BSD for the Nicaraguan pine savanna and rain forest areas, comparing them to temperate zone areas and discussing their predictability.

Antonio Molina R. identified many of the plants in the savanna area in the field, and we collected others for later study at the herbarium of the University of California, Los Angeles. Appendix II groups qualitatively the most conspicuous plants of the savanna study areas and includes a brief description of their appearance and importance to the bird fauna.

Description of Study Areas

We made quantitative measurements of vegetation density in plots designated as Pine Savanna Area 1, Pine Savanna Area 2, and Rain Forest Area, and calculated the FHD for each (Figure 4). These plots were all close together in terms of absolute distance and elevation. I have located each in relation to Waspam, about 75 miles or 120 km northwest of Puerto Cabezas in the Comarca de El Cabo. All had the same elevation, 65 m, except the Rain Forest Area which was 130 m. The Grassland and Rain Forest Areas are the same distance from Waspam though not contiguous; both lie along a curved road, approximately 14 miles or 22 km south southwest of Waspam, with the difference in compass directions too slight for notation.

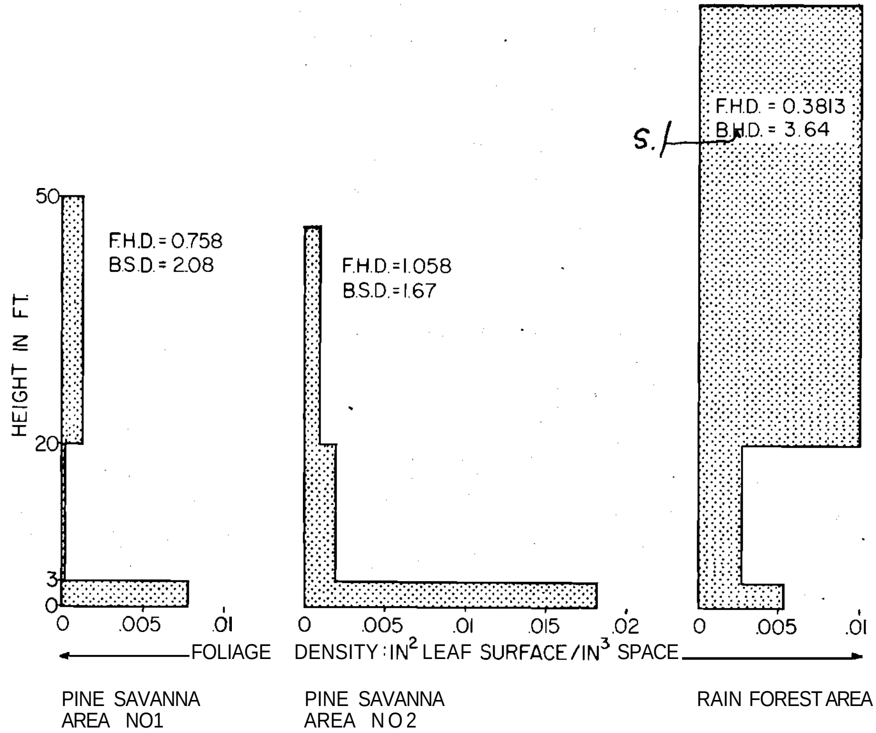

Figure 4. Foliage profiles, foliage height diversity (FHD), and bird species diversity (BSD) for Pine Savanna Areas Nos. 1 and 2 and the Rain Forest Area. See text for explanation.

Pine Savanna Area 1

Leicus Creek, 22.5 km southwest of Waspam; 25 acres, 348 by 348 yards.

Characteristics (Figure 5): Pine trees irregularly spaced, moderately dense; average height of 27 trees above 25 feet, chosen at random, 50.2 ft, extremes 27 to 71 ft; seedling pines and large shrubs sparse; dense ground cover of grasses and sedges; no streams or permanent standing water, but some low lying wet areas; permanent streams within 100 m; dirt road, rarely used, running through area near eastern edge.

Most conspicuous plants: Trees—Pinus caribaea, throughout; Curatella americana, scarce. Shrubs—Byrsonima crassifolia, throughout; Miconia lundelli, throughout; M. albidea, throughout. but less common than M. lundelli. Herbs—Tibouchina belizensis. mostlv in lower areas with slow drainage; Clidemia rubra, throughout; Polygala sp., throughout; Diodia frutescens, throughout; Borreria suaueolens, throughout. Grasses and sedges—Pasoalum humboldtianum, throughout; Panicum sp.. throughout; Aristida sp., throughout; Andropogon sp., edges of road, scarce; Hypolytrum schraderianum, throughout; Bulbostylus paradoxa, throughout; Rhynchospora barbata, throughout; Fimbristylis sp., throughout. Arboreal plants—Psittacanthus mayanus, fairly common; Aechmea bracteata, fairly common; Tillandsia sp., abundant. Ferns-Blechnum sp., in low-lying wet places.

Pine Savanna Area 2

Located 15.3 km south southwest of Waspam; approximately 15 acres of a square 345 by 345 yds, of which about 10 acres was burned in 1965 and lacked trees or shrubs; the burned section, one corner of the square, was excluded from study area.

Characteristics (Figure 6): Pine trees irregularly spaced, moderately dense; average height of 25 trees above 25 ft chosen at random, 46.3 ft, extremes 31.5 to 68 ft; seedling pines numerous, often dense; large shrubs numerous in some sections; ground cover of grasses and sedges denser and higher than in Area 1; standing water in low-lying areas; frequently used dirt road running through northern edge.

Figure 5. Pine Savanna Area No. 1.

Most conspicuous plants: As in Area 1 with the following exceptions: Shrubs—in northern part of area, Miconia scorpioides, M. impetularis, Palicourea guineense, and a few young Xylopia frutescens in small numbers; Tibouchina belizensis in dense stands in the same area; all stands were between 1.5 and 2 m high. Grasses and sedges—Paspalunz humboldtianurn much more luxuriant than in Area No. 1; the smaller plants of the ground cover were fewer.

Pine Savanna Area 3

Located 20 km southwest of Waspam; 25 acres, irregular pentagon, longest side 350 yds.

Characteristics (Figure 7): Similar to Savanna Area 1, but trees and shrubs sparser and ground cover of grasses and sedges lower and less dense; permanent small stream, bordered with dense stands of cane grass (Tripsacum sp.), winding through area; a few low-lying spots that seemed permanently wet support dense stands of Tripsacum, Tibouchina belizensis, and large sword ferns; a few clumps of Sabal palmetto; gravel road, frequently used, outside western edge. No measurements of tree heights or vegetation density.

Grassland

Located 25 km south southwest of Waspam; 5 acres, 155 by 155 yds.

Characteristics (Figure 8): Dense grass and sedges with few shrubs and pine seedlings usually no higher than the grass; average height of dense grass, measured at 15 random points, 1.85 ft; maximum height of sparse blades, about **3** ft; one dead weathered pine about 15 m high in center; conditions varying from low cover and bare ground on dry soil to taller denser cover and some standing water in low areas; surrounding area largely grassy, with sparse growth of small pines near two of the sides.

Most conspicuous plants: Grasses and sedges as in Pine Savanna Area 1; Andropogon in a few small clumps; Byrsonima crassifolia and Tibouchina belizensis sparsely distributed; a few pine seedlings about 1 m high.

Rain Forest Area

Located about 25 km south southwest of Waspam, elevation 130 m; approximately 10 acres, irregular quadrilateral with longest side 300 yds and shortest, 157 yds.

Characteristics (Figures 9 and 10): Many species of broad-leafed hardwood trees; numerous epiphytes, philodendrons, and lianas; bamboo and ***Heliconia*** abundant at edges and in more open areas in forest; several small permanent streams winding through; average height of 10 trees over 25 ft high, selected at random, 74.3 ft, extremes 36 to 142 ft; understory of seedlings, herbs, and small palms (some thorny); terrain slightly contoured, maximum difference in elevation about 10 m; not primeval; evidence of small amount of selective logging probably within past five years; numerous second-growth indicator species; trail along one edge with clearing beyond.

Most conspicuous plants: Species composition greatly mixed; most trees not identified; see Taylor (1963) for characteristic lowland evergreen trees found in the rain forest on the Caribbean slope in Nicaragua.

Avifauna of the Pine Savanna

A relatively small number of bird species use the savanna habitat. Table 1 lists *56* species although we did not record all of these in the study areas. The list does not include water birds and waders that mav occur in and out of the savanna, nor the spring and fall transients that are present only briefly, nor all the species ever recorded in or over the savanna. Rather, the list includes all species that use the characteristic features of the savanna in some ecologically important way, or combination of ways-i.e., foraging, feeding, resting, nesting — with at least some regularity. Because equivocal cases are inevitable, I have provided some explanatory footnotes in Table 1. The categories are:

Permanent residents — resident species whose presence in this general region depends on the presence of the savanna. These birds carry on most or all of their activities in the savanna and are absent from the broad-leafed forest.

Figure 6. Pine Savanna Area No. 2. Note the abundance ot seedlings, and the white board and poles used for foliage measurements.

Figure 7 (above). Pine Savanna Area No. 3.

Figure 8 (below). The Grassland Area.

Wide-ranging residents — resident species that use the savanna frequently and importantly, perhaps exclusively in the case of some individuals, but which, as species, also use adjacent, nonsavanna habitats frequently and importantly.

Summer residents — species that differ from permanent residents only by their absence.

Winter residents — species that nest in temperate North America and occur regularly in the savanna during the winter months.

Regular visitors from adjacent broad-leafed forest-resident species that are widespread in broad-leafed forest or forest edge and regularly range into the savanna and may even nest in the pines; all of these species appear to depend on a broad-leafed forest close by for many or most of their activities.

The avifauna of the savanna areas showed little variation in the resident populations from year to year or season to season, except in Area *2,* In November 1966, when logging began there. I shall discuss the effects of this on the bird population later. Some of the resident birds were apparently paired the year round, and in August 1965 we noted some, including the Vermilion Flycatcher (*Pyrocephalus rubinus*), Common Bluebird, Hepatic Tanager (*Piranga flava*), and Rusty Sparrow (*Aimophila rufescens*), in family groups. Others, such as parrots and the Common Meadowlark, appeared to maintain pairs within flocks and still others, such as the Black-headed Siskin (*Carduelis notata*) and Chipping Sparrow, formed large flocks in the winter months with no evidence of pairing. The only winter resident recorded within the study areas was the Yellow-throated Warbler (*Dendroica dominica*). I shall discuss the interactions between this species and the resident Grace's Warbler later.

We often saw flocks of mixed species, especially in winter, and we noted the tendency for pairs of different species to concentrate in certain areas even at the height of the breeding season in April, leaving other parts of the savanna virtually devoid of birds. We did not determine whether the attraction of other birds as such was the cause of these concentrations or whether the concentrations simply indicated more favorable ecological conditions, not obvious to us.

We estimated the numbers of breeding territories of the species in each of the study areas (Tables 2 and **3)** and used these figures to calculate the bird species diversity for each area. Visitors and migrants, also listed, include other birds recorded in each area, but apparently not within their breeding territories.

Avifauna of the Rain Forest Area

We recorded 116 species within the 10-acre study area. However, we considered less than half of these residents; 14 or 15 were migrants; others we recorded only once. For many species, it is difficult to establish reliable criteria of "residence" in a small section of rain forest. Some are secretive or difficult to see in the crown of tall trees. Others wander in mixed species flocks, following army ant trails or feeding at briefly flowering or fruiting trees. The breeding of different species at different seasons means that some birds are singing on territories while others are silent and inconspicuous.

TABLE 1

Birds of the Pine Savanna in Nicaragua

	Permanent Residents
Accipitridae	*Buteo albicaudatus,* White-tailed Hawk *B. jamaicensis,* Red-tailed Hawk
Falconidae	*Falco sparverius,* American Kestrel *F. femoralis,* Aplomado Falcon *Polyborus cheriway,* Crested Caracara
Phasianidae	*Colinus nigrogularis,* Black-throated Bobwhite
Columhidae	*Columbina minuta,* Plain-breasted Ground Dove
Psittacidae	*Amazona ochrocephala,* Yellow-headed Parrot [1]
Strigidae	*Bubo virginianus,* Great Horned Owl
Trochilidae	*Amazilia cyanocephala,* Red-billed Azurecrown
Picidae	*Dendrocopos scalaris,* Ladder-backed Woodpecker
Tyrannidae	*Pyrocephalus rubinus,* Vermilion Flycatcher *Muscivora tyrannus,* Fork-tailed Flycatcher
Troglodytidae	*Cistothorus platensis,* Sedge Wren
Turdidae	*Sialia sialis,* Common Bluebird
Parulidae	*Dendroica graciae,* Grace's Warbler
Icteridae	*Icterus chysater,* Yellow-backed Oriole *Sturnella magna,* Common Meadowlark
Thraupidae	*Piranga flava,* Hepatic Tanager
Fringillidae	*Carduelis notata,* Black-headed Siskin *Loxia curvirostra,* Red Crossbill *Sicalis luteola,* Yellow Grass-finch [2] *Ammodramus savannarum,* Grasshopper Sparrow *Aimophila rufescens,* Rusty Sparrow *A. botterii,* Botteri Sparrow *Spizella passerina,* Chipping Sparrow
	Wide-ranging Residents
Cathartidae	*Cathartes aura,* Turkey Vulture *C. burrovianus,* Yellow-headed Turkey Vulture *Coragyps atratus,* Black Vulture
Rallidae	*Laterallus ruber,* Ruddy Crake
	Summer Residents
Caprimulgidae	*Chordeiles minor,* Common Nighthawk *Caprimulgus maculicaudus,* Spot-tailed Nightjars [3]

TABLE 1 *(Continued)*

	Winter Residents
Picidae	*Sphyrapicus varius,* Yellow-bellied Sapsucker
Hirundinidae	*Iridoprome bicolor,* Tree Swallow[4]
Parulidae	*Dendroica coronata,* Myrtle Warbler *D. dominica,* Yellow-throated Warbler *D. palmarum,* Palm Warbler
	Visitors from Adjacent Broad-leafed Forest
Accipitridae	*Buteo magnirostris,* Roadside Hawk
Falconidae	*Herpetotheres cachinnans,* Laughing Falcon *Falco rufigularis,* Bat Falcon
Columbidae	*Columba cayennensis,* Pale-vented Pigeon *C. speciosa,* Scaled Pigeon
Psittacidae	*Ara macao,* Scarlet Macaw *Amazona autumnalis,* Red-lored Parrots *Aratinga astec,* Olive-throated Parakeet
Strigidae	*Glaucidium brasilianum,* Ferruginous Pygmy Owl
Nyctibiidae	*Nyctibius griseus,* Common Potoo
Caprimulgidae	*Nyctidromus albicollis,* Pauraque
Picidae	*Piculus rubiginosus,* Golden-olive Woodpecker *Dryocopus lineatus,* Lineated Woodpecker *Melanerpes formicivorus,* Acorn Woodpecker[6]
Tyrannidae	*Tyrannus melancholicus,* Tropical Kingbird[7] *Elaenia flavogaster,* Yellow-bellied Elaenia[7]
Hirundinidae	*Progne chalybea,* Gray-breasted Martin
Corvidae	*Psilorhinus morio,* Brown Jay
Parulidae	*Geothylypis poliocephala,* Gray-crowned Yellowthroat

---

1 Apparently feeds only in broad-leafed trees at the edge of the savanna.

2 Apparently a gregarious species of wandering habits and irregular occurrence.

3 Not recorded from November to March; presumably absent during that time.

4 Recorded only in February 1963 when it was abundant.

5 Found in the savanna as frequently as the Yellow-headed Parrot, but differs in that it uses broad-leafed forest as much as it does the savanna.

6 Uses the savanna only in the vicinity of oaks *(Quercus oleoides).*

7 More likely to range out, even territorially, into the savanna from the broad-leafed forest edge than other tyrannids such as *Contopus cinereus, Myiarchus tuberculifer,* and *Myiozetetes similis.*

For calculating the species diversity, I included only those species that we found nesting or on territories in April 1967, or that we recorded more than once in that month and also in March and November 1966 when we made other censuses. This lowers the list to 37 species, a conservative figure, since we doubtless overlooked some inconspicuous forms at one time or another.

We encountered further difficulties in estimating the number of territories. Hummingbird females, for example, may not nest within the territories of conspicuous males; each male in a group of displaying manakins may not secure a mate and nest within the study area; and the study area may represent only a portion of the entire territory of a nesting pair of kites. Such complications, though they may introduce some error into the estinlates, are unavoidable. In Table **3,** I estimated the number of territories for each of the 37 species believed to be resident in at least part of the study area, and calculated the bird species diversity (BSD) from these figures.

Results

The foliage profiles for all three areas in which we measured the vegetation density agree reasonably well with our impressions of the physiognomy of the total vegetation. The reader may judge this by examining the photographs (Figures 5–10). We may now consider each area from the standpoint of the predicted bird species diversity.

Pine Savanna Area I

The calculated BSD of 2.08 in this study is close to the figure of 1.98, predicted from the formula derived by MacArthur and MacArthur (1961) on the basis of data gathered in file-acre plots of deciduous woodland in temperate North America. One could interpret this result as a confirmation of the prediction, at least as applied to a habitat that is characteristic of temperate regions despite its location in a tropical latitude and climate. However, the Nicaraguan study area encompasses 25 acres instead of only five, as used by the MacArthurs. Even in the 25 acres, only two of the 10 breeding bird species had more than one pair with territories within the study area. With such low densities of breeding pairs, the size of the study plot definitely affects the diversity figures. For example, if we had censused only five acres within Area 1, we could, assuming that the foliage height diversity (FHD) was relatively uniform, have obtained a count of three territories and four species (for example, 1, 1, 0.5, 0.5) with a BSD of only 1.23 -- well below the predicted figure.

The foliage profile and FHD of .731 for five acres of deciduous woodland in Vermont (MacArthur and MacArthur, 1961) appear quite close to the foliage profile and FHD for Pine Savanna Area 1; the Vermont woodland included nine territories of six species; the Nicaraguan Area 1 included 10 territories of nine species. Taken as a whole, the quantitative data suggest that, in terms of bird population density and species diversity, five acres of temperate deciduous woodland is roughly equivalent to 25 acres of tropical pine savanna.

Such comparisons are difficult to evaluate as the pine savanna, in contrast to deciduous woodland, includes only one species of tall tree. Furthermore, pines represent a special type of vegetational resource to which some birds are well-adapted and others not at all. I know of no measurements of FHD in temperate zone pine forests, but there are bird censuses in such habitats from which BSD can be calculated.

Figure 9. Edge of the Rain Forest **Area.**

In Georgia, Norris (1951) censused the breeding birds in 43 acres of mature, but recently burned-over, longleaf-pine forest (*Pinus palustris*) with only a light woody undercover and wire-grass (*Aristida*); this habitat appears similar to the Nicaraguan pine savanna. Eliminating one pair of Cardinals (*Cardinalis cardinalis*) and one pair of Yellow-throated Vireos (*Vireo flavifrons*) that depended on patches of broad-leafed vegetation, Norris recorded 15 species and 82.5 breeding pairs (Table 7). Since 25 is about 0.6 of 43,25 acres should have about 50 pairs and a BSD of 2.13, a figure remarkably close to the BSD of 2.08 for Pine Savanna Area 1, but with five times as many breeding territories.

Assuming (1) that Norris' longleaf-pine area had a FHD similar to that in Savanna Area 1, (2) that the interpolation of figures from 43 to 25 acres is valid, and (3) that the similarities in BSD for the Vermont, Georgia, and Nicaraguan study area are not merely coincidental, it appears that we may expect a BSD of approximately 2.0 in areas of similar foliage profile in (a) temperate deciduous woodland, (b) temperate pine woodland, and (c) tropical pine savanna. But the tropical pine savanna differs in that it is five times as large as the temperate deciduous woodland and includes only one-fifth as many breeding bird territories as the temperate pine woodland. One way or another, the Savanna Area 1 appears to be only one-fifth as "rich" as comparable areas in the temperate zone.

TABLE 2

Species and Numbers of Breeding Territories in the Nicaraguan Pine Savanna

Species	*Area No. 1*	*Area No. 2*	*Area No. 3*
Breeding Species			
Falco sparverius	—	—	0.25
Colinus nigrogularis		0.5	0.25
Ara macao (1967) or *Amazona ochrocephala* (1966)	0.5	—	—
Amazilia cyanocephala	1.0	1.0	—
Dendrocopos scalaris	0.5	—	
Sialia sialis	1.0	—*	—
Dendroica graciae	2.5	2.0	0.5
Geothlypis poliocephala	—	0.5	—
Sturnella magna	1.0	—*	1.0
Piranga flava	1.5	1.5	—
Carduelis notata	1.0	—	—
Aimophila rufescens	1.0	1.0	1.0
Total number of pairs	10.0	6.5	3.0
B.S.D.	2.08	1.67	1.44
Species Recorded, but Apparently Not on Territories			
Coragyps atratus	x	—	—
Herpetotheres cachinnans	x	—	—
Columba speciosa	x	—	—
C. cayennensis	x	x	x
Arnazona autumnalis	x	x	x
Bubo virginianus	x	—	—
Chordeiles minor	x	x	x
Piculus rubiginosus	—	x	—
Dyocopus lineatus	—	x	—
Melanerpes formicivorus	x	—	—
Pyrocephalus rubinus	—	—	x
Progne chalybea	x	x	—
Psilorhinus morio	—	x	—
Dendroica dominica	x	x	x
Loxia curvirostra	x	—	—
Airnophila botterii	—	—	x

*Recorded after logging of area; may or may not have bred there.

Figure 10. Rain Forest Area showing varied tree heights.

Davenport (1964, 1965, 1966) repeatedly censused 18.5 acres of Georgia pine forest with 95 per cent Pinus "caribaea" (= *P. elliottii*), 4 per cent Sweet Gum (*Liquidamber stryaciflua*), and a patchy undercover of shrubs and seedlings with virtually no grasses. His figures for each of three consecutive years show 22 species and 42 territorial males, 20 species and 41 territorial males, 19 species and 50 territorial males. The number of species in Davenport's Georgia area is higher than in Norris' Georgia area, but some of these such as the Yellow-billed Cuckoo (*Coccyzus americana*) and Hooded Warbler (*Wilsonia citrina*) obviously depend on broad-leafed plants.

Davenport's area seems less like the Nicaraguan pine savanna than does Norris'; but in Davenport's area also there appear to be about 50 breeding territories of pine-dwelling birds in 25 acres. Davenport's three-year average is 44.3 territories in 18.5 acres or about 60 in 25 acres. However, Davenport's list includes about 10 species that are wholly, or largely, dependent on broad-leafed vegetation. Very likely, if the larger trees were exclusively pines, these 10 would not occur in the area and there would be close to 50 breeding territories in 25 acres.

One can compare the bird populations of different regions by using the combined weights of all the breeding birds found in equivalent areas of each region. I did this for Savanna Area 1, for the Vermont deciduous woodland of MacArthur, and for the Georgia longleaf-pine forest of Norris. I took the weights of the Nicaraguan savanna birds exclusively from specimens collected there, and obtained the weights for the birds in the Vermont and Georgia areas principally from Hartman (1955) and Norris and Johnston (1958). Though the sample size of each species is sometimes small, the means of the weights are probably adequate for comparison. In practice, it was convenient to average the average weights of males and females of each species and multiply this figure by the number of pairs present. Because pairs were involved, one should double this sum to arrive at the total weight of breeding birds present.

The total weight of the birds for Pine Savanna Area 1 was 468 grams, without the weight of a breeding pair of parrots, which I excluded because they apparently took no food from the savanna and thus were not in the same category as the resident species that fed there exclusively. The weight for the breeding birds in 25 acres of Georgia longleaf-pine forest was 2,680 g, approximately 5.7 times as great. Although these figures are approximations, they conform fairly well to other data that suggest that the tropical pine savanna is only one-fifth as rich in birdlife as a comparable area in the temperate zone.

The weight of the birds from the five-acre deciduous woodland in Vermont is 458 g. This figure, from an area with a vegetational profile similar to that in Savanna Area Number 1, is very close to the figure of 468 g for 25 acres of Area 1 and lends support to the suggestion that, in terms of bird population, 25 acres of tropical pine savanna is ecologically equivalent to five acres of temperate deciduous woodland with a comparable FHD. The three areas had certain taxa in common (Table 8).

I have discussed Savanna Area 1 at length because it appeared to approach the upper limit of numbers of species and individuals that occur in any area of comparable size in the unmixed pine savanna in Nicaragua. Our field parties carefully covered hundreds of acres of this savanna and never encountered a section that appeared to support a greater variety and quantity of birds, even in pure stands of pines that were taller or denser or both.

Pine Savanna Area 2

The presence of a well-developed intermediate layer of pine seedlings and a much denser ground cover results in a FHD of 1.058, and a predicted BSD of 2.59—considerably higher than that for Savanna Area 1. However, the actual BSD, according to our observations was only 1.67, considerably lower than the prediction and lower than the diversity we observed in Area 1.

This is a striking exception to the generalization that the addition of a layer of foliage increases the BSD, but there is a possible ecological explanation. We delimited Area 2 to include onlv acreage that was unburned for many years, thus supporting a higher growth of ground-cover plants and much denser stands of pine seedlings than in Area 1. This difference eliminated suitable habitat in Area 2 for the Common Bluebird and Common Meadowlark, two species found in Area 1, but did not provide conditions favorable for breeding of other local species.

The pine seedlings are strictly a transient formation in this region. They grow rapidly into tall trees or they are destroyed by fires that are apparently both a cause and a consequence of the savanna environment. A dense growth of herbaceous cover in one corner of Area 2 probably accounted for the inclusion within it of part of a territory of the Gray-crowned Yellowthroat (*Geothlypis poliocephala*), a species not adapted to the exploitation of pine seedlings. Thus, the net effect of the increased density of the vegetalion was a reduction in the number of bird species and individuals present.

As the intermediate layer, predominately of pine seedlings, is seldom used by any birds except occasionally by the usually higher ranging Grace's Warbler and Hepatic Tanager, we recalculated the FHD with the assumption that the resident birds recognized only two layers—0 to **3** ft and **3** to 42.26 ft which was the average height of trees higher than 25 ft. This yields an FHD of 0.696 and a predicted BSD of 1.86, a figure considerably closer to our observed BSD of 1.67. It supports the speculation that Area 2 represents essentially a two-layer habitat for birds.

TABLE 3

Birds of the Rain Forest Area

Family	*Species*	*Number of breeding territortes*
	Breeding Pairs	
Tinamidae	*Tinamus major,* Great Tinamou	0.5
Acdpitridae	*Leptodon cayanensis,* Gray-headed Kite	0.25
Columbidae	*Columba nigrirostris,* Short-billed Pigeon	0.5
Trochilidae	*Phaethornis superciliosus,* Long-tailed Hermit	1.5
	P. longuemareus, Little Hermit	2.0
	Thalurania furcata, Green-crowned Woodnymph	2.0
	Hylocharis eliciae, Blue-throated Goldentail	1.0
	Amazilia candida, White-bellied Emerald	0.25
	Chalybura urochrysia, Bronze-tailed Plumeleteer	1.0
Trogonidae	*Trogon rufus,* Black-throated Trogon	1.0
Picidae	*Centurus pucherani,* Black-cheeked Woodpecker	0.5
	Phloeoceastes guatemalensis, Pale-billed Woodpecker	0.5
Dendrocolaptidae	*Dendrocincla fuliginosa,* Plain-brown Woodcreeper	1.0
Furnariidae	*Sclerurus guatemalensis,* Scaly-throated Leafscraper	0.25
Formicariidae	*Thamnophilus punctatus,* Slaty Antshrihe	2.5
	Myrmotherula fulviventris, Fulvous-bellied Antwren	1.0
	M. axillaris, White-flanked Antwren	1.0
	Microrhopias quixensis, Dot-winged Antwren	1.0
	Formicarius analis, Black-faced Antthrush	1.0
	Phaenostictus mcleannani, Ocellated Antthrush	1.0
Pipridae	*Pipra mentalis,* Red-capped Manakin	5.5
Cotingidae	*Laniocera rufescens,* Speckled Mourner	1.0
Tyrannidae	*Megaynchus pitangua,* Boat-billed Flycatcher	1.0
	Terenotriccus erythrurus, Ruddy-tailed Flycatcher	1.0
	Myiobius barbatus, Sulphur-rumped Flycatcher	1.0
	Platyrinchus mystaceus, White-throated Spadebill	0.5
	Pipromorpha oleaginea, Ochre-bellied Flycatcher	3.0
Troglodytidae	*Henicorhina leucosticta,* White-breasted Wood-wren	2.5
Sylviidae	*Polioptila plumbea,* Tropical Gnatcatcher	1.5
Vireolaniidae	*Smaragdolanius pulchellus,* Green Shrike-vireo	1.0
Vireonidae	*Hylophilus decurtatus,* Gray-headed Greenlet	2.5
Parulidae	*Phaeothylypis rivularis,* Buff-rumped Warbler	0.5
Thraupidae	*Euphonia gouldi,* Olive-backed Euphonia	1.0
	Chlorothraupis carmioli, Olive Tanager	2.0
	Habia fuscicauda, Dusky-tailed Ant-tanager	2.5
Fringillidae	*Cyanocompsa cyanoides,* Blue-black Grosbeak	1.0
	Arremon aurantiirostris, Orange-billed Sparrow	0.5
		47.75

TABLE **3** *(Continued)*

Family	*Species*	*Number of breeding territories*
	Visitors and Migrants	
Accipitridae	*Accipiter bicolor,* Bicolored Hawk	
	uteo magnirostris, Roadside Hawk	
Cracidae	*Penelope purpurascens,* Crested Guan	
Phasianidae	*Odontophorus erythrops,* Rufous-fronted Wood-quail	
	Rhynchortyx cinctus, Tawny-faced Quail	
Columbidae	*Columba cayennensis,* Pale-vented Pigeon	
	C. speciosa, Scaled Pigeon	
	Leptotila cassinii, Gray-chested Dove	
Psittacidae	*Ara macao,* Scarlet Macaw	
	Aratinga astec, Olive-throated Parakeet	
Cuculidae	*Piaya cayana,* Squirrel Cuckoo	
	Neomorphus geoffroyi, Rufous-vented Ground-cuckoo	
Trochilidae	*Threnetes ruckeri,* Band-tailed Barbthroat	
	Florisuga mellivora, White-necked Jacobin	
	Amazilia amabilis, Blue-chested Hummingbird	
	Heliothrix barroti, Purple-crowned Fairy	
Momotidae	*Momotus momota,* Blue-crowned Motmot	
Bucconidae	*Notharchus macrorhynchos,* White-necked Puffbird	
	Malacoptila panamensis, White-whiskered Puffbird	
Ramphastidae	*Pteroglossus torquatus,* Collared Aracari	
	Ramphastos sulfuratus, Keel-billed Toucan	
	R. swainsonii, Chestnut-mandibled Toucan	
Picidae	*Piculus simplex,* Rufous-winged Woodpecker	
	Celeus castaneus, Chestnut-colored Woodpecker	
Dendrocolaptidae	*Dendrocincla anabatina,* Tawny-winged Woodcreeper	
	Glyphorynchus spirurus, Wedge-billed Woodcreeper	
	Xiphorhynchus guttatus, Buff-throated Woodcreeper	
Furnariidae	*Automolus ochrolaemus,* Buff-throated Foliage-gleaner	
	Xenops minutus, Plain Xenops	
Formicariidae	*Cymbilaimus lineatus,* Fasciated Antshrike	
	Myrmotherula schisticolor, Slaty Antwren	
	Myrmeciza exsul, Chestnut-backed Antbird	
	Gymnopithys bicolor, Bicolored Antbird	
	Hylophylax naevioides, Spotted Antbird	
	Grallaria fulviventris, Fulvous-bellied Antpitta	
Pipridae	*Manacus candei,* White-collared Manakin	
	Schiffornis turdinus, Thrush-like Manakin	
Cotingidae	*Carpodectes nitidus,* Snowy Cotinga	
	Rhytipterna holerythra, Rufous Mourner	
Tyrannidae	*Contopus* sp., Pewee	
	Onychorhynchus mexicanus, Northern Royal-flycatcher	
	Platyrinchus coronatus, Golden-crowned Spadebill	
	Rhynchocyclus brevirostris, Eye-ringed Flatbill	
	Todirostrum cinereum, Common Tody-flycatcher	
	Oncostoma cinereigulare, Northern Bentbill	
	Ornithion semiflavum, Yellow-bellied Tyrannulet	

TABLE 3 (Continued)

Family	*Species*	*Number of breeding territories*
Corvidae	***Psilorhinus morio,*** Brown Jay	
Troglodytidae	***Thryothorus castaneus,*** Bay Wren	
	Cyphorhinus phaeocephalus, Song Wren	
Mimidae	***Dumetella carolinensis,*** Common Catbird	
Turdidae	***Hylocichla mustelina,*** Wood Thrush	
Sylviidae	***Ramphocaenus melanurus,*** Long-billed Gnatwren	
Vireonidae	***Vireo olivaceus,*** Red-eyed Vireo	
	Hylophilus ochraceiceps, Tawny-crowned Greenlet	
Coerebidae	***Chlorophanes spiza,*** Green Honeycreeper	
	Cyanerpes Eucidus, Shining Honeycreeper	
	Dacnis cayana, Blue Dacnis	
Parulidae	***Mniotilta uaria,*** Black-and-white Warbler	
	Dendroica magnolia, Magnolia Warbler	
	D. pensylvanica, Chestnut-sided Warbler	
	D. castanea, Bay-breasted Warbler	
	Seiurus aurocapillus, Ovenbird	
	S. noueboracensis, Northern Waterthrush	
	S. motacilla, Louisiana Waterthrush	
	Oporornis formosus, Kentucky Warbler	
	Wilsonia canadensis, Canada Warbler	
Icteridae	***Zarhynchus wagleri,*** Chestnut-headed Oropendola	
	Gymnostinops montezuma, hlontezuma Oropendola	
	Cacicus uropygialis, Scarlet-rumped Cacique	
	Zcterus galbula, Baltimore Oriole	
Thraupidae	***Euphonia lauta,*** Yellow-throated Euphonia	
	Tangara larvata, Golden-masked Tanager	
	Ramphocelus passerinii, Scarlet-rumped Tanager	
	Piranga rubra, Summer Tanager	
	Lanio leucothorax, White-throated Shrike-tanager	
	Tachyphonus luctuosw, White-shouldered Tanager	
Fringillidae	***Saltator maximus,*** Buff-throated Saltator	
	Caryothraustes poliogaster, Black-faced Grosbeak	
	Oryzoborus funereus, Thick-billed Seed-finch	

The bird fauna in Area 2 changed as conditions in and around it changed. As previously mentioned, 10 acres of small pine seedlings and grass, adjacent to the 15-acre study plot, were burned about four months before the first census in August 1965, and at that time were devoid of birds. By March 1966, the ground-cover plants in the burned area showed considerable regrowth and we recorded the Common Meadowlark and Common Bluebird as visitors.

Unfortunately, logging operations that coincided with my next visit, in November 1966, removed most of the larger straight pines, knocked down some seedlings, and scattered many sawed-off branches and tree tops. On 28 November, I saw a Golden-olive Woodpecker ***(Piculus rubiginosus)*** and a Lineated Woodpecker ***(Dyocopus lineatus)*** foraging in some of the remaining larger pines, especially those damaged by the logging. I had not recorded them previously and never saw them again in that area. In addition, we saw a Gray-crowned Yellowthroat foraging among fallen pine branches in the center of the area, well away from the corner where this species previously stayed. By 22 April 1967, 20 months after our first census, the bird fauna of Area 2 showed a loss of one pair each of the Red-billed Azurecrown (Amazilia cyanocephala), Grace's Warbler, and Hepatic Tanager, and the addition of one pair of Rusty Sparrows and part of the territory of a pair of Common Meadowlarks; we again noted the Gray-crowned Yellowthroat in the center of the area.

Pine Savanna Area 3

Despite the permanent stream running through it, Area 3 was extremely poor both in numbers of species and numbers of individuals. The 25 acres apparently supported as breeding residents only five species at most and included the entire territories of only two of these. The BSD equaled 1.44, less than either Areas 1 or 2. The low BSD predicts a FHD of about 0.5, which seems reasonable in comparison with Area 1. Except along the stream, the density of the vegetation, both trees and ground cover, was perhaps near the lower limit required by most savanna birds. Thus, the pines were too widely spaced for the Grace's Warbler and Hepatic Tanager; the shrubs, grasses, and sedges were too low and too sparse for most ground-dwelling forms. The openness possibly attracted the American Kestrel (Falco sparverius) and Vermilion Flycatcher, but may not have provided enough food for their support.

Grassland Area

This five-acre area apparently did not include even part of the territories of any breeding birds. We saw the Common Meadowlark and Rusty Sparrow in the vicinity but not within the boundaries of the study area. Only six or seven of the species listed in Table 1 are potential nesters in grassland, and most of these are either sparsely and locally distributed or found only near stream-bordered thickets or wet areas. We walked across many acres of pure grasslands outside the study plot and invariably found birds scarce or absent. I attribute this to the paucity of grassland-adapted species in the isolated habitat and to the apparent scarcity of food for such species.

Rain Forest Area

The FHD, calculated from density measurements at the same three levels as in the pine savanna, is 0.3813. This low figure results from the great difference in the density of the different layers; the one above 20 ft, which averages 54.3 ft high, is very dense compared to the others. Nevertheless, the foliage profile fits my impression of the forest reasonably well.

The predicted BSD with this FHD is only 1.23, but we recorded a BSD of 3.64. MacArthur et al. (1966) also recorded high BSD's—3.393 and 3.378—in similar rain-forest habitats in Panama, and their figures are much higher than predicted from a FHD calculated from measurements at three levels (0–2, 2–25, >25). MacArthur and his associates suggested that birds may distinguish four layers of vegetation (0–2, 2–10, 10–50, >50). A calculation of FHD on the basis of four layers fits better the regression line derived from three-layer measurements in the temperate zone. In support of the four-layer division, they cited Slud (1960), who proposed recognition of five levels of the forest habitat at Finca "La Selva," Costa Rica.

In the Nicaraguan Rain Forest Area, my impression was that the 10 to 50 ft layer did not correspond either to a pattern of foliage density or to a distinct stratum recognized and used by certain species of birds. Because Slud's Costa Rican area included all species of birds that we recorded in the Nicaraguan rain forest plot, and because he based his designation of levels on observations made during a year's continuous residency, I attempted to convert his five semiqualitative divisions into units which, when applied to my study area, permitted a calculation of FHD at five levels.

The resulting conversion (Table 4) gives Slud's terminology and my estimates of the vertical extent of each division. With the five layers, the FHD becomes 1.03 + and the predicted BSD equals 2.54, closer to the observed BSD of 3.64 than when calculated at three levels, but nevertheless low. Actually, only the subdivision of the dense foliage above 20 ft into two layers has much effect on the FHD figure. If we use only four layers (0–3, 3–20, 20–50, 50–74.3) the FHD equals 1.00 and the BSD equals 2.47. However, my field observations do not support the supposition that birds distinguish two layers in the upper levels of the forest. Most bird species found at those levels appeared to range freely from about 20 ft above the ground to the tops of the trees. A comparison of my Nicaraguan census data (Table 4) with Slud's species lists for the middle forest and canopy shows that, in Nicaragua, all canopy species except the Gray-headed Kite (Leptodon cayanensis) and the Green Shrike-Vireo (Smaragdolanius pulchellus) also range through the middle forest level, and all 16 middle forest species also occur either in the canopy or in the high understory level.

We cannot exclude the possibility of subtle partitioning by the birds, but calculations based on further divisions of this type of habitat are bound to raise the figure for FHD and hence the predicted BSD. A better fit of high BSD figures to predicted values is thus inevitable and not necessarily confirmatory. Orians (1969) also doubted that finer division by birds of the layers of the tropical forest is the primary factor responsible for the relatively large number of bird species present, but he now informs me (1971, pers. commun.) that he has new evidence that such partitioning is importantly involved.

The Rain Forest Area of only 10 acres had 37 species on territories and 79 additional species as visitors. These data raise questions about the use of census figures. If an area has more than twice as many visiting species as species on territories, should we omit the "visitors" from calculations of species diversity? These "visitors" use food and other resources of the area, often with apparent regularity; they must affect the approximately equally common "residents" and have an ecological impact on the habitat. Yet measurements of species diversity, based on the number of species with breeding territories in a given area, exclude them. Even ignoring the visitors, the large number of resident breeding species results in a high diversity figure for the rain forest.

Orians (1969) dealt with similar censusing problems in Costa Rica by basing his BSD calculations on "... the total number of species encountered on each of the sites and not upon some measure requiring an estimate of their proportional representation." I share Orians' despair in attempting to get accurate data on the number of territories of rain-forest species in a given area. However, I feel justified in making estimates as my study area was 10 acres — large enough to include fully the territories of many species — and as several observers made many censuses at different seasons over two years.

It is difficult to compare my results with Orians'; he used a different method of measuring the vegetation profile (MacArthur and Horn, 1969) and calculated BSD without estimating proportional representation. His data for a three-acre plot at La Selva, a habitat probably similar to my study area, included FHD (four layers) of .40 and BSD of 1.65. My figures for Nicaragua are quite different on both counts. I have discussed them with Orians and we cannot tell whether our different methods or other factors are primarily responsible.

Discussion

Using the data above and additional information from observations within and near the study areas, I now consider the questions posed in the introduction.

Question 1

What are the precise qualitative and quantitative differences between the avifaunas of measured areas of tropical pine savanna and of adjacent broad-leafed forest?

I have outlined and discussed in part the avifaunal differences between the different study areas and habitat types. I found no species breeding in both the savanna and rain forest study areas, and recorded only three species-Pale-vented Pigeon (Columba cayennensis), Scaled Pigeon (C. speciosa), Brown Jay (Psilorhinus morio) - as visitors in both. The Scarlet Macaw (Ara macao) proved to be a special case. Although it feeds only in broad-leafed forest and we recorded it as a visitor in the Rain Forest Area, one pair nested in Pine Savanna Area 1 in April 1967. Otherwise, despite the proximity of the savanna and rain forest areas and the similarity in many of the large-scale environmental features such as day length, climate, elevation, etc., their avifaunas are almost totally different, both in the numbers of different species and numbers of individuals.

Question 2

Within the tropical savanna, what are the differences between the bird populations in pines with little understory or seedling, pines with more understory and abundant pine seedlings of various heights, and the treeless savanna with grasses, sedges, and a few shrubs?

The pine savanna with little shrubby or herbaceous understory and few seedlings supports a more diverse and abundant avifauna than an area where such growth is prevalent. However, if the pines are too far apart and the ground cover too sparse, the avifauna is also sparse. The treeless grass savanna is particularly impoverished.

Question 3

Are the differences in bird populations in the various habitats predictable on the basis of their foliage profiles as proposed by MacArthur and MacArthur (1961)?

The differences are not predictable purely on the basis of different foliage profiles, but they are accountable on other ecological grounds.

Question 4

How do the bird populations of the tropical habitats compare, in numbers of species and numbers of individuals, with bird populations in temperate-zone habitats?

TABLE 4

Birds of the Rain Forest

Occurrence in one or more of Five Vertical Layers of Vegetation

Residents	*Visitors*	*Migrants*
	Forest Floor (0-3 feet)	
Tinamus major	*Odontophorus erythrops*	*Seiurus aurocapillus*
Sclerurus guatemalensis	*Rhynchortyx cinctus*	*S. noveboracensis*
Formicarius analis	*Leptotila cassinii*	*S. motacilla*
Phaenostictus mcleannani	*Neomorphus geoffroyi*	
*Henicorhina leucosticta**	*Mymeciza exsul*	
Phaeothlypis rivularis	*Gymnopithys bicolor* *	
Arremon aurantiirostris	*Grallaria fulviventris*	
	*Cyphorhinus phaeocephalus**	
	Low Understory (3-6 feet)	
*Phaethornis superciliosus**	*Threnetes ruckeri**	*Dumetella carolinensis*
*P. longuemareus**	*Automolus ochrolaemus**	*Hylocichla mustelina**
*Thamnophilus punctatus**	*Hylophylax naevioides*	*Dendroica magnolia**
Platyrinchus mystaceus	*Manacus candei*	*Oporornis formosus*
*Henicorhina leucosticta**	*Schiffornis turdinus*	
*Habia fuscicauda**	*Thyothorus castaneus*	
*Cyanocompsa cyanoides**	*Cyphorhinus phaeocephalus**	
	*Ramphocaenus melanurus**	
	High Understory (6–20 feet)	
*Phaethornis superciliosus**	*Accipiter bicolor*	*Hylocichla mustelina**
*P. longuemareus**	*Threnetes ruckeri**	*Mniotilta varia*
Thalurania furcata	*Florisuga mellivora*	*Dendroica magnolia.*
Hylocharis eliciae	*Amazilia amabilis*	*D. castanea**
Amazilia candida	*Momotus momota*	*Wilsonia canadensis*
Chalybura urochrysia	*Notharchus macrorhynchos*	
*Trogon rufus**	*Malacoptila panamensis*	
*Phloeoceastes guatemalensis**	*Celeus castaneus**	
*Dendrocincla fuliginosa**	*Dendrocincla anabatina*	
*Thamnophilus punctatus**	*Glyphorynchus spirurus**	
Myrmotherula fulviventris	*Xiphorhynchus guttatus**	
*M. axillaris**	*Automolus ochrolaemus*	
*Microrhopias quixensis**	*Xenops minutus**	
*Pipra mentalis**	*Cymbilaimus lineatus*	
*Laniocera rufescens**	*Myrmotherula schisticolor*	
*Megarynchus pitangua**	*Onychorhynchus mexicanus*	
*Terenotriccus erythrurus**	*Platyrinchus coronatus*	
*Myiobius barbatus**	*Rhynchocyclus brevirostris**	
Pipromorpha oleaginea•	*Todirostrum cinereutn*	
*Polioptila plumbea**	*Oncostoma cinereigulare*	
*Euphonia gouldi**	*Ornithion semiflavum*	
Chlorothraupis carmioli	*Psilorhinus morio**	
*Habia fuscicauda**	*Ramphocaenus melanurus**	

TABLE 4 (Continued)

Residents	*Visitors*	*Migrants*
*Cyanocompsa cyanoides**	*Hylophilus ochraceiceps*	
	Euphonia lauta	
	Ramphocoelus passerinii	
	*Lanio leucothorax**	
	Saltator maximus	
	Oryzoborus funereus	
	Middle Forest *(20–50* **feet)**	
*Columba nigrirostris**	*Buteo magnirostris*	*Contopus* **sp.**
*Trogon rufus**	*Aratinga astec**	*Vireo oliuaceus*
*Centurus pucherani**	*Pteroglossus torquatus**	*Dendroica magnolia**
*Phloeoceastes guatemalensis**	*Ramphastos sulfuratus**	*D. pensyluanica*
*Dendrocincla fuliginosa**	*R. swainsonii**	*D. castanea**
*Myrmotherula axillaris**	*Piculus simplex*	*Icterus galbula*
*Microrhopias quixensis**	*Celeus castaneus**	*Piranga rubra*
*Pipra mentalis**	*Xenops minutus**	
Laniocera rufescens	*Glyphorynchus spirurus**	
*Megarynchus pitangua**	*Xiphorhynchus guttatus**	
*Terenotriccus erythrurus**	*Rhynchocyclus breuirostris**	
*Myiobius barbatus**	*Ornithion semipavum**	
*Pipromorpha oleaginea**	*Psilorhinus morio**	
*Polioptila plumbea**	*Chlorophanes spiza**	
*Hylophilus decurtatus**	*Gymnostinops montezuma**	
*Euphonia gouldi**	*Cacicus uropygialis**	
	*Tangara larvata**	
	Lanio leucothorax•	
	*Tachyphonus luctuosus**	
	*Caryothraustes poliogaster**	
	Canopy (above *50* **feet)**	
Leptodon cayanensis	*Penelope purpurascens*	
*Columba nigrirostris**	*Columba cayennensis*	
*Centurus pucherani**	*C. speciosa*	
*Phloeoceastes guatemalensis**	*Ara macao*	
*Megarynchus pitangua**	*Aratinga astec**	
*Myiobius barbatus**	*Piaya cayana*	
Pipromorpha oleaginea	*Heliothryx barroti*	
*Polioptila plumbea**	*Pteroglossus torquatus**	
Smaragdolanius pulchellus	*Ramphastos sulfuratus**	
*Hylophilus decurtatus**	*R. swainsonii**	
*Euphonia gouldi**	*Carpodectes nitidus*	
	Rhytipterna holerythra	
	*Rhynchocyclus breuirostris**	
	*Chlorophanes spiza**	
	Cyanerpes lucidus	
	Dacnis cayana	
	Zarhynchus wagleri	
	Gymnostinops montezuma	
	*Cacicus uropygialis**	
	*Tangara larvata**	
	*Lanio leucothorax**	
	*Tachyphonus luctuosus**	
	*Caryothraustes poliogaster**	

***Occurs in more than one layer.**

The bird populations of the richest area of tropical pine savanna are equivalent to about one-fifth of the populations in a temperate-zone area of the same size and similar habitat. The populations of 25 acres of tropical pine savanna are also approximately equivalent to the populations in five acres of temperate-zone deciduous woodland with a similar foliage profile.

Question 5

Does competition restrict any species in its use of either habitat?

Competition must influence restriction to habitat to some extent; otherwise one must assume that no species from either the pine savanna or the rain forest would eventually colonize the other habitat even if it lacked an avifauna of its own. Evidence that suggests competitive exclusion or restriction would include (1) direct conflict between potential competitors, (2) incomplete colonization of one habitat by species characteristic of another, or (3) replacement of species characteristic of one habitat by morphologically and behaviorally similar forms in the other.

I never observed any direct conflicts that suggest competition between pine-savanna and rain-forest bird species. The only frequent interspecific conflicts were between Grace's Warblers and Yellow-throated Warblers in the pines. I shall discuss this more fully under Question 8.

Pine Savanna.—Most permanent resident species characteristic of the pine savanna showed no tendency to invade or colonize the rain forest. This is not surprising as most of these species have feeding habits that require open habitat, and some of them appear to be specifically adapted to pine trees. The Ked Crossbill obviously depends on pine seeds; the Chipping Sparrow seems to show a distinct preference for pine foliage (Klopfer, 1963); and the Grace's Warbler is almost completely restricted to pines (Webster, 1961), although there is no obvious reason why, with its bark-searching, foliage-gleaning, and flycatching methods of feeding, it could not gather food successfully in the broad-leafed trees at the forest edge. No other resident species forages in the edge situations the way the Grace's Warbler forages in the pines; yet I have never seen this warbler alight, even momentarily, in any tree except a pine.

The Hepatic Tanager is only slightly less restricted to the pines; occasionally, it goes to other trees or shrubs at the edge of the rain forest. The northern populations of this tanager—western United States to northern Nicaragua—all seem to be pine-forest or pine-oak-forest dwellers; the Nicaraguan lowlands constitute a gap in the range (Howell, 1965), and the southern populations—from Costa Rica into South America—have a wide distribution in non-coniferous forests. The most probable potential competitors of this tanager that occur in the broad-leafed forest in Nicaragua also occur farther south; therefore, it appears unlikely that competition restricts these tanagers to the pine savanna.

Only three pine-savanna species appear to be potential colonizers of the broad-leafed forest in that some individuals regularly visit the broad-leafed forest edge. The Yellow-headed Parrot (Amazona ochrocephala) apparently feeds only along this edge; the Red-billed Azurecrown frequently feeds at flowering plants along the borders of watercourses and other wet places; the Yellow-backed Oriole (Zcterus chysater) most often occurs near the interface of the pines and broad-leafed forest. We saw none of these species deeper in the rain forest, even in the clearings. I shall discuss possible competitive interactions between these and other species below.

The rain-forest and forest-edge species most likely to attempt complete colonization of the savanna are those recorded in Table 1 as regular visitors, and we may group them according to feeding habits: Raptors, three falconiforms and one owl; non-pine feeders, three parrots and two pigeons; bark and tree-trunk feeders, three woodpeckers; aerial insect-feeders, two caprimuligiforms, two tyrannids, and one swallow; insect gleaners, Gray-crowned Yellowthroat; opportunistic omnivore, Brown Jay.

The visiting raptors differ in size and habits from their closest pine-savanna counterparts, but competition with the residents for the limited food resources of the savanna may prevent the visitors from becoming residents. The scarcity of nest holes of suitable size may also be a limiting factor for two of the falcons and the owl.

The visiting species that do not feed in pines depend on habitats other than the savanna for food, although the Pale-vented Pigeon sometimes feeds on mistletoe berries in the pines. The visiting parrots do not appear to require an open habitat, and none, including the resident Yellow-headed Parrot, feeds on pine seeds, a habit that makes Rhynchopsitta of Mexico a true pine-forest bird. Probably the only important competition between visiting non-pine feeders and pine-savanna residents is for nesting holes.

It is difficult to believe that competition from the scarce, small resident Ladder-backed Woodpecker (Dendrocopos scalnris) prevents full occupancy of the pine savanna by the three larger species of visiting woodpeckers. The Acorn Woodpecker (Melanerpes formicivorus) does not venture far from the vicinity of large oaks, and the savanna may not provide adequate resources for resident populations of the other two woodpeckers. The scarcity in the pines of species that excavate large holes may limit the invasions of other hole-nesting species, as mentioned above.

Competition may influence the population size and distribution within the savanna habitat of the aerial insect-catchers, but in this feeding category the savanna has more visitors than residents. I believe that the visitors are restricted because they are unable to sustain themselves in the savanna habitat, with or without competition from residents, except when close to the broad-leafed forest.

The Gray-crowned Yellowthroat is adapted primarily to gleaning insects from herbaceous plants near the ground. Although some of the resident fringillids doubtless obtain some insects from this vegetational stratum, there is no similar adaptive type among the pine-savanna residents. I believe it is not competition that limits this species but a lack of its microhabitat — the herbaceous growth that occurs in the pine savanna only near wet areas.

In the savanna, no resident species resembles the Brown Jay in morphology and behavior. The pines offer little food and the other woody plants are too sparse to provide adequate sustenance for this large jay which forages primarily in trees and shrubs. Brown Jays cannot readily obtain food in the dense savanna grasses and sedges, and open ground is usually quite barren. Hence the species would probably not colonize the pine savanna fully, even in the absence of resident birds.

As competition may be important between superficially dissimilar species and not important between apparently similar ones, it is difficult to say with assurance which forms are truly "replacing" one another in the different habitats. Congeneric status is often a useful criterion as it often indicates a similarity of adaptive characters. Five genera — Buteo, Falco, Amazona, Amazilia, and Icterus — are represented by different species in both types of habitat. I have discussed above the possible competitive interactions between the species of the first three genera. In addition to those species listed in Tables 1 and 3, we frequently recorded the Cinnamon Hummingbird *(Amazilia rutila),* Rufous-tailed Hummingbird *(A. tzacatl),* and the Black-cowled Oriole *(Icterus prosthemelas)* in broad-leafed forest or forest edge near the study areas.

It is not unlikely that the Cinnamon Hummingbird which, like several savanna residents, inhabits arid semi-open regions in most of its range would colonize the pine savanna if the Red-billed Azurecrown were absent. The Rufous-tailed Hummingbird, White-bellied Emerald *(Amazilia candida),* and Blue-chested Hummingbird *(A. amabilis)* are probably not potential colonizers of the pines, but competition from them and the Cinnamon Hummingbird may limit penetration by the Red-billed Azurecrown into the broad-leafed thickets and rain-forest edges.

In the savanna region the Yellow-backed Oriole inhabits primarily the pines, but in the highlands of Nicaragua, it inhabits varied vegetational associations including pines and broad-leafed forest. In the savanna, I observed this species probing in the crevices of pine bark and foraging in the mistletoe and bromeliads in the pines; it also used the oaks, palms, and other broad-leafed trees along creeks and thickets. Although the much smaller Black-cowled Oriole is fairly common along the edge of the rain forest, I never saw the two species together.

If competition is influential in maintaining ecological separation of these two species, I suspect that it limits the local distribution of the Yellow-backed rather than that of the Black-cowled. We did not record the Yellow-tailed Oriole *(Icterus mesomelas),* which is more like the Yellow-backed in size and color than is the Black-cowled, in northeastern Nicaragua. A few Baltimore Orioles *(I. galbula)* visit the pine savanna occasionally in migration and in winter but I saw no indication that this species influences the activities of the Yellow-backed Oriole.

In summary, I believe that the particular adaptations and requirements of each species play a more important role than does interspecific competition in preventing the successful cross-colonization of these adjacent, but very different, habitab. I doubt that many pine-adapted species would colonize the rain forest even if it lacked a resident avifauna, and I also doubt that many rain-forest species could successfully invade the savanna where the sparse vegetation limits both food and cover. Nevertheless, the pine savanna, unlike the rain forest, gives the impression of an unsaturated habitat, one that could accommodate other adaptive types as well as denser populations of some resident species. I shall consider these points in a following section.

Rain Forest.- The rain forest habitat, with its large and diverse avifauna (Table 3), requires a somewhat different analysis. Table 4 shows that, with rare exceptions, every resident species within a given forest level differs clearly from every other species in that level in one or more characteristics relevant to competition — in body size, bill size and/or shape, method of feeding, type of food taken, or the usual microhabitat it occupies.

Among the residents, we recorded only two pairs of congeneric species (species in the same genus) — two hummingbirds, the Long-tailed Hermit *(Phaethornis superciliosus)* and the Little Hermit *(P. longuemareus),* and the Fulvous-bellied Antwren *(Myrmotherula fulviventris)* and the White-flanked Antwren *(M. axillaris).* The two hummingbirds differ greatly in size. The two antwrens are generally similar except for color pattern, but the White-flanked is somewhat smaller, has a more slender bill, and seems to move about more quickly.

The birds of the ecologically complex rain forest appear to reduce or avoid interspecific competition by the same means that we observed in the simpler pine savanna — that is, each resident species differs from the others by distinct morphological and behavioral characters that diminish overlap in foraging and other activities. However, even considerable differences in morphology and in general foraging do not necessarily mean little or no competition. Willis (1966a) and Morse (1967) showed, by field studies, that the feeding activities of greatly different species — the Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) and the Ocellated Antthrush (*Phaenostictus macleannani*), the Brown-headed Nuthatch (*Sitta pusilla*) and the Pine Warbler (*Dendroica pinus*) — are competitive and that the competition may strongly influence foraging behavior. Since these competing species are morphologically dissimilar and belong to different families, one could not have predicted the competition by examining museum skins, by calculations from measurements in Ridgway's "Birds of North and Middle America," or even by observing them casually in the field. Examples such as these impose a measure of caution regarding any conclusions about interspecific competition — or lack of it — between dissimilar species.

The number of species, 37, with at least part of the breeding territory within the 10 acres of rain forest is much greater than the corresponding number in the 25 acres of pine savanna. The figure for the rain forest is also greater than for any area of comparable size in a variety of temperate-zone habitats in North America, as reported in Audubon Field Notes (1966). In data from 86 different censuses, all areas containing more than 30 territorial species were larger, usually much larger, than 10 acres. However, the number of temperate-zone males per species were proportionately greater in the temperate-zone plots than in the rain forest, and the number of visiting species was proportionately less. These data provide one more example of the well-known phenomenon of tropical diversity — more species but fewer individuals of each species than in the temperate zone — for which many population ecologists and other biologists have proposed particular, or general, explanations.

Klopfer and MacArthur (1960; 1961), who dealt specifically with Neotropical birds, proposed that (1) the environmental stability of the tropics favors more stereotyped behavior patterns, which results in smaller, more restricted niches, and (2) this stability in availability of resources permits greater niche overlap, which furthers — or allows — the coexistence of many very similar species and thus increases diversity. They assumed that non-passerilles are more stereotyped in behavior than passerines and claimed that the proportion of individuals of non-passerines to passerines increases with decreasing latitude, thus supporting their hypothesis. They also noted that some tropical congeneric species that may feed together differ only slightly in bill length and presumably use many of the same food resources — an example of niche overlap. Winterbottom (1964), Simpson (1964), and Schoener (1965) discussed these suggestions critically, and I shall consider them later in relation to the pine-savanna populations.

It is difficult to compare the proportion of non-passerines to passerines in the Nicaraguan rain forest with the Klopfer and MacArthur data because their figures are for territorial males per species per 100 acres. Considering the patchy and local distribution of many rain-forest species, I believe that extrapolating the census data from my 10-acre study area by multiplying by 10 would be highly misleading and that the censusing of an additional 90 acres of similar habitat would undoubtedly add many species, both non-passerine and passerine, in irregular abundance.

Considering only the data for 10 acres, one finds a high proportion of non-passerines to passerines — about 24 per cent of the resident males were non-passerines. However, more than half of these were hummingbirds, and if we exclude them, the proportion of non-passerines to passerines is less than 10 per cent. These data clearly do not test the validity of the Klopfer and MacArthur proposal dealing with the non-passerine to passerine ratio. Furthermore, only two pairs of congeneric species resided in the study area and one cannot safely account for the high degree of diversity on the basis of coexistence of groups of similar species with overlapping requirements that finely partition the available resources.

MacArthur et al. (1966) censused seven different plots in Panama including both young and mature forest. Out of a combined total of over 90 species, only three pairs of congeneric species held territories in a subplot large enough to include 25 pairs of birds. In all three pairs — Keel-billed Toucan (Ramphastos sulfuratus) and Chestnut-mandibled Toucan (R. swainsonii), Buff-throated Woodcreeper (Xiphorhynchus guttatus) and Black-striped Woodcreeper (X. lachrymosus), and Yellow-billed Elaenia (Elaenia flavogaster) and Lesser Elaenia (E. chiriquensis)-the species differ considerably in size.

Skutch (1966) carefully censused the breeding birds of a 3.75-acre area in Costa Rica for each of three successive years. Of the three-year total of 38 species, he found only the following congeneric forms: Blue-chested Hummingbird and Rufous-tailed Hummingbird, one nest of each in one year; Social Flycatcher (*Myiozetetes similis*) and Gray-capped Flycatcher (*M. granadensis*), both with several nests in two out of three years; and Golden-masked Tanager (*Tangara larvata*), Silver-throated Tanager (*T. icterocephala*), Bay-headed Tanager (*T. gyrola*), and Speckled Tanager (*T. chrysophrys*), two or three of the four species nesting each year. Skutch censused a partly cleared, relatively predator-free area that included planted fruit trees and a feeding tray continuously supplied with bananas. His censuses, like those of MacArthur et al. (1966), indicate that, in a specific small area, the high diversity of species is not caused by great numbers of similar congeneric forms.

Visitors. — The large number of visitors recorded in the Nicaraguan study (Table **3)** includes a number of congeners of the resident species as well as other similar forms. From a list based on specimens collected in such an area, one could draw the seemingly reasonable but erroneous conclusion that the area supported a large number of very similar species as coexisting nesting birds.

In a specific area at any given time of year, the visitors may be (1) nonbreeding birds — either immatures or adults that have nested or will nest; or (2) breeding birds with territories in another area but with a wide cruising range, or which join mixed species flocks that may wander widely, following army ant trails or feeding in trees and shrubs that flower and fruit profusely but briefly. (See Willis, 1965b, regarding superabundance of insect food exposed by army ants.)

My term "breeding resident" may be somewhat imprecise and ambiguous, for the residents of one area may be visitors in another. However, similar and potentially closely-competing species, although living in the same geographical area, may have their breeding territories so spaced out and scattered that there is little spatial overlap between them except when these species exploit superabundant food. Whether such spacing results from active competition and aggression between species or from slight differences in habitat preference may vary with the species in question. Given the great complexity of the vegetation and the patchy distribution of microhabitats in a tropical rain forest, one would expect that—in a group of similar species—some would have an advantage over others only in certain microhabits; other species would be less specialized; and one or a few quite versatile. This means that some species would be rare and local, others more abundant in varying degrees, and perhaps one or a few almost ubiquitous. Such distributional patterns are particularly frequent in the tropics.

Question 6

Considering the composition of the bird species in both habitats, what may we infer about competition, niche size and overlap, and the partitioning of resources between species and between individuals within a species?

As the number of permanent and summer-resident bird species in the savanna is small, we may consider the entire avifauna instead of only those species recorded in the study areas.

Even rather small differences in body size, in food-getting appendages, or in behavior may reduce or eliminate overlap among birds in the use of critical resources within a shared environment. (See Grant, 1968, for a recent review.) Given such differences ". . . there can be as many species as there are proportions of the resources that can be counted on from season to season" (MacArthur and Levins, 1964).

Table 5 groups the breeding birds of the pine savanna according to their principal food habits; I have omitted the wide-ranging cathartid vultures and the erratic Yellow Grass-finch (*Sicalis luteola*). With the exception of the buteos and some of the fringillids, every species in each group is clearly distinct from every other on the basis of the kind, size, or location of the food it takes or the manner in which it obtains the food. With this virtual absence of feeding overlap among the resident birds, the pine savanna provides a model of a habitat with a minimal—perhaps subminimal—number of species representing different adaptive types.

Of the 27 forms listed, there are only three pairs of congeneric species: White-tailed Hawk (*Buteo albicaudatus*) and Red-tailed Hawk (*B. jamaicensis*); Aplomado Falcon (*Falco femoralis*) and American Kestrel; Rusty Sparrow and Botteri's Sparrow (*Aimophila botterii*). The two buteos are similar in size and foraging habits; the White-tailed Hawk is much more abundant than the Red-tailed Hawk. Stevenson and Meitzen (1946) characterized the White-tailed Hawk in Texas as an opportunistic feeder that frequently foraged at the edges of prairie fires; it fed on insects and all classes of small vertebrates, frequently including meadowlarks and Common Bobwhites (*Colinus virginianus*). Obviously the Nicaraguan savanna provides the kind of foraging conditions and food resources that the White-tailed exploits successfully. The Red-tailed Hawk feeds primarily on rodents, at least in open habitats, but rodents and other mammals are scarce in the savanna. The evidence suggests that the White-tailed Hawk is better adapted to the Nicaraguan savanna environment than is the Red-tailed Hawk, and competition between the two may limit their relative abundance.

The two species of the genus *Falco* differ considerably in size; the Aplomado Falcon weighs about three times as much as the American Kestrel. Great disparity in size is frequent in cases of congeneric sympatry in this family (Schoener, 1965) and these two species probably compete very little, if at all.

Rusty Sparrows and Botteri's Sparrows also differ greatly in size, and I have considered this difference in relation to all six fringillids found in the pine savanna. Within a relatively similar intrafamilial group of species, meas-

TABLE 5

Pine Savanna Resident Birds grouped according to Food Habits

Species	*Habits*
	Carnivorous
Buteo albicaudatus	Potentially competitive
Buteo jamaicensis	
Falco femoralis	Large; scarce; feeds on birds?
Falco sparverius	Small; common; partly insectivorous
Polyborus cheriway	Carrion-feeder
Bubo virginianus	Large; nocturnal; rare
	Insectivorous
Chordeiles minor	High-flying, semi-nocturnal aerial feeder
Caprimulgus maculicaudus	Low-flying, nocturnal aerial feeder
Amazilia cyanocephala	Takes smallest arthropods, also nectar
Dendrocopos scalaris	Arboreal feeder; drilling, probing, gleaning
Pyrocephalus rubinus	Flycatches in pine stands
Muscivora tyrannus	Flycatches in open grass savanna
Cistothorus platensis	Restricted to marshes
Dendroica graciae	Largely restricted to foliage and small branches
Icterus chrysater	Arboreal icterid
Sturnella magna	Terrestrial icterid
	Omnivorous (seeds and/or fruits, insects)
Colinus nigrogularis	Terrestrial, scratches in litter; moderately large
Columbina minuta	Terrestrial, gleans from surface; small
Sialia sialis	Arboreal-terrestrial; slender bill used primarily for grasping
Piranga flava	Arboreal; heavy bill used for grasping and cutting
	Frugivorous-herbivorous
Ara macao	Do not feed in pine savanna
Amazona ochrocephala	
	Granivorous
Carduelis notala	All fringillids; see Figure 10
Loxia curvirostra	
Ammodramus savannarum	
Aimophila rufescens	
Aimophila botterii	
Spizella passerina	

urements of body weight, wing length, and bill length and depth should indicate general body size, extent of aerial activity, and feeding habits, respectively (Figure 11). The non-concordant variation in these morphological characters suggests differences in feeding activities that would lessen interspecific competition, and field observations support this idea: the Red Crossbill is a food specialist; the Black-headed Siskin and Chipping Sparrow seem to eat primarily the seeds of *Hypolytrum* and *Andropogon*, respectively; the Rusty Sparrow is much larger and wider ranging in its habits than either the Botteri's Sparrow or the Grasshopper Sparrow (*Ammodramus savannarum*). The Botteri's and Grasshopper Sparrows differ in size, but they were too secretive for detailed observation of their feeding behavior.

Table 6 gives mean measurements of wing length, body weight, and bill length for both sexes of a group of pine-savanna species for which I have such data. For each set of measurements, I calculated the per cent difference between the means for males and females by dividing the smaller figure by the larger and subtracting the quotient from one. The per cent differences are usually small, exceeding 10 per cent in some dimension in only three species-Ladder-backed Woodpecker, Yellow-backed Oriole, and Common Meadowlark. The oriole and meadowlark belong to the family Icteridae, in which the sexes often show great size dimorphism. In the woodpeckers, sexual dimorphism in size is not the rule, but measurements for various populations of Ladder-backed Woodpeckers given in Ridgway (1914) show that the male Ladder-backed Woodpecker is usually larger than the female. Thus, in these three species, size dimorphism is consistent with the trend in other conspecific populations.

In most savanna species, the low per cent difference between the sexes in culmen length is notable and is usually less than that shown in wing length and body weight. Only in the three most dimorphic species does this difference exceed six per cent. Schoener (1965) suggested that a ratio of larger to smaller bill length of 1.14 or more indicates a reduction of interspecific competition through the partitioning of food resources between the larger- and smaller-billed forms. Presumably, such differences in bill size between males and females of the same species would also lessen the competition between them for food.

Among the pine-savanna residents only the Ladder-backed Woodpecker shows a ratio of bill lengths between the sexes as great as 1.14. In the Yellow-backed Oriole, the ratio is 1.07, and in the Common Meadowlark, 1.08. This suggests a reduction in competition between the sexes in the woodpecker, but I have too few observations of this scarce species to evaluate the possibility. In the other savanna species, the lack of a "significant" intraspecific difference in bill length between sexes suggests that males and females must be using essentially the same food resources. If there is a meaningful degree of competition between the sexes, it may be partly responsible for the low densities of individuals in the savanna.

The scarcity of congeneric forms and the apparent minimizing of competition between resident species suggests an insular avifauna and the savanna as an ecological island. Compared to the montane pine forests of Honduras and Nicaragua, the lowland savanna has a much greater annual rainfall and a higher mean temperature, with the low extremes much higher. We might expect it to be more productive and support more bird species, as is the case with the lowland versus highland areas of tropical broad-leafed forest (Orians, *1969).* Nevertheless, a number of arboreal species reside in the montane pine forest of Honduras and/or Nicaragua that are absent from the lowland pines: White-breasted Hawk *(Accipiter chionogaster),* Mountain Trogon *(Trogon mexicanus),* Common Flicker *(Colaptes auratus),* Hairy Woodpecker *(Dendrocopos villosus),* Strong-billed Woodcreeper *(Xiphocolaptes prorneropirhynchus),* Greater Pewee *(Contopus pertinax),* Steller's Jay *(Cayanocitta stelleri),* Brown Creeper *(Certhia familiaris),* Solitary Vireo *(Vireo solitarius),* Olive Warbler *(Peucedramus taeniatus),* and Painted Redstart *(Myioborus pictus).* On the other hand, none of the arboreal residents and visitors of the lowland pine savanna is absent from the montane pines except the Aplomado Falcon, the Yellow-headed Parrot, and the Vermilion Flycatcher.

In several instances, the savanna avifauna includes close counterparts of montane species and competitive exclusion could explain the absence of at least some of these from the lowlands, but for some species this is not evident. In any case, the montane pine habitat clearly includes more bird species than the lowland pines. Some of the exclusively montane species possibly invaded the savanna at times and failed to establish themselves, but it is difficult to see why some such invasions—if they occurred—were not successful. It is also hard to understand why some of the savanna residents are not more abundant. For example, bark-gleaning is virtually unexploited except by the Grace's Warbler on the smaller upper branches and to some extent by the wintering Yellow-throated Warbler. Besides these warblers, the montane forest also includes the large Strong-billed Woodcreeper and the small Brown Creeper, both bark-gleaners and both absent from the lowland pines. No woodcreepers ever venture into the savanna from the broad-leafed forest.

The Ladder-backed Woodpecker is the only resident woodpecker in the pine savanna, and most other populations of this widespread species do not occur in coniferous forest. This small-billed form gleans and flakes off bark on small branches; it also drills in typical woodpecker fashion and gleans the dry bases of bromeliads. It is inexplicably scarce; I estimate a maximum density of less than one pair per 100 acres, and Monroe *(1968)* did not encounter any Ladder-backed Woodpeckers in the Honduran portion of the savanna.

The case of the Vermilion Flycatcher is similar. This species does not inhabit pines in most of its range and it is not abundant in the savanna. Yet it is the only small tyrannid resident in the lowland pines—the larger Fork-tailed Flycatcher *(Musczvora tyrannus)* is primarily a grass-savanna bird.

The Red Crossbill has no vertebrate competitors of any kind for the pine seeds; yet the crossbills are very rare. We collected six specimens and saw others on only two other occasions despite intensive searching.

When an island is inhabited by the same but fewer species of birds as are found on the mainland, the diminished interspecific competition may permit the insular populations to expand the dimensions of their niches beyond those of their mainland counterparts. I am familiar with the habits of most of the pine-savanna species in other, "mainland," parts of their ranges, and I watched for indications of niche expansion in the seemingly unsaturated savanna environment. One can consider the presence of typically "non-pine" species such as the Ladder-backed Woodpecker and the Vermilion Flycatcher as examples of niche expansion, but within the pine savanna their activities seemed the same as in any other open habitat. I did not detect any notable differencesin the ecology of other species, and if any have developed, they are certainly inconspicuous.

TABLE 6

Sexual Dimorphism in Size in some Pine Savanna Residents

Species	Sex	No.	$\bar{x}$ wing length	Per cent difference	No.	$\bar{x}$ body weight	Per cent difference	No.	X culmen from nostril	Per cent difference
Falco sparverius	M	13	166.8	3 5	7	73.9	9.2	13	10.15	4.25
	F	11	172.8		5	81.3		11	10.6	
Colinus nigrogularis	M	8	89.0	<1	3	113.5	5.6	8	8.26	<1
	F	4	90.7		1	120.7		4	8.22	
Amazilia cyanocephala	M	8	56.8	3.7	3	(4.5,4.9,6.4)	—	9	16.7	2.9
	F	9	54.7		0			8	17.2	
Dendrocopos scalaris	M	3	85.7	1.9	3	26.1	5.4	3	14.6	12.4
	F	9	84.1		8	24.7		6	12.8	
Pyrocephalus rubinus	M	13	71.0	3.8	7	14.3	<1	13	9.84	0
	F	11	68.3		4	14.5		10	9.85	
Sialia sialis	M	17	95.7	2.3	11	29.5	2.4	17	9.5	0
	F	14	93.5		11	30.2		14	9.5	
Dendroica graciae	M	10	57.5	4.0	3	7.9	1.3	10	7.44	1.8
	F	6	55.2		2	7.8		6	7.58	
Icterus chrysater	M	4	104.2	10.4	2	60.2	13.4	4	17.3	6.65
	F	5	93.4		2	52.15		4	16.15	

TABLE *6* (Continued)

Species	*Sex*	*No.*	$\bar{x}$ *wing length*	*Per cent difference*	*No.*	$\bar{x}$ *body weight*	*Per cent difference*	*No.*	$\bar{x}$ *culmen fromnostril*	*Per cent difference*
Sturnella magna	*M*	11	96.0	9.0	6	82.15	24	11	19.9	7.6
	F	9	87.4		5	62.9		9	18.4	
Piranga flava	M	10	88.4	2.4	4	34.45	5	12	13.23	<1
	F	7	86.3		1	32.8		6	13.35	
Carduelis notata	*M*	10	62.4	4.6	9	10.6	2.8	10	10.6	3.8
	F	5	59.5		6	10.3		5	10.2	
Loxia curoirostra	M	*3*	86.7	3.4	0	—	—	3	17.2	1.2
	F	3	83.8		3	33.3		3	17.0	
Ammodramus savannarum	*M*	3	54.1	3.4	3	15.3	5.9	3	7.3	4.0
	F	1	52.3		1	14.4		1	7.6	
Aimophila rufescens	*M*	11	68.9	7.0	7	35.8	8.7	10	10.7	1.0
	F	7	64.1		2	32.7		7	10.8	
A. botterii	M	8	55.3	1.1	3	19.5	—	8	8.3	3.6
	F	2	54.7		0	—		2	8.0	
Spizella passerina	M	8	65.9	4.4	6	11.6	4.3	8	7.35	5.2
	F	8	63.0		9	11.1		10	6.97	

All weights in grams (g); measurements in millimeters (mm).

I also watched for evidence of niche-narrowing in this tropical savanna that would permit coexistence of more species of similar morphology and habits, and again I found no clear-cut examples. One possible case of niche-narrowing, the apparent dependence of the Black-headed Siskin on ***Hypolytrum*** seeds, seems more an example of the simple use of one of the few abundant foods in a generally impoverished habitat than of the partitioning of resources in response to competition. I feel that the composition of the avifauna in the savanna results more from historical accident than from direct contemporary competition, a point I shall develop later.

Question 7

How do the proportions of non-passerines to passerines and suboscines to oscines differ in the two habitats and how may one interpret the differences?

As mentioned above, Klopfer and MacArthur (1960) suggested that the greater environmental stability in the tropics favors more stereotyped behavior patterns, resulting in smaller and more restricted niches that in turn lead to fewer individuals of each "stereotyped" species in a given area. On the other hand, birds with less stereotyped behavior would have larger niches and a greater ability to share more varied resources and this, in turn, would lead to more individuals of each species in a given area.

Although not explicitly stated, Klopfer and MacArthur imply that reduced niche sizes also permit more different species to inhabit a particular area. Klopfer (1962:84) subsequently made this suggestion. To support this hypothesis, they attempted to show that the behavior of a high proportion of tropical species is more stereotyped and that they have smaller niches than temperate-zone species. The authors proposed that non-aquatic non-passerines, being phylogenetically older than the passerines, must have a more limited "central nervous capacity" than the passerines. This should reduce their ability to modify their behavior in response to changing environmental conditions resulting in more restricted niches. The behavior of the phylogenetically younger passerines should be less stereotyped, leading to broader niches and greater abundance of individuals in unstable environments.

Klopfer and MacArthur further proposed that an increase in the proportion of non-passerines to passerine individuals — not necessarily species — from temperate to tropical areas would support their hypothesis of a tendency for more birds to have smaller, more restricted niches in the tropics. They selected 45 breeding bird censuses, taken in a variety of habitats from northern Canada to southern Mexico, and presented the data as the number of territorial males per 100 acres per species for both passerines and non-passerines. They used these figures to calculate for each area the ratio of passerines to non-passerines and the per cent of individuals which are non-passerines. The authors interpreted the figures as showing an increase in the proportion of non-passerines to passerines from north to south, thus supporting their hypothesis.

The figures vary greatly from area to area and it is difficult to distinguish clear trends even when plotted arithmetically on a graph. Only the last eight census areas are definitely tropical, and three are prairie habitats. There does appear to be a tendency for an increase in the "per cent of individuals which are non-passerine" from north to south, and a decrease in the number of passerine territorial males per 100 acres per species (Klopfer and MacArthur, 1960:295). However, I can find no clear indication of any regular increase toward tropical latitudes in the number of non-passerine territorial males per

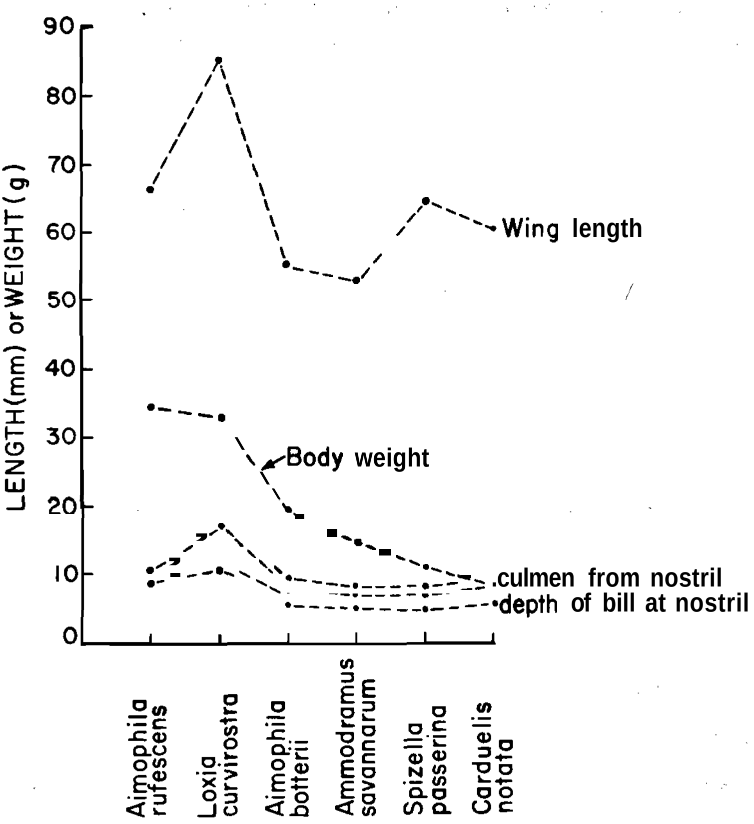

Figure 11. Body weight and measurements of pine savanna fringillids, arranged in order of decreasing body weight.

100 acres per species. This means that the increase in the proportion of non-passerines to passerines results from a decrease in the density of individuals of passerine species and not from an increase in the density of non-passerines. Therefore, the following chain of inferences is not supported by the authors' figures: (1) a higher proportion of non-passerines to passerines is found in a more stable (tropical) environment; (2) this is due to more restricted niches among non-passerines; (3) this in turn allows more species of non-passerines to inhabit a given area; (4) resulting in a greater diversity of species in the tropics. Klopfer and MacArthur (1960) rejected the possibility that tropical passerines might have more stereotyped behavior and thus smaller niches than non-tropical species as contrary to the assumption that passerines as a group have a higher order of central nervous organization and are consequently more plastic in behavior.

Even if future censuses in neotropical areas show more non-passerine territorial males per 100 acres per species than in the temperate-zone areas, I suggest that this type of census does not provide an appropriate test of Klopfer and MacArthur's hypothesis. In the approximately 15 families of non-aquatic non-passerines found in the Nearctic region, almost all the species are as large or larger than most passerines. The important exceptions are the swifts and hummingbirds (Apodiformes), especially the hummingbirds (Trochilidae). Since large non-colonial birds generally require large territories, one would expect fewer individuals of non-passerines than of passerines in a 100-acre area regardless of niche size. In the neotropics, an abundance of hummingbirds often boosts considerably the number of non-passerine species and individuals per 100 acres. The hummingbirds are adapted primarily to tropical conditions and represent the only family in which most species are smaller than most passerines.

Large, raptorial non-passerines are also more abundant and diverse in the tropics; this could be the direct result of more abundant and diverse prey types (a part of the phenomenon to be explained) rather than an indication of more restricted niches. Thus, apart from the highly questionable assumption that non-passerines are, by definition, more stereotyped behaviorally than passerines, I feel that rough comparisons of census data from very different habitats, without considering the avifaunal composition in some detail, are not meaningful.

Comparison of Pine Savanna in Georgia and Nicaragua.—I suggest that that a meaningful ecological question would be: Are individuals of bird species, particularly passerines, less abundant in tropical habitats than individuals of *similar* species in *comparable* temperate-zone areas and, if so, why? *I* have made such a comparison using data from the Nicaraguan pine savanna and from similar habitats in the temperate zone where the climate is less stable.

Although I did not census any single area greater than 25 acres in the pine savanna, I feel confident in estimating the bird populations that would probably occur in a 100-acre sample, based on several 25-acre censuses and all of my observations. In Table 7 I have compared my census data with Norris' (1951) extrapolated figures for 100 acres of Georgia pine forest, excluding those pairs that depended entirely on patches of broad-leafed vegetation.

The two areas have one species, five additional genera, and two more confamilial forms in common. The list of bird species shows that my study plot in Nicaragua is somewhat more open in aspect than is Norris' plot in Georgia. Nevertheless, both areas support the same number of species—15. The greater number of non-passerine species in the tropical area results from the inclusion of two open-country species, the American Kestrel and Common Nighthawk, common to both geographic regions but not occurring in the Georgia plot, and one hummingbird that feeds at flowering mistletoe and bromeliads not present in the Georgia pines.

The total number of territorial males per 100 acres per species is much higher in the temperate-zone area for both non-passerines and passerines. This is particularly striking in the passerines except for the Common Bluebird, which favors more open habitats. The higher ratio of non-passerines to passerine in the tropical area is due to the low density of individual passerines per species and not to an increase in the density of non-passerines. After allowing for the slight differences in the habitats, the data show that, even though the number of species is approximately the same, the density of individuals per species is generally much greater in the temperate area than in the tropical area. This fundamental aspect of the phenomenon of tropical diversity is worth considering in detail.

Despite my criticism of Klopfer and MacArthur (1960), I agree with one of their major proposals—that birds tend to have narrower niches in the tropics than in temperate regions, resulting in lower densities of individuals in the tropics, but irrespective of whether the birds are non-passerines or passerines.

Of the species listed for the Nicaraguan pine savanna, almost all are strictly confined to that habitat at all seasons. Few, if any, of the birds listed for the Georgia pines are so restricted. A comparison of the closely related congeneric forms common to both areas makes this clear. The Common Bobwhite in Georgia uses much more varied habitat than the Black-throated Bobwhite (*Colinus nigrogularis*) in Nicaragua; the same is true of the Downy Woodpecker (*Dendrocopos pubescens*) and Ladder-backed Woodpecker, and of the Summer Tanager (*Piranga rubra*) and Hepatic Tanager. Even species characteristic of the temperate pine woods, such as the Pine Warbler and Bachman's Sparrow (*Aimophila aestivalis*) frequently range into other habitats, especially in winter (Bent, 1953; Weston, 1965, 1968). Many of the Georgia species are migratory and occupy different habitats in winter. In the Nicaraguan list, only the Common Nighthawk is migratory. In summary, the evidence shows that the pine-dwelling birds in the temperate zone are much less restricted to this habitat than their tropical counterparts. This means that the temperate-zone birds have broader niches by any definition of the term. Having a broader niche — and the concomitant ability to use a wide variety of available resources — would not necessarily enable a species to achieve a high population density if it is confined to a habitat where the spectrum of resources is narrow and limited in quantity. We have no measure of the variety and abundance of resources available to birds in the two pine areas, but the resources are presumably greater in the temperate area, at least in spring and summer, in view of the fact that the number of breeding birds is five times greater than in the tropical pines. However, I doubt that the Georgia pines could maintain a winter population equal to that of the warm seasons.

Norris did not census his area in winter, but the two most abundant species, the Pine Warbler and Bachman's Sparrow, form winter flocks and range out into other habitats, and three other abundant breeders — the Great Crested Flycatcher (*Myiarchus crinitus*), Eastern Wood Pewee (*Contopus virens*), and Summer Tanager — migrate to non-pine tropical areas.

Davenport (1964, 1965, 1966) censused his Georgia pine area in winter and found that about half of an average of 20 breeding species migrated out, and that the number of individuals of permanent resident species was much less in winter than in summer. Even an influx of wintering migrants did not bring the number of individuals of all species up to the level found during the summer. Clearly, the pine-dwellers in the temperate zone use their capacity for broader niche exploitation to occupy other habitats when changes of season make it advantageous.

In contrast, the bird populations in the Nicaraguan savanna change very little throughout the year. In August, the young birds increase the numbers of individuals of permanent residents, and in winter some North American migrants arrive. They compete only partly, if at all, with the residents. However, the permanent residents do not seem to change the dimensions of their niches with the seasons and many appear to remain paired and to maintain the same home ranges throughout the year. In an impoverished habitat such as the pine savanna, this leads inevitably to a wide spacing and low density of individuals.

One could propose that the environment in the Nicaraguan pine savanna with its wet and dry seasons and frequent fires is actually just as unstable and

TABLE 7

Comparison of Pineland Bird Populations

*Georgia**		*Nicaragua*	
Species	*Territorial males (pairs) per 100 acres*	*Species*	*Territorial males (pairs) per 100 acres*
	Non-Passerines		
		Falco sparverius	0.25
Colinus virginianus	5.8	*Colinus nigrogularis*	3.0
		Chordeiles minor	1.0
		Amazilia cyonocephala	3.0
Centurus carolinus	1.2		
Dendrocopos pubescens	4.7	*Dendrocopos scalaris*	0.25
Total	11.7		7.50
	Passerines		
Myiarchus crinitus	14.0	*Pyrocephalus rubinus*	0.5
Contopus virens	21.0	*Muscivcrra tyrannus*	0.25
Cyanocitta cristata	11.6		
Parus carolinensis	2.3		
Parus bicolor	4.7		
Sitta pusilla	9.3		
Sialia sialis	2.3	*Sialia sialis*	4.0
Polioptila caerulea	2.3		
Vireo flavifrons	2.3		
Dendroica pinus	30.3	*Dendroica graciae*	10.0
Piranga rubra	10.5	*Piranga flava*	6.0
		Icterus chrysater	0.25
		Sturnella magna	5.0
		Carduelis notata	2.0
Aimophila aestivalis	69.9	*Aimophila rufescens*	5.0
		Spizella passerina	1.0
Total	180.5		34.00
	Mean abundance; territorial males per 100 acres per species		
Non-passerines (n-p)	3.9		1.5
Passerines (p)	15.0		3.4
p/n-p	3.8		2.3

***Data from Norris, 1951.**

rigorous as the environment in the Georgia areas, and that this instability causes a low diversity and low population density. However, the dry season is only relatively dry; there is usually some rain as well as permanent streams and ponds. Fires are also characteristic of the temperate pinelands, including Norris' study area in Georgia. Periodic burning is a management technique for increasing quail populations and, incidentally, those of meadowlarks and some sparrows (*Aimophila*). In fact, in habitats where fires are frequent and natural, periodic burning is not a disaster and may even help to maintain or increase bird populations, including those of ground-nesting species (Komarek, 1966; Lawrence, 1966; Stoddard, 1932). It is, therefore, improbable that the stress of fires in the Nicaraguan savanna is equivalent to the climatic stress in the temperate zone.

Thus, in two very similar habitats, the one with an equable tropical climate supports a much sparser bird population than the one with a more variable temperate climate. I attribute a large part of the difference to the use of broader niches, at different seasons, by the temperate-zone species. In the northern temperate regions, which have only become habitable for their present avifauna within the last few thousand years, selection naturally favored broad-niche species that could adapt to marked seasonal changes.

Specialization to a pine-forest environment involves a narrowing of niche dimensions. In tropical regions, where selective pressures for maintaining broad niches are slight and countered by competition with established residents in the broad-leafed forest, the narrowing could reach an extreme. This may have happened in the tropical pine savanna, where most species appear to be of northern derivation. Although this specialization to narrow niches may have reduced the numbers of individuals, it has not led to a greater diversity of species; that requires more niches.

Slud (1960) pointed out that the ratio of suboscine to oscine passerines increases from North America through Central America to the equatorial forests of South America. His interpretation is that suboscines evolved in conjunction with humid lowland tropical forests and are more numerous and diverse than oscines in such associations, but they diminish northward as that habitat diminishes in extent and complexity. The suboscine to oscine ratio also drops in open and drier habitats, even in equatorial regions, suggesting that the oscines in general may be better adapted to such environments. These phenomena may relate to the fact that suboscines are almost entirely insectivorous or frugivorous or both whereas oscines include many types that feed on hard dry seeds. In the Nicaraguan study areas, suboscines comprise most of the rain forest passerines but there were no suboscines in Pine Savanna Areas I and 2; the only permanent-resident suboscine species in the unmixed savanna are the Fork-tailed and Vermilion Flycatchers, and as Orians (1969) pointed out, flycatchers (tyrannids) are the most successful suboscine family in temperate environments. The savanna includes six or seven (including the Yellow Grass-finch) permanently resident species of fringillids, but in the otherwise richer Rain Forest Area we recorded only five species of fringillids, of which only the Black-faced Grosbeak and Orange-billed Sparrow spent much time inside the forest as opposed to the edge. As open and drier habitats generally include many plants with seeds that lack an edible outer covering, such habitats predictably support more seed-husking or seed-cracking species—usually oscines—than do humid forests.

Question 8

What is the ecological effect of wintering North American migrants on the resident birds in both habitats?

The influence of North American migrants on the resident avifauna of the Nicaraguan study areas appears to be negligible with one striking exception — the Yellow-throated Warbler — which I shall discuss below.

We recorded 15 North American migrants in the Rain Forest Area (Table 3) — one species each in the families Tyrannidae (assuming that the pewee, Contopus sp. is a migrant), Mimidae, Turdidae, Vireonidae, Icteridae, Thraupidae, and nine species in the Parulidae. Other than the Catbird (*Dumetella carolinensis*), Summer Tanager, Magnolia Warbler (*Dendroica magnolia*), and Chestnut-sided Warbler (*D. pensylvanica*), the migrants appeared to be only casual visitors. The Catbird, a thicket-inhabiting bird, is the only mimid that occurs in Nicaragua. The Summer Tanager and Chestnut-sided Warbler usually occur in the higher levels of the forest; the Magnolia Warbler may occur at all levels, but is usually less than 20 feet above ground. As most of the resident species forage at the lower levels, one might expect this warbler to encounter severe conflict with the residents, yet it was the most abundant of the North American wintering species.

None of the migrants was numerous; we seldom saw as many as three individuals in a census of the 10-acre area. I never noticed any aggression between the migrants and resident forms, and from this negative evidence I presume there is little important competition between them. Willis (1966b), in a study of interactions between migrant passerines and resident ant-following species in the rain forest on Barro Colorado Island, Panama, concluded that the migrants do not restrict the residents; rather, the residents restrict the migrants to the use of sporadically superabundant food.

In the pine savanna, we recorded only five species of winter residents (Table 1). The Yellow-bellied Sapsucker (*Sphyrapicus varius*) was scarce and we never observed it interacting with other woodpeckers. The sapsucker also ranged into the broad-leafed forest, and with its ability to feed on sap and cambium, it probably does not compete importantly with the permanent residents. We recorded the Tree Swallow (Iridoprocne bicolor) only in one year; this aerial feeder had no competitors over the savanna in winter.

Three species of warblers are present in winter in addition to the permanent-resident Grace's Warbler. The Palm Warbler (*Dendroica palmarum*), a ground-feeder, is scarce; the Myrtle Warbler (*D. coronata*) is common, but in this region is primarily a "flycatcher" at middle and lower levels as well as a shrub- and ground-feeder. Neither of these warblers appears to compete importantly with the Grace's Warbler. The Yellow-throated Warbler, however, feeds in trees at the same levels as the Grace's Warbler, and the two species show quite similar color patterns. Although the Yellow-throated Warbler winters in non-coniferous forest on the Pacific slope of Nicaragua, we did not observe it outside the pine savanna on the Caribbean slope and Russell (1964) listed it as common in the pines in British Honduras.

In the Nicaraguan savanna, the Yellow-throated Warbler arrives at least by mid-August and was present until late March 1966, but not in mid-April 1967. The Yellow-throated Warbler and Grace's Warbler often foraged in the same general area or in the same tree. In fact, we found the two species close together so frequently that mere coincidence seems unlikely. The Grace's Warbler often attacked the larger Yellow-throated Warbler but not viceversa;

the Yellow-throated Warbler usually retreated only as far as was necessary to avoid further attacks and resumed foraging.

The two are potentially competitive, but clear-cut differences in morphology and feeding behavior probably account for their successful coexistence for at least eight months of the year. The Yellow-throated Warbler is larger and has a longer bill than the Grace's Warbler. Three specimens of the Yellow-throated Warbler, collected in the Nicaraguan savanna, had a mean wing length of 64.7 mm, about 8 mm longer than the mean for the savanna population of the Grace's Warbler (Table 5). Measuring only the specimens collected in the Nicaraguan savanna, the mean culmen-from-nostril length of three Yellow-throated Warblers was 9.6 mm and the mean for 16 Grace's Warblers, 7.5 mm, giving a ratio of 1.28, well above the ratio of 1.14 suggested by Schoener (1965) as the minimum ratio indicative of partitioning of food resources by their size or dimensions.

TABLE 8

Shared Taxa of Birds in three Different Latitudinal and Ecological Areas

Family	*Genus/Species*	*Vermont (temperate deciduous woodland)*	*Georgia (Pine forest)*	*Nicaragua (Pine savanna)*
Picidae	***Dendrocopos***	X	X	X
Sittidae	***Sitta***	X	X	
Turdidae	***Sialia sialis***		X	X
Vireonidae	***Vireo***	X	X	
Parulidae	***Dendroica***	X	X	X
Thraupidae	***Piranga***		X	X
Fringillidae	***Aimophila***		X	X

There is some overlap in their foraging activities in that both species worked over the branches and foliage of the pines and did some flycatching; there were also well-marked differences. Most of the time, the Grace's Warbler moved out from the tree trunk along the upper surface of small branches of larger trees, taking food from the bark and then gleaning the bases of the needle clusters. It usually foraged on branches that did not exceed, roughly, the diameter of its own body, enabling it to reach around most of the branch with its bill without having to hang upside down. On the few occasions when we saw Grace's Warblers foraging on large branches, they seemed able to cling only momentarily to the undersides before falling away. The Grace's Warbler very seldom foraged on tree trunks, but frequently sallied after flying insects and captured some as large as small dragonflies (Odonata).

In the Nicaraguan savanna, the Yellow-throated Warbler exploits the bark-gleaning niche that appears largely unfilled by any resident species. Unlike the Grace's Warbler, the Yellow-throated often frequents the larger branches and tree trunks, where it reaches into crevices with its long, slender bill. It moves over vertical trunks and along the underside of branches in much the same manner as the Black-and-white Warbler (*Mniotilta varia*), a species that winters in the adjacent broad-leafed forest but almost never ventures into the pines.

A comparable situation exists in the pine forests in the southern United States where Ficken et al. (1968) studied competition between the Yellow-throated Warbler and the Pine Warbler. The ratio of the bill lengths of Yellow-throated Warbler/Pine Warbler is 1.24—very close to that shown for Yellow-throated Warbler/Grace's Warbler in Nicaragua. The population of Yellow-throated Warblers studied by Ficken et al. used the longer bill in probing cones of Pinus taeda, one of the three species of pines present; they did not see the Pine Warbler probe cones and showed that its bill and skull morphology would make this activity ineffective. In the Nicaraguan pines, we never saw either warbler probe cones, but the longer bill of the Yellow-throated Warbler allows it to probe into deeper bark crevices and exploit a food source unavailable to the Grace's Warbler. Whether or not the Yellow-throated and Grace's Warbler could coexist as breeding species, particularly in an area with only one species of pine, is a moot question. In April, when the Yellow-throated Warbler was absent, the Grace's Warbler appeared to explore the bark crevices of the larger branches and trunks more often, but it seemed poorly adapted for this type of feeding. It also foraged frequently among the small pines and seedlings, but did not seem to obtain much food from them.

In summary, the evidence suggests that the Yellow-throated Warbler during its winter residency exploits a foraging mode that is not used in the savanna during the breeding season. I doubt that the presence of the Yellow-throated Warbler lowers the population density of the Grace's Warbler but we need more data to be certain.

Question 9

What historical factors may have been responsible for the difference in the avifauna of the two habitats?

Although one cannot entirely separate the influences of historical from ecological factors in determining the composition of the avifaunas of the savanna and rain forest areas, distinctions are possible. Given the same contemporary ecological conditions, a different history might have produced different avifaunas.

The rain forest of the Caribbean slope of Nicaragua probably has been essentially continuous with that of Costa Rica, Panama, and much of South America since the end of the Pliocene period. The bird species are mostly of tropical affinity, and the varied composition of the avifauna is not surprising.

The Nicaraguan pine savanna is probably of relatively recent origin. It may be no older than the cut-and-burn agricultural practices of the aboriginal Indians; or, it may date back to the last glacial period which presumably caused the pine forest to extend into tropical latitudes. A reasonable guess is that the age of the Nicaraguan pine savanna is between 1.000 and 10,000 years.

The length of time that the lowland pine savanna has been isolated from other pine-forest habitats—assuming that some connection once existed-must be less than the age of the pine-savanna habitat as such. The presence of well marked subspecies of birds representing several different orders and families indicates a high degree of isolation (Howell, 1965; Monroe and Howell, 1966; Monroe, 1968).

The Nicaraguan pine savanna represents a relatively recent, terminal, and isolated segment in the tropics of a specialized habitat that is more characteristic of high-latitude regions; one would expect its avifauna to include a depauperate sample of primarily temperate-zone species adapted to a temperate-zone environment, and to lack many other potentially successful adaptive types. I suggest that the absence of many of the potentially adaptive types is a consequence of historical accident and not of ecological unsuitability; other actually or potentially pine-adapted species have simply not reached the area, or have not reached it in sufficient numbers at the right season, to establish themselves. If the tropical conditions of the lowland pines were generally unfavorable to species derived from the north-temperate zone, one would not expect to find the Red Crossbill and Chipping Sparrow. On the other hand, species of the humid lowland forest have always had ample opportunity to occupy the pines, but none has succesfully or completely taken this step.

Of the permanent-resident pine-savanna species that are probably not of temperate-zone origin, the only tropical forms we find in the savanna are those that are adapted elsewhere in their ranges to open and sometimes arid or semi-arid habitats. This fact again emphasizes the recency of the habitat, for several species of the humid forest edge that frequently use open vegetational associations are only visitors to the savanna despite the apparently vacant niches.

The apparent trend is that birds of tropical affinity are gradually invading the savanna while pine-savanna birds are not invading the broad-leafed forest. Even such a versatile form as the American Kestrel has not yet begun to occupy the numerous clearings in the broad-leafed forest that seem to offer suitable foraging conditions and no obvious competitors. In this meeting of characteristically temperate-zone and tropical-zone habitats, there is no evidence of general adaptive superiority of species of temperate-zone origin.

In summary, the sharp ecological differences between the pine savanna and rain forest environments account in the main for their avifaunal differences, but historical factors—the antiquity and continuity of the rain forest and the recency and isolation of the pine savanna—are probably responsible for many important details in the composition of their avifaunas.

Latitudinal Gradients and Species Diversity

Question 10

What relevance do the answers to these questions have to the subject of latitudinal gradients in bird species diversity?

When I began this study in 1965, one of my objectives was to contribute to the understanding of latitudinal gradients in species diversity. Since that time, the theoretical question of why there are such gradients has been beaten, if not to death, at least to the point of greatly reduced viability. Two recent symposia (Lowe-McConnell, 1969; Brookhaven Symposia in Biology Number 22, 1969) include numerous sophisticated mathematical models and brilliant analogies that deal with many aspects of tropical diversity. The conclusions that I reached from my data include some that are very close to those of Slobodkin and Sanders (1969) in their contribution to the latter symposium, and in such instances I will frequently paraphrase and use terms from their excellent and lucid review, without pretense of originality. Actually, many of the ideas supported by those authors are virtually traditional, but are worth reiterating as they are often doubted or denied.

My data from the rain forest study area confirm as expected that this type of habitat supports a greater diversity of bird species than does temperate forest, but also show that the diversity is much greater than that predicted from a foliage profile based on three or even five layers. Either the hypothesis that bird species diversity can be predicted from foliage profile is insufficient, or the vegetation measurement and bird censusing techniques are inadequate for the complex tropical rain forest. Predictable or not, the high diversity figure merits closer examination.

In avian taxonomy, the families are generally less broadly inclusive than those in other classes of vertebrates and tend to comprise very similar adaptive types. Members of many avian families are therefore likely to be readily recognizable variations on an ancestral adaptive theme, and the theme may be identifiable as to its probable region of origin. An adaptive pattern that importantly involves sallying after flying insects or feeding on nectar almost certainly evolved in the tropics, where these food resources are available the year round. In contrast, a pattern that often includes high resistance to cold, opportunistic foraging modes, and even storage and recovery of seasonally abundant food is likely to have evolved in high latitude regions. Thus, although avian families may be rather finely split taxonomically, the family thereby gains in usefulness in tracing evolutionary histories.

An analysis of the distribution of birds in Central America (Howell, 1969) shows that, in some families, the number of species decreases from temperate to tropical regions whereas in other families the reverse is true. For example, the Corvidae (ravens, crows, jays) and the Paridae (chickadees, tits) show greater species diversity in the temperate zone than in the tropics, and the Trochilidae (hummingbirds) and the Tyrannidae (New World flycatchers) show the opposite trend in diversity. The families Corvidae and Paridae probably originated in the temperate zone, and the hummingbird and flycatcher families probably arose in the tropics. Some taxa in each of these families have successfully colonized habitats in climatic zones other than the one in which the group probably originated, but the overall tendency is for a lessening of species diversity from the environment of probable origin toward its periphery. Although groups adapted to temperate zone conditions tend to decrease or increase in species diversity with decreasing or increasing latitude, respectively, the number of species in the tropical-adapted groups is so much greater that their increase or decrease completely overshadows the trend of the temperate zone groups. If one considers only the total number of species in each of a series of regions, the conclusion is that the class Aves shows increasing species diversity with decreasing latitude, but this is a composite of opposing trends.

A basic question, therefore, is: "Why are there so many species in tropical-adapted avian groups?" I assume that rates and mechanisms of speciation are adequate to produce at least as many species as the environment can support in both temperate and tropical forests, and the question pertains to the factors that make possible the continued existence of such large numbers of species in the latter habitat. A frequently offered answer is that there are more and perhaps narrower niches in the tropics, but as Slobodkin and Sanders (1969) point out, this type of argument is circular even if the statement is true. As we recognize and define niches by the presence of occupying species, many species must mean many niches. However, few species could mean either fewer niches, or some unoccupied niches, or larger niches for fewer but more broadly adapted species. If there are more and narrower niches in the tropics than in the temperate zone, one must explain why there are more, and why there are so many different species occupying them.

Slobodkin and Sanders (1969) discussed species diversity in terms of severity and predictability of environments. By a "predictable" environment they mean one in which the variances of environmental properties around their mean values are relatively low and predictable, both spatially and temporally. Severity of conditions leads to low diversity, but given predictability of conditions many kinds of animals can adapt physiologically or behaviorally and persist. Coping with unpredictable conditions requires a broader range of adaptation, and species that lack that capacity will be eliminated; even fewer can survive conditions both unpredictable and severe. The latter type of environment should have the lowest diversity of species, and a predictable and benign environment should have the highest diversity. The tropical rain forest approximates such an environment as it is highly predictable and lacks extremes of temperature and aridity. Applying these concepts to birds, one may summarize as follows:

1. In the New World equatorial regions, the predictable and benign humid lowland forest has existed in varying extent for the duration of the evolutionary history of birds.

2. In this habitat, many species may persist—even if rare—that could not survive in unpredictable and severe conditions characteristic of higher-latitude environments. The humid tropical forest not only supports broad-niche species but tends to accumulate a variety of narrow-niche specialists. The latter are often sparsely distributed but so well-adapted to their microhabitats that they are able to maintain themselves in competition with invading or newly-evolved jack-of-all-trades species.

3. In the less predictable and often severe temperate zone, narrow-niche specialists may also invade or evolve, but if dependent on a few critical conditions or resources that disappear with drastic climatic change—seasonal or through geologic time—such species will be eliminated. Unpredictable conditions also favor the evolution of broadly-adapted forms.

4. Humid tropical forests thus support a great number of bird species, many with low population densities, occupying a great variety of niches. In the temperate zone and higher latitude regions, relatively few but broadly-adapted species partition the environmental resources. When such resources are abundant, partitioning by relatively few species leads to large numbers of individuals of each.

A frequent criticism of such proposals is that they fail to account for the great diversity of tropical plant species required for the great variety of niches, thus begging the question or merely pushing it back one step. However, the same reasoning that may explain diversity of animal species seems equally applicable to diversity of plant species, and Janzen (1970) has shown that, in the tropics, heavy predation on seeds and seedlings near the parent plant may account for the absence of pure stands, and consequently the greatly mixed distribution of plant species in tropical forests.

The Nicaraguan pine savanna is virtually as predictable as the adjacent rain forest but is less benign. There is much less shade, evaporation rates are higher, the soil is leached and poorer in organic nutrients, and there are extensive fires in the dry season. This periodic burning may not be detrimental to pine- and grassland-adapted birds, but it certainly constitutes severe physical stress for many plants, insects, and other invertebrates and possibly for some reptiles and small mammals. It definitely limits invasion of the savanna by many broad-leafed plant species and thus restricts the variety of possible niches there; in Slobodkin and Sanders' terms, the pine savanna lacks the geometrical complexity and spatial heterogeneity of the rain forest.

Paine (1966) showed that predation on invertebrates in the rocky-intertidal zone favored species diversity by preventing the monopoly of resources by one or a few species, and proposed that predation is a generally important influence on species diversity. MacArthur (1969) used similar reasoning in suggesting that high predation in the tropics leads to high species diversity there. The Nicaraguan savanna avifauna includes a higher proportion of predatory birds than does the adjacent rain forest or temperate pinelands, but bird species diversity is low. Possibly most of the raptors in the savanna do not feed primarily on birds, but some do in part. Other potential predators on birds such as snakes and carnivorous mammals appear to be extremely scarce in the savanna, and Paine's and MacArthur's proposals may be valid for other habitats where such types are abundant.

The sparse avifauna of the tropical pine savanna at first seems to contradict the principle that predictable and relatively benign habitats will have greater species diversity than less predictable and more severe habitats, for temperate zone pinelands are in the latter category but support breeding bird faunas at least as diverse as in the tropical pines and have greater numbers of individuals. I attribute the relatively low population density of the pine savanna birds in part to the fact that most of them do not or cannot invade the adjacent broad-leafed forest and use the more abundant resources there. As previously mentioned, the equivalent temperate pineland birds often range into other habitats, at least seasonally. Thus, the dimensions of the niches of many of the tropical pine savanna birds are narrower, but narrower niches alone have not brought about greater species diversity. The Nicaraguan pine savanna is also relatively recent in age and lies at the periphery of this type of habitat; given enough time, more species of pine-adapted or open-country birds might reach the savanna and establish themselves. It is also possible that, for the same reasons, potential foods for birds are presently scarce there and might ultimately increase. Thus, in the Nicaraguan savanna, the conditions usually associated with low latitudes—predictable and benign climate, low population densities and narrow niches of resident bird species—are as yet insufficient to bring about high species diversity because of the low variety of niches and the isolation from the pool of species potentially able to establish themselves there.

Even if the savanna were not a recent formation, however, I do not believe it could ever approach the high species diversity of the adjacent rain forest. The rain forest habitat has varied resources for nectar, fruit, and insect eaters, and a highly varied foliage physiognomy. Its bird population is primarily derived from groups of tropical South American origin and descendants of the pre-Pleistocene avifauna of tropical North and Central America. Recurrent periods of aridity in the Pleistocene isolated segments of humid lowland forest and this probably augmented the differentiation of many similar forest-adapted tropical bird species, especially in South America (Haffer, 1969). Some of these have doubtless extended their ranges north through the now continuous rain forest of the Caribbean slope, at least part of which has probably existed throughout the Cenozoic era.

Pleistocene glaciation in North America forced the ranges of many species far to the South and eliminated others, leaving an avifauna largely of temperate-adapted types including those specialized for exploitation of coniferous forests and grasslands. The Nicaraguan savanna represents the southernmost extent ever reached in the New World by the pinelands habitat, and its bird species are largely of temperate zone origin and constitute a depauperate sample of the avifauna of the temperate pinelands that has reached tropical latitudes primarily at high elevations. The few bird species of probable tropical origin that have colonized the lowland pine savanna are not fully pine-adapted; they only take advantage of its open aspect, or obtain food from tropical epiphytes. In a sense, the pine savanna represents the worst of two worlds—too recent and too remote for colonization by most temperate pine-adapted birds, and too austere ecologically for most tropical forest birds.

All this leads to the scarcely original but common-sense conclusion that high species diversity depends on a constellation of conditions that are most likely but not invariably to be found at tropical latitudes, and when one or more of these conditions is absent—as is likely in higher latitudes—species diversity declines. I have discussed some of these conditions previously and I cannot hope to recognize and list all the possible ones. Probably the influential factors vary with the case under scrutiny, and we may never achieve a general and comprehensive theory to account for all gradients in species diversity. As MacArthur (1969) points out "...statistical events like species diversity often have complex and multiple explanations. Hence, there is no reason that the validity of any of the [possible] explanations need preclude any of the others."

For the situations I have tried to analyze, there are certainly multiple explanations. In addition, at least among Central American birds, there are opposing gradients of species diversity in groups of temperate and tropical origin where temperate environments extend into tropical latitudes and interdigitate with attenuated tropical environments. Lumping the total number of species found at a given latitude gives the misleading impression of a relatively uniform gradient of increasing species diversity from north to south. Therefore, in attempting to explain gradients in bird species diversity, one must consider not only a wide range of ecological parameters but also the geologic history of the region in question and the distributional and evolutionary .history of the species under study. The same precaution may prove fruitful in analyzing the species diversity patterns of other organisms as well.

Summary

I used the method of MacArthur and MacArthur (1961) to measure the vegetation density at three levels in two areas of pine savanna and one area of rain forest, and I calculated foliage profiles and foliage height diversities (FHD) for each area. I have described the methods in detail. From censuses of birds in the three areas made at different times of the year, I calculated resident bird species diversity (BSD) and compared these results with the figures predicted by the equation BSD = 2.01 FHD + .46, derived from temperate-zone data by MacArthur and MacArthur (1961).

Bird species diversity in one savanna area with sparse seedlinps and shrubs approximated the predicted value only when it included 25 acres instead of the five used in the temperate-zone study. In a second savanna area with numerous seedlings, the FHD was greater but the observed BSD was lower than that predicted from it. This suggests that the seedling layer eliminated some bird species but added none. When the area was treated as a two-layered habitat, the predicted BSD and the observed value were much closer. In the rain forest area the observed BSD was much greater than that predicted from the FHD even when the latter was calculated from five instead of three layers of vegetation.

A census of a five-acre grassland in the savanna in April yielded no nesting birds although grassland species were then in breeding condition. This result indicates low population densities and patchy distribution of grass-dwelling birds.

I compare my results with data from temperate-zone forests, both deciduous and pine, and discuss the possible influences of competition, niche size, and related ecological and historical factors on bird species diversity. I conclude that the avifaunas of the pine savanna and adjacent rain forest are almost totally different, largely because of different adaptations and distributional histories, and that there are fewer niches for birds in the pines than in the adjacent rain forest. As expected, the tropical rain forest area-has a greater number of bird species but fewer individuals per species than have temperate-zone forest areas of comparable size. I attribute this to the greater variety of niches for birds in the tropical forest, many of which are occupied by narrow-niche specialists that can persist under mild and equable conditions but could not survive more rigorous temperate-zone conditions and the competition from species well-adapted to them. Unexpectedly, the tropical pine savanna area has no greater species diversity and has lower densities of individuals than have temperate pineland areas of comparable size. From the data on the pine savanna, I conclude that: (1) in similar habitats, at different latitudes, a more predictable and benign climate does not necessarily result in an increase in the number of bird species or of individuals; (2) some bird species in tropical areas have a smaller range of foraging activities and habitat usage than their temperate zone equivalents, but this does not necessarily lead to greater species diversity although it may result in a lower density of individuals; **(3)** bird species diversity varies in different groups in different habitats at the same latitude — for example, diversity of fringillid species is greater in the pine savanna than in the rain forest, whereas suboscine passerines show a much greater diversity in the latter habitat; lumping all bird species at a given latitude into a single total conceals such distinctions; (4) the geological history of the Central American region and the evolutionary history of its bird life have influenced the avifaunal differences between the pine savanna and adjacent rain forest and also the nature of the latitudinal gradient in bird species diversity.

Acknowledgments

National Science Foundation grants GB **3683** and GB **3783** supported the field work in Nicaragua. I am very grateful to the personnel of the Nicaraguan Long Leaf Pine Lumber Company ("Nipco"), particularly the Robinson family of New Orleans, Louisiana, and to W. H. Barry, Mr. and Mrs. John H. Roberts, and many others at the company's Nicaraguan facilities. Mr. and Mrs. H. H. John of the United Nations FAO office in Puerto Cabezas provided assistance and information. Lt. Col. Fritz Halsell of the Administracion de Aduana at Puerto Cabezas facilitated clearing equipment through customs. Spicer Lung of the Managua office of Pan American Airways expedited shipments of specimens and made travel arrangements with efficiency. I regret that space does not permit the listing of many others in Nicaragua who helped us in innumerable ways, and I am deeply appreciative to all. Mildred Mathias and D. S. Verity identified botanical specimens and clarified nomenclatural problems. The comments and criticisms of M. L. Cody, J. M. Diamond, B. L. Monroe, Jr., G. H. Orians, D. R. Paulson, and S. M.

Russell were a great benefit although we do not necessarily agree on all points. My field companions inclyded Monte Lloyd, who aided in making and analyzing the vegetation measurements, Antonio Molina R., Escuela Agricola Panamericana, Tegucigalpa, Honduras, whose knowledge of Central American plant life provided both aid and inspiration, and T. W. Brown, who collected herpetological specimens and aided in many ways. My special gratitude goes to L. F. Kiff, F. G. Stiles, and J. E. Zoeger, who participated with great skill and dedication in the most arduous parts of the field work and shared freely their ideas on tropical ecology.

APPENDIX 1

Method Used in Obtaining Foliage Height Diversity (FHD) and Bird Species Diversity (BSD)

Within each study area we marked 20 random points by using a table of random numbers for distances along two coordinates of a quadrilateral, and for each of these points we selected a compass direction, from 0 to 360, also from the table of random numbers. We took a white board, **30** by **30** inches, to each point and then moved either the board or the observer in the compass direction until the board appeared half-covered with foliage. The vegetation density is inversely proportional to the distance between the observer and the board; that is, the greater the distance, the less dense the vegetation. Assuming a random distribution of leaves, we express the vegetation density as $K = \frac{\log_e 2}{D}$ where K is the area of leaf surface/volume of space and D is the distance between the observer and the board, when the board appears half obscured by vegetation.

We repeated this measuring procedure for each of the 20 points for three different levels above ground and averaged the figures for each level. The number and vertical extent of the levels are necessarily arbitrary. We chose three, with dimensions that correspond roughly to a low layer of grasses and herbs, an intermediate layer of shrubs and seedlings, and a high layer of the crowns of the larger trees. One then plots the mean density figures for each level against the height to form the foliage profile (Figure 4). The maximum height on the graph is the average height of a group of randomly chosen trees that are higher than the upper limit of the intermediate layer. If the investigator delimits the levels appropriately, the foliage profile should agree with his subjective impression of the vegetation of the area.

Using data on vegetation density in the different layers, MacArthur calculated foliage height diversity (FHD) using Shannon's function $FHD = -\sum_{i=1}^{S} p_i \log_e p_i$ where S represents the number of layers of vegetation measured, and p_i the proportion of the total vegetation density represented by the ith layer. The figure approaches a maximum when the layers approach equal density, declines when the distribution of foliage is more unequal, and reaches zero if only one layer is present (log. $1 = 0$).

The same formula provides a measure of bird species diversity (BSD) when S equals the number of bird species in an area and p_i equals the proportion of the total number of birds, or of breeding pairs, present that are represented by the ith species. A maximum diversity figure is approached when there are many breeding species present in equal numbers, and diversity equals zero if only one species is present. For examples and discussion of the use of this equation as a measure of diversity, see Lloyd and Ghelardi (1964), MacArthur (1964), Pianka (1966), McIntosh (1967), and Lloyd et *al.* (1968).

The size of MacArthur's study areas was at first five acres, a reasonable size for an accurate census and one that permits comparison with other census data which are often obtained in five acres or multiples of five. In later work, in habitats that had sparse bird populations, MacArthur compared census plots that included 20 to 25 pairs of birds regardless of acreage.

MacArthur and Mac.Arthur (1961) found that, in a number of temperate-zone habitats, a plot of FHD against BSD yielded a series of points clustered about a straight line. Consideration of plant species diversity in relation to BSD did not reduce scatter of points or provide a better fit by a straight line. From this the authors concluded that, at least in the habitats they studied, they could predict the BSD from the FHD without considering the species composition of the vegetation. Their equation is $BSD = 2.01\ FHD + .46$. However, MacArthur (1964) pointed out that, in some special habitats and with some bird species that are food specialists, the proposed relationship between FHD and BSD might not hold.

We measured the vegetation characteristics of two pine savanna areas and one rain forest area by MacArthur's method with the following specifications and modifications:

1. We kept the white board, 30 by 30 inches, at the random points and the observer moved away from it.

2. We delimited three vegetation layers—0 to 3 ft, 3 to 20 ft, and 20 ft to the average height of trees over 25 ft. We selected these limits primarily on the basis of the characteristics of the savanna; the densest grass and sedge growth in the study area seldom exceeded 3 ft, and the lowest branches of the mature pines were usually about 20 or 25 ft; this left an intermediate layer between 3 and 20 ft. We could not distinguish a similarly "natural" division in the rain forest, but since no other spacing of layers seemed any better, we used the same divisions. We held the board at the following levels for measurements: 0 to 3 ft—one edge resting on the ground: 3 to 20 ft—approximately 6 ft above ground; 20 ft and above—atop a 24-foot aluminum pole.

3. For determinations above 20 ft, the observer either climbed a tree or used a ladder. When he could use neither of these methods, he backed away and estimated from the ground which foliage cluster, alone or in combination, would half obscure the board and then measured the distance from the board to this cluster. In the pine savanna, above 20 ft, sometimes only one or two foliage clumps intervened between the observer and the board. When the closest foliage clump covered less than half the board and this, combined with the second, covered more than half, we used the following calculation of foliage density:

$$\tfrac{1}{2}\,(\log_e(1 - p_1))\,/d_1 + (\log_e(1 - p_2))\,/d_2 = K$$

p1 = proportion of board covered by first clump; d1 = distance to first clump; p2 = proportion covered by two clumps combined; d, = distance from point to second clump.

4. There was very little foliage in the intermediate layer in one of the savanna areas; sometimes the trunk of only one pine intervened between the observer and the board without half covering it or there were numerous straight trunks that covered no part of it. Feeling that we were missing 17 feet of vertical tree trunk, an important vegetational component, we made additional measurements to take this into account.

Using a forester's wedge prism with a basal area factor (BAF) of 10 at each random point, we recorded the number of trees whose trunks appeared displaced to the side by an amount less than the apparent trunk width, measured the circumference of these trees, and calculated the bark surface of that part of their trunks within the intermediate layer. We combined these figures with those for the vegetation density based on area of leaf surface when constructing the foliage profile.

5. The dense foliage of the rain forest above 20 ft sometimes completely obscured the board for an observer only a short distance away. Trial and error testing in comparably dense foliage at eye level indicated that 30 inches was a reasonable figure for the mean distance at which the board would be half obscured. Thus, for such points we assumed that D equalled 30 in.

We censused all study areas repeatedly for birds during each visit with the exception of the grassland area which we censused only twice, both times in April. One or two observers began before, or shortly after, sunrise to record species seen or heard within the area. In the pine savanna, the observer usually started at one corner, walked along one edge to the opposite corner, moved up one side a few meters, and then walked back parallel to his first crossing. By repeated crossings he could census a 25-acre area in about one and one-half hours.

We used a different method in the rain forest area where there were no obvious or recent trails. We first cut a trail around the area by following compass lines and then a random pattern of trails through it, trying to strike a balance between penetrating the densest parts and keeping the disturbance of the vegetation to a minimum. Some measure of our success, by human standards, is the fact that we often became disoriented within the 10-acre plot even after we believed we were familiar with the trails.

We censused the grassland area first on 22 April by walking back and forth across it as in the pine savanna. On 25 April, two of us dragged an 80-foot rope, stretched between us, across the entire area. Since neither method yielded a single bird, we concluded that no species nested in the grassland plot, nor used it importantly at that time of year.

We made censuses from dusk up to 18:00 or 20:00 hours several times in one pine savanna and twice in the rain forest area during April 1967. In the savanna we found no birds except the Common Nighthawk (Chordeiles minor) overhead. We also recorded this species in the daytime. We heard no owls and our repeated attempts to call up or eyeshine owls were unsuccessful. We detected no nocturnal birds in the rain forest area although we collected a Mottled Owl (Ciccaba virgata) nearby and heard, but did not identify, another owl of medium to large size just outside the area.

APPENDIX 2

Conspicuous Plants of the Savanna Study Areas and Their Importance to the Bird Fauna

Trees

Pinus caribaea, Pinaceae; most abundant tree; used to some extent, at least, by almost all savanna birds.

Curatella americana, Dilleniaceae; low and spreading, often less than 2 meters high; indicator of burned-over conditions; abundant; seldom used by birds except for perching; Yellow-bellied Sapsucker ***(Sphyrapicus varius)*** workings noted occasionally.

Xylopia frutescens, Ammonaceae; a few examples, less than 2 m in height, of this broad-leafed forest tree in wet areas; no use by birds observed in this early growth stage.

Shrubs

Byrsonima cmassifolia, Malpighiaceae; usually less than 0.5 m high, but small tree size at edges of broad-leafed forest; large berries eaten by many birds.

Miconia lundelli; M. albidea, M. scorpioides, M. impetularis, Melastomataceae; listed in order of increasing size, about 0.5 m to as much as 2 m, and decreasing abundance; all, especially the first two, important sources of berries eaten by birds.

Palicourea guineense, Rubiaceae; up to 2 m high, found in savanna only near edge of broad-leafed forest; red flower clusters used by hummingbirds.

Sabal sp., Palmaceae; palmetto. usually in dense clumps at edge of wet areas; important cover for sparrows, particularly Botteri's Sparrow ***(Aimophila botterii).***

Herbs

Tibouchina belizensis, Melastomataceae; abundant; may be 2 m high; sometimes in stands; provides some cover; no observed use of seeds by birds.

Clidemia rubra, Melastomaceae; abundant; less than 1 m high; no observed use by birds for cover or food.

Polygala sp., Polygalaceae; ***Borreria swaveolens, Diodia frutescens,*** Rubiaceae; ***Cassia diphylla,*** Leguminosae; all abundant, usually less than 0.3 m high, of scattered distribution; no observed use by birds.

Grasses and Sedges

Tripsacum sp., Gramineae; cane-grass, dense stands 1.5 to 2 m high in wet places, espeaally edges of broad-leafed forest; provides cover; seeds eaten by birds.

Paspalum humboldtianum, Gramineae; most abundant grass, almost everywhere in dense dumps up to one m high; provides cover; seeds small, no observed use by birds.

Panicum sp., ***Aristida*** sp., Gramineae; wiry grasses; both abundant, mixed with ***Paspalum,*** but smaller—usually not over 0.5 m high; provide cover; no observed use of seeds by birds.

Andropogon sp., Gramineae; broom-sedge grass; less abundant than other grasses; up to one m high; usually at edges of roads, trails, and other cleared areas; provides cover and seeds; seeds used especially by Chipping Sparrows ***Spizella passerina.***

Hypolytrum schraderianum, Cyperaceae; abundant; often in dense stands, up to 1.5 m high but usually lower; provides cover; fruiting heads present at all seasons; seeds appear to be principal food of Black-headed Siskin ***(Carduelis notata),*** probably important to other fringillids, especially Rusty Sparrows ***(Aimophila rufescens).***

Rhynchospora barbata, Bulbostylis paradoxa, Fimbristylis sp., Cyperaceae: abundant; usually less than 0.5 m high; provide cover, no observed use of seeds by birds.

Arboreal Plants

Psittacanthus mayanus, Loranthaceae; a mistletoe, fairly common in pines; red flowers in March-April, used by Red-billed Azurecrown ***(Amazilia cyanocephala);*** berries in August, eaten by pigeons ***(Columba*** sp.), probably by other birds.

Aechmea bracteata, Bromeliaceae; fairly common in pines: up to 0.6 m in diameter, holds much water and plant debris; fauna includes large ants, mosquitoes and other insects, frogs ***(Hyla staufferi);*** many birds probe into these bromeliads, possibly for both water and food; flowering stalks used by Red-billed Azurecrown.

Tillandsia sp., Bromeliaceae; abundant in pines; smaller than ***Aechmea,*** usually less than 0.25 m in diameter, but often with similar fauna; visited by many birds, but apparently especially important to Ladder-backed Woodpecker ***(Dendrocopos scalaris)*** which probes and gleans them.

Ferns

Blechnum sp., Blechnaceae; sword fern; sometimes abundant in wet places, absent elsewhere; no observed use by birds, but must provide some cover.

LITERATURE CITED

BENT, A. C.
1953 Life histories of North American wood warblers. Bull. U. S. Natl. Mus., 203

BLYDENSTEIN, J.
1967 Tropical savanna vegetation of the llanos of Colombia. Ecology, 48:1-15.

DAVENPORT, L. B., JR.
1964 Audubon Field Notes, 18:394-395, 561.
1965 Audubon Field Notes, 19:423, 596.
1966 Audubon Field Notes, 20:467, 623.

DENEVAN, W.M.
1961 The upland pine forests of Nicaragua. Univ. California Publ. Geogr., 12: 251-320.

FICKEN, R. W., M. S. FICKEN, and D. H. MORSE
1968 Competition and character displacement in two sympatric pine dwelling warblers (Dendroica, Parulidae). Evolution, 22: 307-314.

GRANT, P. R.
1968 Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Systematic Zool., 17: 319-333.

HARTMAN, F.A.
1955 Heart weight in birds. Condor, 57: 221-238.

HAFFER, J.
1969 Speciation in Amazonian forest birds. Science, 165(3889):131-137.

HOWELL, T. R.
1965 New subspecies of birds from the lowland pine savanna of northeastern Nicaragua. Auk, 82:438-464.
1969 Avian distribution in Central America. Auk, 86:293-326.

JANZEN, D. H.
1970 Herbivores and the number of tree species in tropical forests. Amer. Nat., 104:501-528.

JOHANNESSEN, C. L.
1963 Savannas of interior Honduras. Ibero-Americana, 46:1-160.

KLOPFER, P. H.
1962 Behavioral aspects of ecology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
1963 Behavioral aspects of habitat selection: the role of early experience. Wilson Bull., 75:15–22.

KLOPFER, P. H., and R. H. MACARTHUR
1960 Niche size and faunal diversity. Amer. Nat., 94: 293-300.
1961 On the causes of tropical species diversity: niche overlap. Amer. Nat., 95: 223-226.

KOMAREK, R.
1966 A discussion of wildlife management, fire and the wildlife landscape. Proc. 5th Annual Tall Timbers Fire Ecology Conf.:177-194.

LAWRENCE, G. E.
1966 Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. Ecology, 47:278-291.

LLOYD, M., and R. J. GHELARDI
1964 A table for calculating the "equitability" component of species diversity. Jour. Animal Ecol., 33:217-225.

LLOYD, M., J. H. ZAR, and J. R. KARR
1968 On the calculation of information-theoretical measures of diversity. Amer. Midland Nat., 79:257-272.

LOWE-MCCONNELL, R.H., Editor
1969 Speciation in tropical environments. Biological Jour. Linnean Soc. London, 1:1-246.

MACARTHUR, . H.
1964 Environmental factors affecting species diversity. Amer. Nat., 98:387-397.
1969 Patterns of communities in the tropics. *In:* Speciation in tropical environments, R. H. Lowe-McConnell, ed. Biological Jour. Linnean Soc. London, 1:19-30.

MACARTHUR, . H.. and H. S. HORN
1969 Foliage profile by vertical measurements. Ecology, 50: 802-861.

MACARTHUR, . H., and R. LEVINS
1964 Competition, habitat selection, and character displacement in a patchy environment. Proc. Natl. Acad. Sci., 51:1207-1210.

MACARTHUR, . H., and J. W. MACARTHUR
1961 On bird species diversity. Ecology, 42:594598.

MACARTHUR, H., J. W. MACARTHUR, and J. PREER
1962 On bird species diversity.II. Prediction of bird census from habitat measurements. Amer. Nat., 96:167-174.

MACARTHUR, R., H. RECHER, and M. CODY
1966 On the relation between habitat selection and species diversity. Amer. Nat.. 100: 319-332.

MCINTOSH, R. P.
1967 An index of diversity and the relation of certain concepts to diversity. Ecology, 48: 392404.

MONROE, B. L., JR.
1968 A distributional survey of the birds of Honduras. A.O.U. Monograph, No. 7.

MONROE, B. L., JR., and T. R. HOWELL
1966 Geographic variation in Middle American parrots of the ***Amazona ochrocephala*** complex. Occas. Papers Mus. Zool. Louisiana State Univ., 34:1-18.

MORSE. D. H.
1967 Foraging relationships of brown-headed nuthatches and pine warblers. Ecology, 48: 94-103.

MUNRO, N.
1966 The fire ecology of Caribbean pine in Nicaragua. Proc. 5th Annual Tall Timbers Fire Ecology Conf.:67-83.

NORRIS , R. A.
1951 Distribution and populations of summer birds in southwestern Georgia. Occas. Papers, Georgia Ornith. Soc., No. 3.

NORRIS, R. A., and D. W. JOHNSTON
1958 Weights and weight variations in summer birds from Georgia and South Carolina. Wilson Bull., 70:114–129.

ORIANS, G. H.
1969 The number of bird species in some tropical forests. Ecology, 50:783-801.

PAINE, R. T.
1966 Food web complexity and species diversity. Amer. Nat., 100:65-75.

PARSONS, J. J.
1955 The Miskito pine savanna of Nicaragua and Honduras. Ann. Assoc. Amer. Geogr., 45:36-63.

PIANKA, E. R.
1966 Latitudinal gradients in species diversity: a review of concepts. Amer. Nat., 100:33-46.

RADLEY J,
1960 The physical geography of the east coast of Nicaragua. M.A. thesis, Dept. Geogr.. Univ. California, Berkeley.

RIDGWAY, R.
1902 The birds of North and Middle America. Bull. U.S. Natl. Mus., 50, pt. 2.
1914 The birds of North and Middle America. Bull. U.S. Natl. Mus., 50, pt. 6.

RUSSELL, S. M.
1964 A distributional study of the birds of British Honduras. A.O.U. Monograph, No. 1.

SCHOENER, T. W.
1965 The evolution of bill size differences among sympatric congeneric species of birds. Evolution, 19:189–213.

SIMPSON, G. G.
1964 Species density of North American recent mammals. Syst. Zool., 15:57-73.

SKUTCH, A. F.
1966 A breeding bird census and nesting success in Central America. Ibis, 108:1-16.

SLOBODKIN, L. B., and H. L. SANDERS
1969 On the contribution of environmental predictability to species diversity. In: Brookhaven Symposia in Biology, No. 22:82-95.

SLUD, P.
1960 The birds of Finca "La Selva," Costa Rica: a tropical wet forest locality. Bull. Amer. Mus. Nat. Hist., 121:49-148.

STEVENSON, J. O., and L. H. MEITZEN
1946 Behavior and food habits of Sennett's white-tailed hawk in Texas. Wilson Bull., 58:198–205.

STODDARD, H. L.
1932 The bobwhite quail, its habits, preservation, and increase. Scribner's, New York.

TALBOT, L. M.
1964 The biological productivity of the tropical savanna ecosystem. Publ. Internatl. Union Conserv. Nat., New Series, No. 4:88-97.

TAYLOR, B. W.
1963 An outline of the vegetation of Nicaragua. Jour. Ecol., 51:27-54.

WEBSTER, J. D.
1961 A revision of Grace's Warbler. Auk, 78:554-566.

WESTON, F. M.
1965 A survey of the birdlife of northwestern Florida. Bull. Tall Timbers Res. Sta., No. 5.
1968 ***Airnophila aestivalis*** ssp. ***In:*** Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Bull. U.S. Natl. Mus., 237, pt. 2.

WILLIS, E. O.
1966a Interspecific competition and the foraging behavior of plain-brown woodcreepers. Ecology, 47:667-672.
1966b The role of migrant birds at swarms of army ants. Living Bird, 5:187-231.

WINTERBOTTOM, J.M.
1964 Note on the relative abundance of passerine and non-passerine birds in Africa south of the equator. Amer. Nat., 98:450-452.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF CALIFORNIA
LOS ANGELES, CALIFORNIA 90024